Published in:

European Journal of Agronomy 123: 126206

https://doi.org/10.1016/j.eja.2020.126206

A fruit growth approach to estimate oil content in olives

Álvaro López-Bernal[a,*] (g42lobea@uco.es), Anabela A. Fernandes-Silva[b] (anaaf@utad.pt), Victorino A. Vega[c] (victorianoa.vega@juntadeandalucia.es), Juan C. Hidalgo[c] (jcarlos.hidalgo@juntadeandalucia.es), Lorenzo León[c] (lorenzo.leon@juntadeandalucia.es), Luca Testi[d] (lucatesti@ias.csic.es), Francisco J. Villalobos[a,d] (ag1vimaf@uco.es)

[a] Departamento de Agronomía, Universidad de Córdoba, Campus de Rabanales, Edificio C4, 14071, Córdoba, Spain

[b] Departamento de Agronomia and Centre for the Research and Technology of Agro-Environmental and Biological Sciences, CITAB, University of Trás-os-Montes and Alto Douro, UTAD, Quinta de Prados 5000-801 Vila Real, Portugal

[c] Instituto de Investigación y Formación Agraria y Pesquera (IFAPA-Centro Alameda del Obispo), Av. Menéndez Pidal s/n, 14080, Córdoba, Spain

[d] Instituto de Agricultura Sostenible (IAS), Consejo Superior de Investigaciones Científicas (CSIC), Av. Menendez Pidal s/n, 14080, Cordoba, Spain

*Corresponding author: g42lobea@uco.es

Abstract

Harvest timing in olive orchards has a strong effect on the quality and quantity of oil yield, but many farmers still lack simple and affordable quantitative tools for rationally deciding appropriate harvest dates. This study presents and tests a conceptual model for predicting fruit oil content (O_f, g oil fruit^{-1}) from inexpensive measurements of fruit dry weight (w_f). The model presents two physiologically relevant parameters, the fruit dry weight at the onset of the oil accumulation phase (w_{f0}) and the ratio of accumulated oil per unit of fruit dry weight increase during the oil accumulation period (β), the latter assumed invariable throughout ripening. A compilation of data on w_f and O_f dynamics collected from four experiments including six olive cultivars and contrasting conditions of water supply and crop load was used to test the model. Our results suggest that β could be fairly independent of crop load or watering regime and, probably, genetically controlled. By contrast, w_{f0} is clearly affected by both the cultivar and the availability of assimilates for fruit growth preceding oil accumulation, which makes it orchard- and year-specific. According to those premises, once cultivar-specific β values are available w_{f0} could be easily calibrated by either a single determination of O_f and w_f at any time during the oil accumulation phase (Approach A) or by directly measuring w_{f0} if the date for the onset of oil accumulation can be estimated (Approach B). Validation tests with an independently calibrated β showed an excellent performance for reproducing O_f patterns from w_f data using Approach A. Approach B satisfactory predicted oil accumulation rates, but absolute estimates of O_f were less reliable. Regardless of the calibration approach, the model is easy to implement and has a minimal cost, which satisfies the demand for inexpensive tools for monitoring oil accumulation dynamics.

Keywords: cultivar variability, fruit growth and development, crop modelling, oil accumulation, *Olea europaea* L.

1. Introduction

The recognition of the nutritional characteristics and health benefits of olive oil has led to an increased demand for this product, which has triggered the expansion of this tree crop in the last decades, both in traditional growing regions in the Mediterranean basin and new areas around the world. Covering more than 10 Mha nowadays, olive orchards represent one of the main oil crops worldwide (FAOSTAT, 2017).

As in any other oil crop, oil yield results from the product of fruit/seed number, fruit/seed weight and oil concentration at maturity. Understanding the dynamics of these components may be useful for establishing the optimal harvest date, as it is a pivotal agronomical decision that determines the yield and quality of olive oil, the two major revenue determinants in olive orchards (Mailer et al., 2007; Trentacoste et al., 2012).

In olive trees, oil synthesis takes place mainly in the parenchymatic cells of the fruit mesocarp (Rapoport and Moreno-Alías, 2017), but it is not until pit hardening has been completed that oil accumulation starts properly becoming the main sink for the assimilates allocated to fruits (Beltrán et al., 2017; Rapoport et al., 2013; Rapoport et al., 2017). Existing evidence suggest that the rate of oil accumulation is very high in late summer/early autumn and then decreases until the fruit reaches physiological maturity (Beltrán et al., 2005; García-Martos and Mancha, 1992; Trentacoste et al., 2010). However, both oil accumulation rate and ripening duration are substantially affected by fruit load (Barone et al., 1994; Dag et al., 2011, Fernández et al., 2015, 2018), cultivar characteristics (Camposeo et al., 2013; Lavee and Wodner, 1991) and both environmental and agronomical conditions (Gucci et al., 2019; Lazzez et al., 2011; Mailer et al., 2007). The concurrent effects of these factors challenge the definition of simple rules for determining the date at which fruits reach their maximum oil content.

Establishing rational criteria for deciding the best harvest date still represents a major challenge due to the existence of several trade-offs acting simultaneously. On the one hand, late harvests obviously ensure achieving high oil contents while simultaneously favor low fruit detachment force (Beltrán et al., 2017; Gamli and Eker, 2017), which can be critical for the harvesting operation for some cultivars. On the other hand, harvesting early prevents yield losses associated to natural fruit abscission and leads to oils of higher quality due to higher contents of some minor components that are responsible of some of the nutraceutical, organoleptic and gastronomic attributes of olive oil, such as polyphenols and tocopherols (Aguilera et al., 2017; Alagna et al., 2012; Caponio et al., 2001; Dag et al., 2011). In fact, the increasing pressure for obtaining oils of the maximum quality is already promoting an advance in the harvest date among the olive oil production sector.

In any case, farmers still lack simple inexpensive methods that allow them to decide the harvest date with some rational basis. In the best case, oil concentration is determined from fruit samples and compared to threshold values indicating on how far the orchard is from exploiting its oil accumulation potential (Zipori et al., 2016). This information is used to decide whether harvest should start or not. Obviously, recurrent olive samplings are required during the autumn to have a clear idea on how oil accumulation develops, which comes at an unaffordable cost for many farmers. The maturity index, based on fruit color (Beltrán et al., 2017), has also been used as an orientating approach for the decision-making of harvest timing, but the correlation between color and oil concentration is poor in many genotypes (Mickelbart and James, 2003; Navas-Lopez et al., 2019). Many other physiological and biochemical parameters such as fruit respiration (Ranalli et al., 1998), fruit detachment force (Almeida et al., 2016; Camposeo et al., 2013), changes in oil composition (Beltrán et al., 2017) and sugar content kinetics (Trapani et al., 2016) have also been related to optimal harvesting periods, but they are more difficult to implement in practice and still require further research to assess the robustness of their relationships with oil concentration.

The aim of this article is to provide and test new simple approaches for predicting oil content dynamics based on inexpensive measurements of fruit dry weight that could be easily used by growers as a support for deciding the optimal harvest timing. Briefly, we consider that, since the start of oil accumulation, fruit oil content, "O_f" (g oil fruit^{-1}), can be linearly related to fruit dry weight "w_f" (g fruit^{-1}) as:

$$O_f = \beta\,(w_f - w_{f0}) = \beta\, w_f - \beta\, w_{f0} \qquad (1)$$

Where w_{f0} (g fruit^{-1}) is the fruit dry weight at the onset of oil accumulation (i.e. at the end of pit hardening) and β (g oil g^{-1}) is the amount of oil accumulated per g of fruit dry weight increase since the start of oil accumulation (Fig. 1). w_{f0} should depend on fruit growth rate from bloom to the end of pit hardening and must be cultivar dependent. β may also be cultivar-specific, but we hypothesize that it remains constant during the whole oil accumulation period and that it is independent of any factor affecting the availability of assimilates for fruit growth such as water status or crop load. This would imply that the oil content of fruits increases proportionally to fruit dry weight from the end of pit hardening to maturity, irrespective of the fact that fruit growth rates can vary with time or among trees of the same cultivar subjected to different conditions. Under these assumptions, recurrent measurements of w_f could be easily used for tracking O_f dynamics throughout the oil accumulation period.

The specific goals of this study are: (i) to test in different olive cultivars that oil accumulation represents a fixed fraction of fruit growth (i.e. constant β), evaluating likely genotypic differences in this trait, (ii) to test whether β is independent of factors affecting fruit growth rates, particularly, crop load and water status, and (iii) to propose and test simple approaches derived from the conceptual model for predicting oil accumulation dynamics based on inexpensive measurements of w_f, assessing its strengths and weaknesses. A compilation of data on fruit dry weight and oil accumulation dynamics coming from four experiments with young-potted and mature field-grown olive trees are used to address these objectives.

2. Materials and methods

2.1. Experiment 1

Experiment I was performed in 2017 with 2 years-old trees of five olive cultivars: ‘Arbequina’, ‘Picual’, ‘Arbosana’, ‘Frantoio’ and ‘Changlot Real’ growing outdoors in 25-L pots at the Institute for Sustainable Agriculture (IAS-CSIC, Córdoba, Spain, 37.8ºN, 4.8ºW, 90m altitude). The substrate of the pots was composed of a mixture of sand (30 %), silt (15 %) and peat (55 %). Ten trees per cultivar were planted in the winter of 2016 and maintained under appropriate growing conditions since then by applying drip-irrigation and slow-release fertilizers. In particular, enough irrigation was supplied to cover the maximum evapotranspiration. Water requirements were established from ad hoc periodical measurements of 24-h weight loss of the tree pots. The main meteorological variables were recorded throughout the experiment with an automated weather station located 500 m apart. The climate in the area is typically Mediterranean, with 580 mm of average rainfall mainly concentrated between autumn and spring, and 1390 mm of average reference evapotranspiration (ET_0).

In 2017, four trees per cultivar were selected for the experimental measurements. Samples of five fruits per tree were collected at different moments of the fruit growing cycle starting on July 19th and finishing in December 15th. After collecting the samples, the fruits were weighted for determining their fresh weight and, then, oven dried for 42 h at 105 ºC to obtain w_f. Their oil content was subsequently measured using a NMR oil analyser (Del Río and Romero, 1999).

2.2. Experiment II

Experiment II was conducted through the years 2011, 2012 and 2013 within a 22.2-ha commercial hedgerow olive (cv. 'Arbequina') orchard located in 'La Harina' farm (20 km to the southeast of Córdoba, Spain, 37.7°N, 4.6°W, 170 m altitude). The orchard was planted in 2005 with 4 × 1.5 m tree spacing over a soil of clayish texture classified as a Vertisol (López-Bernal et al., 2015).

Four irrigation treatments were established using a randomized complete block experimental design with four replicates. Each of the 16 plots consisted of 40 trees in four adjacent rows. The irrigation treatments included a fully irrigated control (FI) that applied enough water to satisfy the maximum ET assuming a maximum crop coefficient of 0.75. The remaining treatments consisted of two similar regulated deficit irrigation treatments (D1 and D2) differing in the timing of the imposed water deficit and in its severity (Table S1), to which we added an additional treatment mimicking the irrigation applied by the manager of the commercial orchard (MI). The annual amounts of applied irrigation are shown for each treatment and year in Table 1, along with cumulative values of rainfall and ET_0. Monthly values of those variables are also presented in the Supplementary Material (Table S1). Information on how the FI, MI and D2 irrigation treatments affected tree water status, trunk growth, transpiration and assimilation is available in López-Bernal et al.

(2015). Crop load was high in 2011 and 2013, and low in 2012, irrespective of the irrigation treatment (Table 1).

The time courses of w_f and O_f were periodically monitored every year from midsummer (July-August) to the orchard harvest date (late November-early December) in randomly hand-picked samples of 72 fruits per irrigation treatment and block. Fruits were always taken from the six central trees of the plots (12 fruits per tree). Fresh and dry weight of fruits and their oil content were measured as in Experiment I.

2.3. Experiment III

Measurements were performed in 2014 in a 12-year old organic commercial olive (cv. 'Cobrançosa') orchard located at "Vilariça" Valley (Trás-os-Montes, Portugal, 41.3 °N, 7.0 °W, 150 m altitude), a typical olive growing area of Northeast Portugal. The climate in the area is Mediterranean (IPMA, 2015), with an average rainfall of 520 mm concentrated from autumn to spring, and 1130 mm of average ET_0. The soil is classified as Eutric Leptosols developed on metamorphic rocks (schists), of sandy loam texture. Tree spacing was 7 x 7 m and the experimental design was a complete randomized block, replicated three times. Each plot contained four central olive trees surrounded by 14 border trees and all measurements were made on the central trees of each plot.

Since 2013, five irrigation treatments were imposed in the orchard:

- FI: fully irrigated control, for which the water applied equaled the difference between the maximum (estimated) ET and rainfall.
- PRD: partial root drying system applying the same irrigation dose as FI to one half of the root system, with the irrigated and drying halves of the root-zone alternating every two weeks.

- SD40: sustained deficit irrigation that regularly received 40% of the water applied to FI
- RD75: regulated deficit irrigation that received 75% of the water applied to FI, with a midsummer deficit period from mid-July to mid-August, reducing irrigation to 15% of FI.
- RD40: regulated deficit irrigation that received the same seasonal amount of irrigation as SD40 with a midsummer deficit period without irrigation from mid-July to mid-August.

Measurements of w_f and O_f were performed for each treatment at three different dates in 2014 (October 2nd, October 20th and November 12th), using samples of 40 fruits per tree (three trees per treatment). That year crop load was low with no noticeable differences among irrigation treatments. Determinations of oil content were based on Soxhlet extraction (Donaire et al., 1977).

2.4. Experiment IV

Experiment IV was conducted in a 10-year old commercial olive (cv. 'Cobrançosa') orchard located at Vilariça Valley (Trás-os-Montes, Portugal, 41.3 °N, 7.0 °W, 240 m altitude), in the same area as the previous experiment. The soil is classified as Eutric Leptosols developed on metamorphic rocks (schists), of sandy loam texture. Tree spacing was 6 x 6 m. The design of the experimental plot consisted of three adjacent blocks, each of these made of four rows with twenty olives trees, where only the six central trees were used for sampling. Three irrigation treatments were imposed during three consecutive seasons starting in 2004: full irrigation (FI), that received a seasonal water equivalent to 100% estimated crop evapotranspiration; sustained deficit irrigation (SD30), that received a volume of water equivalent to 30% of FI; and a rainfed treatment (RF).

In 2006, samples of 40 fruits per tree in 4 trees per treatment were collected periodically from September to December to monitor the dynamics of w_f and O_f. The latter was determined by Soxhlet extraction. That year crop load was the highest of the three experimental seasons, with FI and RF showing the highest and lowest fruit numbers, respectively (Fernandes-Silva et al., 2010).

Further information describing the orchard characteristics, the climatic conditions during the experiment, the irrigation amounts applied to each treatment and their impacts on the water status and productivity of the trees is provided in Fernandes-Silva et al. (2010).

2.5. Hypothesis testing

Linear regression analyses of O_f versus w_f were performed to test whether β can be assumed both constant during the ripening period (i) and independent of the carbon availability for fruit growth (ii). As these assumptions refer to the oil accumulation phase only, data with oil concentrations below 5 % on a dry matter basis were, whenever present, excluded from the analyses. According to the conceptual model (Eqn. 1), β was estimated from the slope of the linear fit and w_{f0} was deduced from the intercept (as it should equal the product of β and w_{f0}).

In Experiment I, regressions were performed for each cultivar independently, allowing us to compare the differences in the resulting linear models. Water stress and crop load presumably affect the availability of assimilates for fruit growth, so separate regressions were conducted for each irrigation treatment in Experiments III and IV, and for each combination of “irrigation treatment” x “year” in Experiment II. Finally, the regression lines were compared experiment by experiment, evaluating the statistical significance of the differences in the slopes and intercepts among the linear fits with the software Statistix 10 for Windows (Analytical Software, Tallahassee, FL, USA).

An additional quantitative assessment of the sensitivity of model parameters to carbon availability was performed in Experiment II. Estimates of tree assimilation (López-Bernal et al., 2015) and records of crop load (Table 1) were used to calculate the cumulative values of assimilation per fruit (A_f, g C fruit^{-1}) for periods preceding (June 18th to July 18th, A_{f1}) and following (August 2nd to September 26th, A_{f2}) the onset of the oil accumulation phase. The dependency of w_{f0} and β on carbon availability was assessed from plots of their apparent values (obtained from the linear fits) versus A_{f1} and A_{f2}, respectively. The choice of the starting and ending dates of the two periods was constrained by both the availability of assimilation records for the three years and the uncertainty regarding the timing of the onset of oil accumulation. We left a gap between the two periods on purpose because, under the conditions of Southern Spain, the start of the oil accumulation phase has been reported to start 10-12 weeks after full bloom (Beltrán et al., 2017; García and Mancha, 1992), with the average flowering date for 'Arbequina' in Córdoba being May 10th (De Melo-Abreu et al., 2004) (unfortunately, the actual dates of full bloom were not recorded in Experiment II).

2.6. Testing model's predictive power in practice

If the conceptual model presented in Eqn. 1 is sound in practice, then oil accumulation dynamics could be easily predicted from routinely measurements of w_f. Any increase in w_f over time can be translated into an increase in O_f by multiplying by β. Furthermore, absolute values of O_f can also be theoretically estimated if a) oil concentration is measured once on a representative sample of fruits at any time during the oil accumulation phase or, b) if w_f is sampled around the date at which the oil accumulation phase starts in midsummer (when $w_f = w_{f0}$). These two simple approaches (hereafter referred as 'Approach A' or 'Approach B') were tested for the cultivar 'Arbequina'.

The dataset of Experiment I was used for calibrating the value of β, while that of Experiment II was selected for validation. In Approach A, the intercept of the model (O_{f0}) is calibrated, for each combination of "irrigation treatment" x "year", as:

$$O_{f0} = O_{fj} - \beta\, w_{fj} \qquad (2)$$

where w_{fj} and O_{fj} are the average dry weight and oil content of a representative sample of fruits taken on day 'j'. For testing purposes, O_{f0} was calculated from the measured values of w_{fj} and O_{fj} that were the closest to October 1st each year ('j' was October 5th in 2011, October 1st in 2012 and September 24th in 2013).

In Approach B, O_{f0} was determined from the product of β and w_{f0}, the latter estimated for each combination of "irrigation treatment" x "year" from the time course of w_f, assuming three fixed-date scenarios for the onset of the oil accumulation phase: July 20th, August 1st and August 10th. We selected these dates due to the aforementioned uncertainty regarding the onset of oil accumulation.

Model performances in reproducing measured oil dynamics were assessed using mean absolute error (MAE; from 0 to +∞, optimum 0), root mean square error (RMSE; from 0 to +∞, optimum 0) and coefficient of residual mass (CRM, from -∞ to +∞, optimum 0):

$$\mathrm{MAE} = \sum_{i}^{n} |S_i - M_i| / n \qquad (3)$$

$$\mathrm{RMSE} = \sqrt{\sum_{i}^{n} (S_i - M_i)^2 / n} \qquad (4)$$

$$\mathrm{CRM} = 1 - \sum_{i}^{n} S_i / \sum_{i}^{n} M_i \qquad (5)$$

Where M_i is the ith measured oil, S_i is the ith simulated *oil* and n is the number of O_f measurements.

3. Results

3.1. Model's proof of concept

The linear regression fits performed for each and every independent dataset of O_f – w_f were always highly significant (P<0.001), with the determination coefficient ranging from 0.72 (Experiment IV, FI) to 0.999 (Experiment II, MI in 2013) and averaging 0.940 (Table 2).

3.2. Carbon availability effects

The time courses of w_f and O_f in Experiment II (cv. 'Arbequina') exhibited considerable differences among years and irrigation treatments (Figure 2). On the one hand, the year of low crop load (2012, Table 1) always led to fruits of higher weight and oil content than its high crop load counterparts. On the other, FI showed higher values of w_f and O_f in 2012 and 2013 than D1 and D2, although slight differences were noticed among treatments in 2011. MI presented similar patterns of w_f and O_f to those of FI in 2011 and 2012, but it was the treatment with the lowest values in 2013. These differences in the patterns of fruit growth and oil accumulation among treatments were in consonance with the differences in water status and assimilation rates reported by López-Bernal et al. (2015) in the same experiment. In any case, estimates of A_f revealed that inter-annual differences in crop load had a higher weight on the carbon availability per fruit than the differences in water status among treatments (Fig. 3).

The values of β, estimated as the slope of the linear fits of O_f versus w_f, averaged 0.79 g oil g^{-1} and ranged from 0.70 to 0.87 g oil g^{-1} (Table 2). All treatments averaged similar β, and no significant differences among them were found when they were compared within each year (Table S2). By contrast, the tests revealed statistically lower β for 2013 in relation to

2011 and 2012 in most cases (Table S2) and a slight direct relationship was found between this parameter and A_{f2} (Fig. 3A). The slope resulting from the linear regression between β and A_{f2} was significant (P<0.02), although its value was low. No single combination of "irrigation treatment" x "year" showed significant differences in β in relation to the value obtained in Experiment I for the same cultivar (Table 2).

The intercept of the set-specific linear fits ranged from -0.34 to -0.15 g oil fruit^{-1} (average -0.25 g oil fruit^{-1}) (Table 2). Significant differences were usually found when comparing the same treatment among years and when comparing the treatments in each year, except for 2011 (Table S2). The high variability in the intercepts was mainly driven by large differences in w_{f0}. In this regard, its apparent values ranged from 0.21 to 0.39 g fruit^{-1} (Table 2, average 0.31 g fruit^{-1}). The highest w_{f0} were observed in the low crop load year (irrespective of the treatment), and deficit irrigation treatments resulted in lower values than FI in 2012 and 2013. Moreover, the apparent estimates of w_{f0} presented a robust correlation with A_{f1} (r^2 = 0.84, P<0.001, Fig. 3B).

'Cobrançosa' datasets generally showed no statistical differences when the slope or the intercept of the linear fits were compared among either irrigation treatments or experiments (Table S3, Fig. 4). Even if non-significant, differences in the estimates of w_{f0} between experiments were considerable, averaging 0.33 g fruit^{-1} in Experiment III and 0.57 g fruit^{-1} in Experiment IV (Table 2). Slightly higher values of β were also found in Experiment IV, irrespective of the treatment. In the FI treatments, β yielded 0.49 g oil g^{-1} in Experiment III and 0.62 g oil g^{-1} in Experiment IV.

3.3. Cultivar effects

No statistical differences were found among cultivars for β in Experiment I (Table S4), its values ranging from 0.75 (‘Arbequina’) to 0.82 (‘Arbosana’) g oil g^{-1} (Table 2). The linear fits of O_f versus w_f were parallels, evidencing clear differences in their intercepts (Fig. 5, Table S4). In this regard, w_{f0} ranged from 0.26 (‘Arbosana’) to 0.60 (‘Picual’) g $fruit^{-1}$. With the exception of the treatments FI and SD30 in Experiment IV, the slope of the fits obtained for ‘Cobrançosa’ was always significantly lower than those observed for the five cultivars tested in Experiment I (Fig. 5, Table 2).

3.4. Performance of Approach A in predicting oil accumulation dynamics

Using the dataset of Experiment I for calibrating the slope of the model for ‘Arbequina’ led to β = 0.75 g oil g^{-1} (Table 1). As the intercept of the model is considered to be affected by carbon availability per fruit, it was obtained from pair measurements of *w* and *oil* around October 1st for each set in Experiment II (Eqn. 2). Its values were the lowest in 2012 and the highest in 2013, ranging from -0.28 to -0.17 g oil $fruit^{-1}$.

Using the routine measurements of w_f during the oil accumulation phase to feed the model, O_f predictions agreed very closely with observations irrespective of the year and irrigation treatment, as shown by the vicinity of the plots to the 1:1 line in Fig. 6. The satisfactory performance of Approach A for reproducing O_f dynamics is also supported by the low values of MAE (0.008 g oil $fruit^{-1}$), RMSE (0.013 g oil $fruit^{-1}$) and CRM (0.01), the latter indicating a negligible bias.

3.5. Performance of Approach B in predicting oil accumulation dynamics

In Approach B, the model intercept is calibrated from the product of the slope (0.75 g oil g^{-1}, obtained from the independent set of ‘Arbequina’ in Experiment I) and w_{f0}, the latter being estimated for three hypothetical date scenarios for the start of the oil accumulation phase. Using this procedure, the intercept averaged -0.21, -0.24 and -0.26 g oil fruit^{-1} for the date scenarios July 20th, August 1st and August 10th, respectively. Regardless of the date scenario, the intercepts were always the lowest in 2012 and the highest in 2013.

Model performance was the best in overall terms assuming August 1st as the date for the onset of oil accumulation, with MAE, RMSE and CRM being 0.021 g oil fruit^{-1}, 0.027 g oil fruit^{-1} and 0.09, respectively (Table 3). However, the best date scenario was different when each year was analyzed independently. For instance, the model made the best predictions of oil for the year 2011 under the date scenario of July 20th, while August the 10th was the best for reproducing oil accumulation dynamics in the year 2013 (Fig. 7).

4. Discussion

This study presents a simple conceptual model in which oil accumulation is linearly related to fruit growth on a dry matter basis. The two model parameters can be associated with physiologically relevant traits: the slope (β) is the fraction of dry weight growth that accumulates in the fruit as oil, while the intercept is given by the product of β and fruit dry weight at the start of the oil accumulation phase (w_{f0}). All the plots of O_f versus w_f compiled in the four experiments of this article exhibited satisfactory linear fits ($P<0.001$) with high determination coefficients (Table 2), which demonstrates the applicability of the model.

Understanding the factors that affect model parameters is a pivotal step to assess how it can be used in practice for predicting oil accumulation dynamics. In Experiment II (‘Arbequina’), β was significantly lower in 2013 than in 2011 and 2012 in most cases (Table S2). This result might have been related with a lower assimilate availability per fruit in 2013 (Fig. 3), contrary to our starting hypothesis, but the likely effect of carbon availability on β is of limited importance actually (or at least it was so for the range of A_f covered in Experiment II). This is evidenced by the excellent performance of Approach A in reproducing oil accumulation dynamics for all the independent datasets (Fig. 6, Table 3) even if a fixed and independent value of β was always used. The lack of statistical differences among irrigation treatments in Experiments III and IV also support the premise of a negligible effect of carbon availability on β for 'Cobrançosa' (Fig. 4, Table S3). We must acknowledge, however, that assessing differences in A_f among treatments or experiments in those datasets was not possible with the available experimental information.

Despite slight and non-significant differences among cultivars being noticed in Experiment I, the values of β obtained for 'Cobrançosa' in Experiments III and IV revealed substantially lower values. Consequently, β might be genotypically controlled, which would imply that this parameter requires cultivar-specific calibration.

Significant cultivar variability was also observed for w_{f0} in Experiment I, which was somehow expected as differences in fruit size among cultivars are usually evident from a few weeks after flowering (Beltrán et al., 2017; Lavee and Wodner, 1991). This fact originates, mainly, from genotypic differences in the rates of cell division (Hammami et al., 2011). Besides cultivar variability, w_{f0} also seems to be significantly determined by carbon availability as evidenced by results in Experiment II, where high crop load and water deficits led to lower values (Fig. 3, Table 2). Both the high rates of cell division and expansion in the first weeks following flowering and the production of lignin during pit hardening are metabolically expensive processes (Hammami et al., 2011, 2013; Rapoport et al., 2017), which explains why any limitation in the availability of assimilates is expected to reduce w_{f0}. As a corollary, w_{f0} can vary every season even for the same orchard and cultivar, so it is a parameter that requires both year- and orchard-specific calibration.

Two approaches for calibrating w_{f0} are implicitly proposed in this paper assuming that β is both independent of carbon availability and genotypically-controlled. If the cultivar-specific value of β is available, the first approach (Approach A) just requires a single measurement of w_f and O_f from a representative fruit sample at any time during the oil accumulation phase to calibrate w_{f0}. The second (Approach B) prevents the need for oil determinations requiring, instead, measuring w_f at the date at which the oil accumulation phase begins. Both approaches can potentially yield excellent results, as demonstrated by the model performance tests conducted for Experiment II (Table 3, Fig. 6, Fig. 7). However, it must be noted that choosing the date of the onset of oil accumulation is rather challenging, as it varies from year to year, which translates into substantial bias in subsequent model predictions (Fig. 7, Table 3). The economic advantage of Approach B (no single O_f determination is needed) comes, therefore, at the cost of limited reliability in relation to Approach A when an absolute estimate of O_f is required. Nevertheless, we must note also that both approaches will yield equally reliable estimates of the rate of oil accumulation in the period between consecutive measurements of w_f.

The development of simple methods to predict the onset of oil accumulation seems a desirable target for future research. So far, measurements of pit breaking resistance with penetrometer devices (Rapoport et al., 2013) might provide a good indication of the ideal date for measuring w_{f0}, as oil accumulation is likely to start when pit hardening (and its competition for assimilates against the mesocarp) is reaching an end (Beltrán et al., 2017; Rapoport et al., 2017), but such measurements might be too laborious to be applied by farmers. On the other hand, a simple model for predicting the onset of oil accumulation based on thermal time has been proposed for several cultivars in the arid environment of Mendoza, Argentina (Trentacoste et al., 2012). Unfortunately, the model has not been validated in the Mediterranean area and remains empirical, as acknowledged by their developers. In this regard, a simple thermal time approach might not be entirely satisfactory for predicting the onset of oil accumulation, as there are evidences pointing that the duration of pit hardening is affected by water stress (Hammami et al., 2013).

Beyond detailed technical examinations of parameter calibration, the model presented in this study is of the greatest relevance for the olive growing sector, as most farmers still lack inexpensive methods for following oil accumulation dynamics and rational criteria to decide the most appropriate harvest date accordingly. The best approach for monitoring oil accumulation dynamics to date depends on periodical determinations of oil concentration, which can be expensive for small growers. Our results suggest that recurrent measurements of w_f might be enough to predict oil accumulation dynamics reducing the number of determinations of oil concentration to a minimum (i.e. to "one" single determination if Approach A is used). Moreover, even if oil concentration cannot be determined, the model is able to predict oil accumulation rates (any increase in w_f can be easily converted into O_f multiplying by β) and theoretically yields approximate estimates of O_f if w_f is measured around the date at which the oil accumulation starts (Approach B). Another implicit point in our conceptual model is that the growth of w_f should stop once the fruit reaches its maximum O_f. From the practical point of view, this implies that the maximum oil content could be determined when w_f reaches a plateau. However, we must acknowledge that the absence of late harvests in our experiments prevented us to probe that point thoroughly.

Despite our results being promising, the conceptual model and its derived practical applications require further testing under contrasting environmental and agronomical conditions including different cultivars in order to better assess their reliability. In this regard, many studies report that oil accumulation rates decrease under high temperatures (Lavee et al., 2012; García-Inza et al., 2014; Rondanini et al., 2014; Benlloch-González et al., 2019; Nissim et al., 2020). These observations might suggest that β is reduced at high temperatures, but the evidences available are not fully conclusive because the reduced oil accumulation rates may as well be the result of a decrease in fruit dry weight accumulation. In any case, we are confident that many researchers could easily contribute to the testing of the model under contrasting temperatures, environments or agronomical management conditions using already collected datasets of w_f and O_f. Finally, the model may also be used within a process-based model of olive orchards like OliveCan, which currently lacks a mechanistic simulation of oil production (López-Bernal et al., 2018).

5. Conclusion

This paper presents a conceptual model that estimates the oil content of olive fruits (O_f) as a fixed proportion (β) of their dry weight increase since the onset of the oil accumulation phase (w_f-w_{f0}). A compilation of datasets of paired oil content and weight determinations from experiments with different cultivars and conditions of water status and crop load supports the validity of the model. The two parameters of the conceptual model (β and w_{f0}) are physiologically-relevant traits and can be obtained from the slope and intercept of linear regressions of O_f on w_f. Our results indicate that β could be cultivar-specific but remains fairly unaffected by factors modulating the availability of carbon per fruit, such as crop load or water stress. On the contrary, the fruit dry weight at the onset of oil accumulation (w_{f0}) is both genotypically-controlled and dependent on crop load and photosynthesis during the earlier stages of fruit growth, which implies that it requires orchard- and year-specific calibration. Fortunately, the model allows for easily determining w_{f0} from a single determination of O_f and w_f at any date during the oil accumulation phase provided that a cultivar-specific value of β is available (Approach A), or, alternatively, it can be measured directly if the date of the onset of oil accumulation can be estimated (Approach B). Overall, these model features indicate that oil accumulation rates could be estimated reliably from inexpensive measurements of w_f during autumn. This opens the door for providing olive growers with simple affordable methods to estimate O_f, which is a critical indicator for establishing optimal harvesting periods. Prior to that, further research testing the validity of our findings for different environmental conditions and/or new cultivars would be highly desirable.

Acknowledgements

This work was supported by the Spanish Ministry of Economy and Competitiveness [project AGL-2015-69822] and also by National Funds by FCT - Portuguese Foundation for Science and Technology [project UIDB/04033/2020]. The former project provided the funding for setting up Experiment I. Experiment II was performed under the framework of a project [P10-AGR-6456] funded by the Andalusian Regional Government. Experiment III was supported by the PRODER program of the Portuguese Ministry of Agriculture [project PA-44662-IF0019]. Experiment IV was funded by the AGRO-INIA program of the Portuguese Ministry of Agriculture [project AGRO175] and by the PhD fellowship [SFRH/BD/18441/2004] awarded to AF-S by the Foundation for Science and Technology of the Portuguese Ministry of Science, Technology and Education. AL-B enjoyed a JAE-Pre PhD scholarship during Experiment II (funded by CSIC) and a 'Juan de la Cierva-Formación' postdoctoral fellowship (funded by the Spanish Ministry of Economy and

Competitiveness, grant number [FJCI-2015-24109]) during the execution of Experiment I. We gratefully acknowledge the contribution of Dr. Francisco Orgaz in designing Experiment II and the excellent assistance by Estrella Muñoz, Marcos Orgaz and José Luis Vázquez in Experiment I.

References

Aguilera, M.P., Uceda, M., Beltrán, G., (2017) La calidad del aceite de oliva, in: Barranco, D., Fernández-Escobar, R., Rallo, L. (Eds.), El cultivo del olivo. Mundi-Prensa, Madrid, Spain, pp.839-868.

Alagna, F., Mariotti, R., Panara, F., Caporali, S., Urbani, S., Veneziani, G., Esposto, S., Taticchi, A., Rosati, A., Rao, R., Perrotta, G., Servili, M., Baldoni, L., 2012. Olive phenolic compounds: metabolic and transcriptional profiling during fruit development. BMC Plant Biol. 12, 162. https://doi.org/10.1186/1471-2229-12-162.

Almeida, A., Figueiredo, T., Fernandes-Silva, A., 2016. Evolution of factors affecting mechanical olive harvesting. Acta Hortic. 1139, 575-579. https://doi.org/10.17660/ActaHortic.2016.1139.99.

Barone, E, Gullo, G., Zappia, R., Inglese, P., 1994. Effect of crop load on fruit ripening and olive oil (*Olea europaea* L.) quality. J. Hortic. Sci. 69, 67-73. https://doi.org/10.1080/14620316.1994.11515250.

Beltrán, G., Aguilera, M.P., Del Río, C., Sánchez, S., Martínez, L., 2005. Influence of fruit ripening process on the natural antioxidant content of Hojiblanca virgin olive oils. Food Chem. 89, 207-215. https://doi.org/10.1016/j.foodchem.2004.02.027.

Beltrán, G., Uceda, M., Hermoso, M., Frías, L., (2017) Maduración, in: Barranco, D., Fernández-Escobar, R., Rallo, L. (Eds.), El cultivo del olivo. Mundi-Prensa, Madrid, Spain, pp.187-212.

Benlloch-González, M., Sánchez-Lucas, R., Bejaoui, M.A., Benlloch, M., Fernández-Escobar, R., 2019. Global warming effects on yield and fruit maturation of olive tres growing under field conditions. Sci. Hortic. 249, 162-167. https://doi.org/10.1016/j.scienta.2019.01.046.

Camposeo, S., Vivaldi, G.A., Gattullo, C.E., 2013. Ripening indices and harvesting times of different olive cultivars for continuous harvest. Sci. Hortic. 151, 1-10. https://doi.org/10.1016/j.scienta.2012.12.019.

Caponio, F., Gomes, T., Pasqualone, A., 2001. Phenolic compounds in virgin olive oils: influence of the degree of olive ripeness on organoleptic characteristics and shelf-life. Eur. Food Res. Technol. 212, 329-333. https://doi.org/10.1007/s002170000268.

Dag, A., Kerem, Z., Yogev, N., Zipori, I., Lavee, S., Ben-David, E., 2011. Influence of time of harvest and maturity index on olive oil yield and quality. Sci. Hortic. 127, 358-366. https://doi.org/10.1016/j.scienta.2010.11.008.

Del Río, C., Romero, A.M., 1999. Whole, unmilled olives can be used to determine their oil content by nuclear magnetic resonance. HortTechnology 9, 675-680. https://doi.org/10.21273/HORTTECH.9.4.675.

Donaire, J., Sanchez-Raya, A.J., Lopez-George, J.L., Recalde, L., 1977. Estudes physiologiques et biochimiques de l'olivier: I. variation de la concentration de divers metabolites pendant son cycle evolutif. Agrochim. 21, 311-321.

FAOSTAT, 2017. http://www.fao.org/faostat/en/#data (accessed 20 May 2020)

Fernandes-Silva, A.A., Ferreira, T.C., Correia, C.M., Malheiro, A.C., Villalobos, F.J., 2010. Influence of different irrigation regimes on crop yield and water use efficiency of olive. Plant Soil 333, 35-47. https://doi.org/10.1007/s11104-010-0294-5.

Fernández, F.J., Ladux, J.L., Hammami, S.B.M., Rapoport, H.F., Searles, P.S., 2018. Fruit, mesocarp and endocarp responses to crop load and to different estimates of source: sink ratio in olive (cv. Arauco) at final harvest. Sci. Hortic. 234, 49-57. https://doi.org/10.1016/j.scienta.2018.02.016.

Fernández, F.J., Ladux, J.L., Searles, P.S., 2015. Dynamics of shoot and fruit growth following fruit thinning in olive trees: same season and subsequent season responses. Sci. Hortic. 192, 320-330. https://doi.org/10.1016/j.scienta.2015.06.028.

Gamlı, Ö.F., Eker, T., 2017. Determination of harvest time of Gemlik olive cultivars by using physical and chemical properties. J. Food Meas. Charact. 11, 2022–2030. https://doi.org/10.1007/s11694-017-9585-3.

García-Inza, G.P., Castro, D.N, Hall, A.J., Rousseaux, M.C., 2014. Responses to temperature of fruit dry weight, oil concentration, and oil fatty acid composition in olive (*Olea europaea* L. Var. 'arauco'). Eur. J. Agron. 54, 107-115. https://doi.org/10.1016/j.eja.2013.12.005.

García-Martos, J.M., Mancha, M., 1992. Evolución de la biosíntesis de lípidos durante la maduración de las variedades de aceituna ‘Picual’ y ‘Gordal’. Grasas y Aceites 43, 277-280.

Gucci, R., Carusso, G., Gennai, C., Esposto, S., Urbani, S., Servili, M., 2019. Fruit growth, yield and oil quality changes induced by deficit irrigation at different stages of olive fruit development. Agric. Water Manage. 212, 88-98. https://doi.org/10.1016/j.agwat.2018.08.022.

Hammami, S.B.M., Costagli, G., Rapoport, H.F., 2013. Cell and tissue dynamics of olive endocarp sclerification vary according to water availability. Physiol. Plantarum 149, 571-582. https://doi.org/10.1111/ppl.12097.

Hammami, S.B.M., Manrique, T., Rapoport, H.F., 2011. Cultivar-based fruit size in olive depends on different tissue and cellular processes throughout growth. Sci. Hortic. 130, 445-451. https://doi.org/10.1016/j.scienta.2011.07.018.

IPMA, 2015. http://www.ipma.pt/pt/oclima/normais.clima/ (accessed 20 May 2020)

Lavee, S., Wodner, M., 1991. Factors affecting the nature of oil accumulation in fruit of olive (*Olea europaea* L.) cultivars. J. Hortic. Sci. 66, 583-591. https://doi.org/10.1080/00221589.1991.11516187.

Lavee, S., Haskal, A., Avidan, B., 2012. The effect of planting distances and tree shape on yield and harvest efficiency of cv. Manzanillo table olives. Sci. Hortic. 142, 166-173. https://doi.org/10.1016/j.scienta.2012.05.010.

Lazzez, A., Vichi, S., Kammoun, N.G., Arous, M.N., Khlif, M., Romero, A., Cossentini, M., 2011. A four year study to determine the optimal harvesting period for Tunisian Chemlali olives. Eur. J. Lipid Sci. Technol. 113, 796-807. https://doi.org/10.1002/ejlt.201000474.

López-Bernal, Á., García-Tejera, O., Vega, V.A., Hidalgo, J.C., Testi, L., Orgaz, F., Villalobos, F.J., 2015. Using sap flow measurements to estimate net assimilation in olive trees under different irrigation regimes. Irrig. Sci. 33, 357-366. https://doi.org/10.1007/s00271-015-0471-7.

López-Bernal, Á., Morales, A., García-Tejera, O., Testi, L., Orgaz, F., De Melo-Abreu, J.P., Villalobos, F.J., 2018. OliveCan: a process-based model of development, growth and yield of olive orchards. Front. Plant Sci. 9, 632. https://doi.org/10.3389/fpls.2018.00632.

Mailer, R.J., Ayton, J., Conlan, D., 2007. Influence of harvest timing on olive (*Olea europaea*) oil accumulation and fruit characteristics under Australian conditions. J. Food Agric. Environ. 5, 58-63.

Mickelbart, M.V., James, D., 2003. Development of a dry matter maturity index for olive (*Olea europaea*). N. Z. J. Crop Hortic. Sci. 31, 269–276. https://doi.org/10.1080/01140671.2003.9514261.

Navas-Lopez, J.F., León, L., Trentacoste, E.R., de la Rosa, R., 2019. Multi-environment evaluation of oil accumulation pattern parameters in olive. Plant Physiol. Biochem. 139, 485-494. https://doi.org/10.1016/j.plaphy.2019.04.016.

Nissim, Y, Shloberg, M., Biton, I., Many, Y., Doron-Faigenboim, A., Zemach, H., Hovav, R., Kerem, Z., Avidan, B., Ben-Ari, G., 2020. High temperature environment reduces olive oil yield and quality. PLoS ONE 15, e0231956. https://doi.org/10.1371/journal.pone.0231956.

Ranalli, A., Tombesi, A., Ferrante, M.L., De Mattia, G., 1998. Respiratory rate of olive drupes during their ripening cycle and quality of oil extracted. J. Sci. Food Agric. 77, 359-367. https://doi.org/10.1002/(SICI)1097-0010(199807)77:3<359::AID-JSFA43>3.0.CO;2-R.

Rapoport, H.F., Hammami, S.B.M., Rosati, A., Gucci, R., 2017. Advances in olive fruit cell and tissue development. Acta Hortic. 1177. https://doi.org/10.17660/ActaHortic.2017.1177.29.

Rapoport, H.F., Moreno-Alías, I., 2017. Botánica y morfología, in: Barranco, D., Fernández-Escobar, R., Rallo, L. (Eds.), El cultivo del olivo. Mundi-Prensa, Madrid, Spain, pp.35-64.

Rapoport, H.F., Pérez-López, D., Hammami, S.B.M., Agüera, J., Moriana, A., 2013. Fruit pit hardening: physical measurement during olive fruit growth. Ann. Appl. Biol. 163, 200-208. https://doi.org/10.1111/aab.12046.

Rondanini, D.P., Castro, D.N., Searles, P.S., Rousseaux, M.C., 2014. Contrasting patterns of fatty acid composition and oil accumulation during fruit growth in several olive varieties and locations in a non-Mediterranean region. Eur. J. Agron. 52, 237-246. https://doi.org/10.1016/j.eja.2013.09.002.

Trapani, S., Migliorini, M., Cherubini, C., Cecchi, L., Canuti, V., Fia, G., Zanoni, B., 2016. Direct quantitative indices for ripening of olive oil fruits to predict harvest time. Eur. J.. Lipd Sci. Technol. 118, 1202-1212. https://doi.org/10.1002/ejlt.201500317.

Trentacoste, E.R., Puertas, C.M., Sadras, V.O., 2010. Effect of fruit load on oil yield components and dynamics of fruit growth and oil accumulation in olive (*Olea europaea* L.). Eur. J. Agron. 32, 249-254. https://doi.org/10.1016/j.eja.2010.01.002.

Trentacoste, E.R., Puertas, C.M., Sadras, V.O., 2012. Modelling the intraspecific variation in the dynamics of fruit growth, oil, and water concentration in olive (*Olea europaea* L.). Eur. J. Agron. 38, 83-93. https://doi.org/10.1016/j.eja.2012.01.001.

Zipori, I., Bustan, A., Kerem, Z., Dag, A., 2016. Olive paste oil content on a dry weight basis (OPDW): an indicator for optimal harvesting time in modern olive orchards. Grasas y Aceites, 67, e137. https://doi.org/10.3989/gya.0764152.

Tables

Table 1. Annual values of rainfall, reference evapotranspiration (ET_0) and applied irrigation and fruit number for each irrigation treatment in Experiment II (FI, full irrigation; MI, manager irrigation; D1, regulated deficit irrigation 1; D2, regulated deficit irrigation 2).

Year	Rain	ET_0	Applied irrigation (mm)				Fruit number (fruits m^{-2})			
	(mm)	(mm)	FI	MI	D1	D2	FI	MI	D1	D2
2011	514	1229	465	326	306	243	859	745	779	772
2012	660	1266	591	376	471	240	307	391	387	406
2013	770	1178	536	144	277	219	1123	1116	1063	1055

Table 2. Results from independent linear regression analyses of fruit oil content (O_f, g fruit^{-1}) versus fruit dry weight (w_f, g fruit^{-1}) for each combination of "irrigation treatment" x "year" x "cultivar" in the four experiments. Note that the slopes of the linear regression lines are equivalent to β. The apparent dry weight at the start of oil accumulation (w_{f0}) is calculated from the slopes and intercepts of linear fits. The last two columns ($P_{intercept}$ and P_{slope}) show whether the slopes and intercepts differ statistically from the apparent value obtained for the olive cultivar 'Arbequina' in Experiment I.

Experiment	Year	Cultivar	Treatment	n	Intercept (g fruit^{-1})	Slope (β) (g oil g^{-1})	r^2	w_{f0} (g)	$P_{intercept}$	P_{slope}
I	2017	Arbequina	FI	52	-0.22	0.75	0.88	0.29		
I	2017	Picual	FI	52	-0.48	0.80	0.80	0.60	***	n.s.
I	2017	Arbosana	FI	52	-0.21	0.82	0.92	0.26	***	n.s.
I	2017	Frantoio	FI	52	-0.33	0.74	0.96	0.45	***	n.s.
I	2017	Changlot	FI	52	-0.36	0.79	0.89	0.45	***	n.s.
II	2011	Arbequina	FI	5	-0.24	0.79	0.99	0.30	n.s.	n.s.
II	2011	Arbequina	MI	5	-0.26	0.84	1.00	0.31	n.s.	n.s.
II	2011	Arbequina	D1	5	-0.26	0.84	1.00	0.30	n.s.	n.s.
II	2011	Arbequina	D2	5	-0.26	0.84	1.00	0.31	n.s.	n.s.
II	2012	Arbequina	FI	7	-0.32	0.83	1.00	0.38	***	n.s.
II	2012	Arbequina	MI	7	-0.34	0.87	0.99	0.39	***	n.s.
II	2012	Arbequina	D1	7	-0.28	0.79	0.99	0.35	***	n.s.
II	2012	Arbequina	D2	7	-0.30	0.75	0.99	0.39	**	n.s.
II	2013	Arbequina	FI	8	-0.21	0.75	0.99	0.28	n.s.	n.s.
II	2013	Arbequina	MI	8	-0.15	0.72	1.00	0.21	***	n.s.
II	2013	Arbequina	D1	8	-0.18	0.72	1.00	0.25	n.s.	n.s.
II	2013	Arbequina	D2	8	-0.16	0.70	1.00	0.23	*	n.s.
III	2014	Cobrançosa	FI	9	-0.15	0.49	0.99	0.31	***	***
III	2014	Cobrançosa	PRD	9	-0.18	0.50	0.85	0.36	***	***
III	2014	Cobrançosa	RD75	9	-0.17	0.50	0.98	0.35	***	***

III	2014	Cobrançosa	RD40	9	-0.14	0.49	0.97	0.29	***	***
III	2014	Cobrançosa	SD40	9	-0.18	0.52	0.93	0.35	***	***
IV	2006	Cobrançosa	FI	20	-0.38	0.61	0.72	0.62	***	n.s.
IV	2006	Cobrançosa	SD30	20	-0.40	0.67	0.96	0.60	***	n.s.
IV	2006	Cobrançosa	RF	20	-0.28	0.57	0.91	0.49	***	**

Table 3. Performance of Approach A and Approach B (for three scenarios for the onset of oil accumulation) in reproducing fruit oil content (O_f) dynamics. MAE is mean absolute error, RMSE is root mean square error and CRM is coefficient of residual mass.

Parameter	Approach A	Approach B		
		July 20th	August 1st	August 10th
n	80	80	80	80
MAE (g oil fruit^{-1})	0.008	0.027	0.021	0.032
RMSE (g oil fruit^{-1})	0.013	0.031	0.027	0.040
CRM	0.01	-0.15	0.09	0.23

Figures

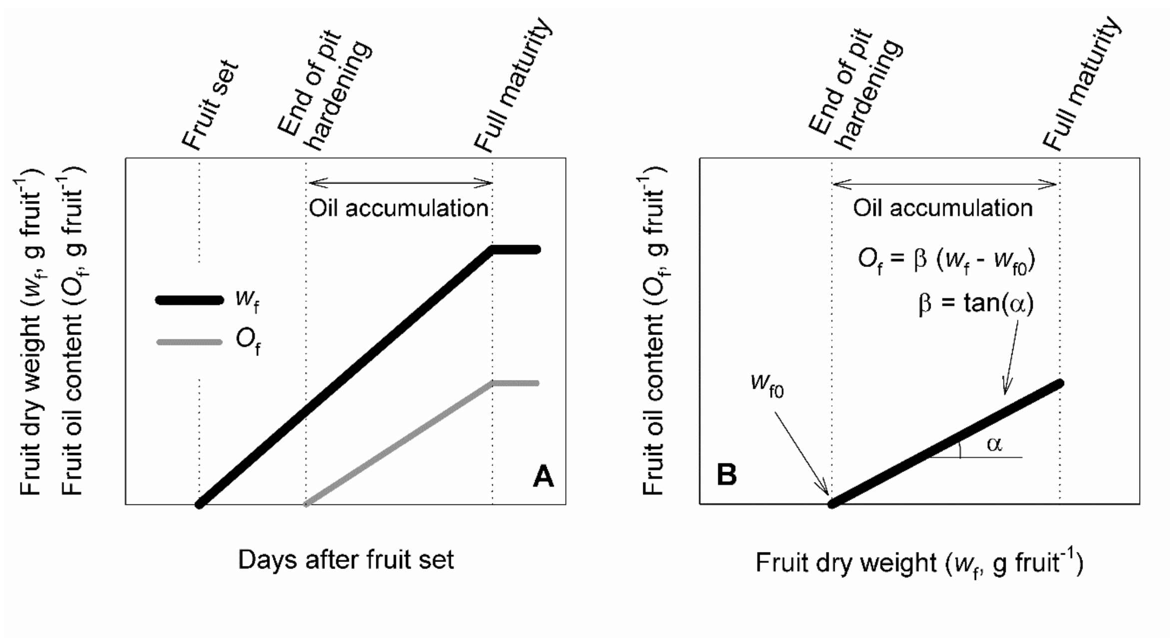

Fig. 1. Graphical description of the main features of the conceptual model. Panel A shows a simplified time course of fruit dry weight (w_f) and oil content (O_f) from fruit set to full maturity. While the former increases throughout this period, oil accumulation only starts when the metabolically expensive pit hardening process has been completed. Panel B shows the plot of O_f versus w_f assuming that the amount of oil accumulated per unit of dry weight increase (β) is constant during oil accumulation. Under these conditions, O_f is linearly related to w_f from the end of pit hardening to full maturity. The slope of the $O_f – w_f$ relationship during this period is indeed the parameter β while the intercept with the X-axis represents the fruit dry weight at the onset of oil accumulation (w_{f0}). Thus, both β and w_{f0} are physiologically relevant parameters that can be used to formulate a linear model to estimate O_f dynamics from those of w_f during the oil accumulation period.

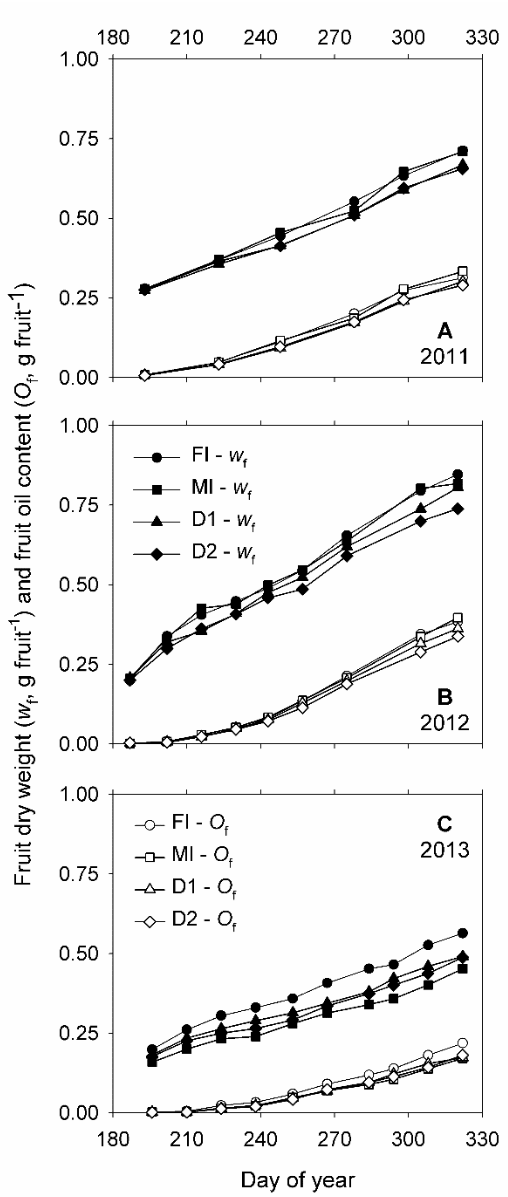

Fig. 2. Time course of fruit dry weight (w_f, closed circles) and fruit oil content (O_f, open circles) in 2011 (**A**), 2012 (**B**) and 2013 (**C**) in Experiment II. Each type of symbol corresponds to a different irrigation treatment: circles, squares, triangles and diamonds for FI (full irrigation), MI (management irrigation), D1 (deficit irrigation 1) and D2 (deficit irrigation 2), respectively.

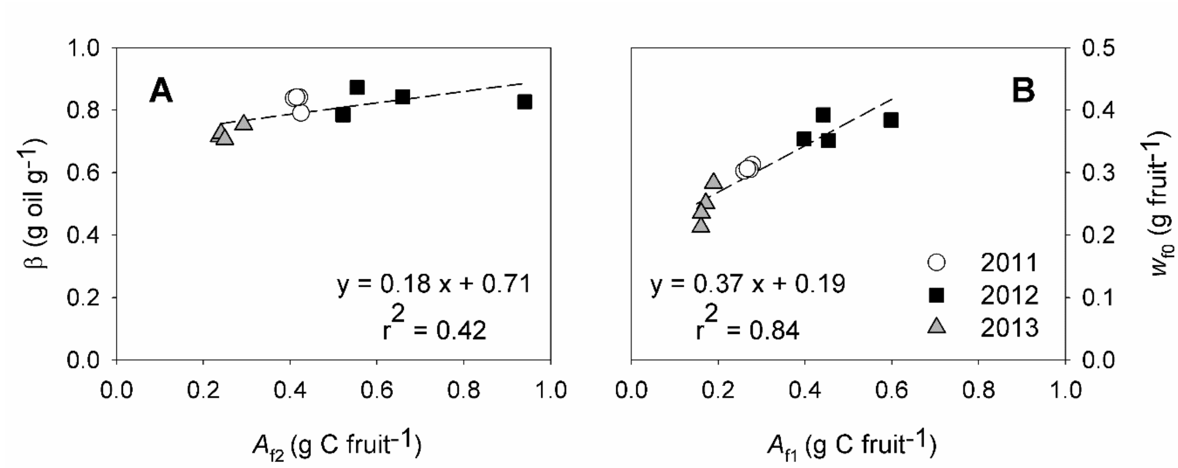

Fig. 3. Relationships between the fraction of fruit dry weight increase allocated to oil accumulation (β) and cumulative assimilation per fruit from August 2nd to September 26th (A_{f2}, A) and between fruit dry weight at the onset of oil accumulation (w_{f0}) and cumulative assimilation per fruit from June 18th July 18th (A_{f1}, B). Data are grouped in years (circles, squares and triangles for 2011, 2012 and 2013, respectively).

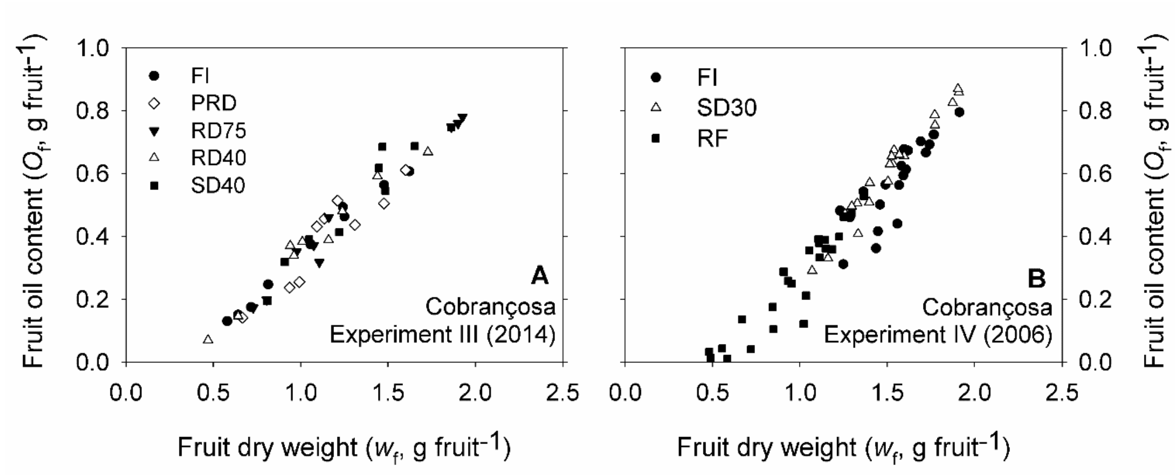

Fig. 4. Plots of fruit oil content (O_f) versus fruit dry weight (w_f) for the olive cultivar 'Cobrançosa' in Experiments III (A) and IV (B). Each type of symbol corresponds to a different irrigation treatment (FI, full irrigation; PRD, partial root drying; RD75, regulated deficit irrigation applying 75 % of FI; RD40, regulated deficit irrigation applying 40 % of FI; SD40, sustained deficit irrigation applying 40 % of FI; SD30, sustained deficit irrigation applying 30 % of FI; RF, rainfed).

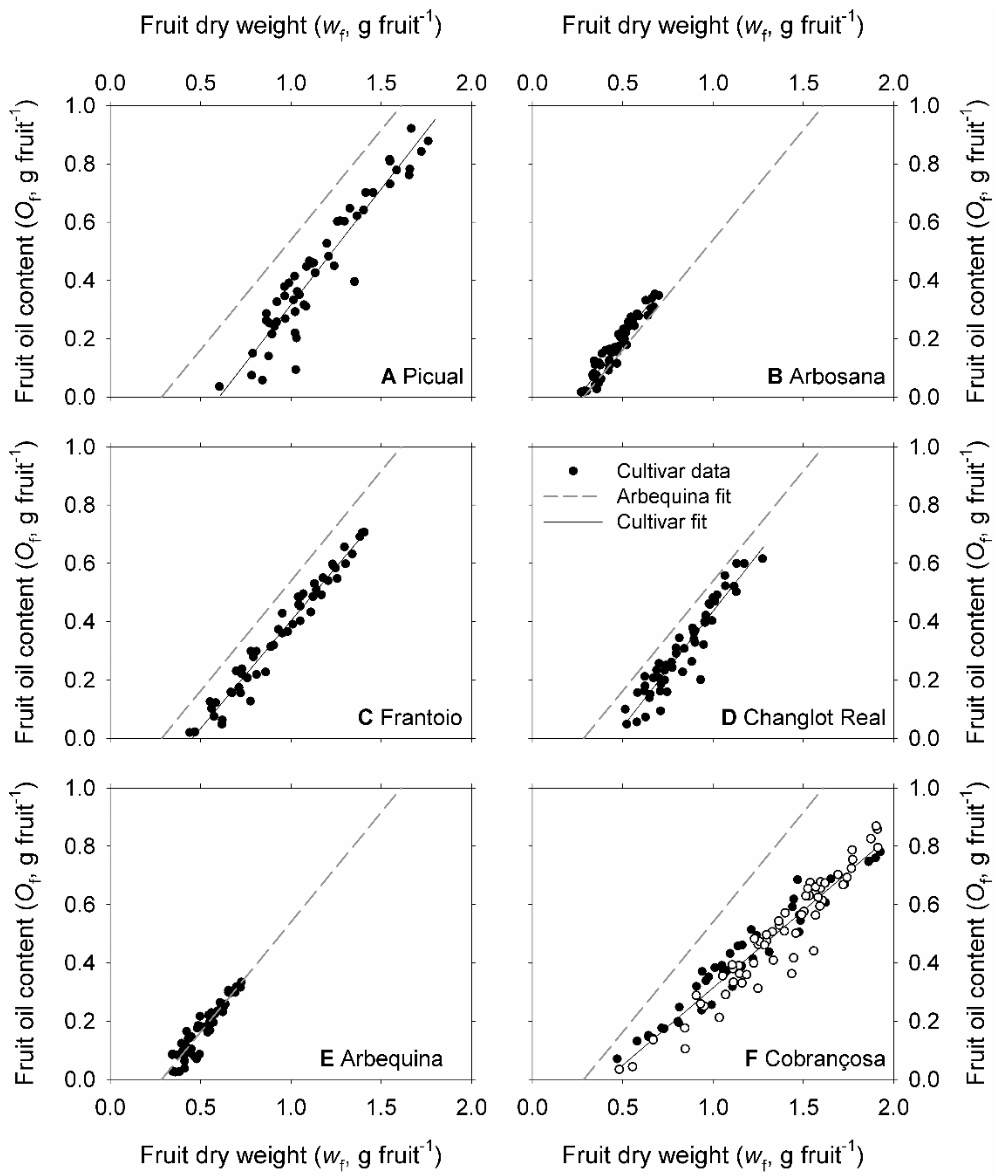

Fig. 5. Plots of fruit oil content (O_f) versus fruit dry weight (w_f) for the olive cultivars 'Picual' (A), 'Arbosana' (B), 'Frantoio' (C), 'Changlot Real' (D), 'Arbequina' (E) and 'Cobrançosa' (F). Data for 'Picual', 'Arbosana', 'Frantoio', 'Changlot Real' and 'Arbequina' come from Experiment I. Data for 'Cobrançosa' comes from Experiment III (closed symbols) and Experiment IV (open symbols), mixing all irrigation treatments. The linear fit obtained for 'Arbequina' in Experiment I is shown in all panels with a grey dashed line to serve as a reference.

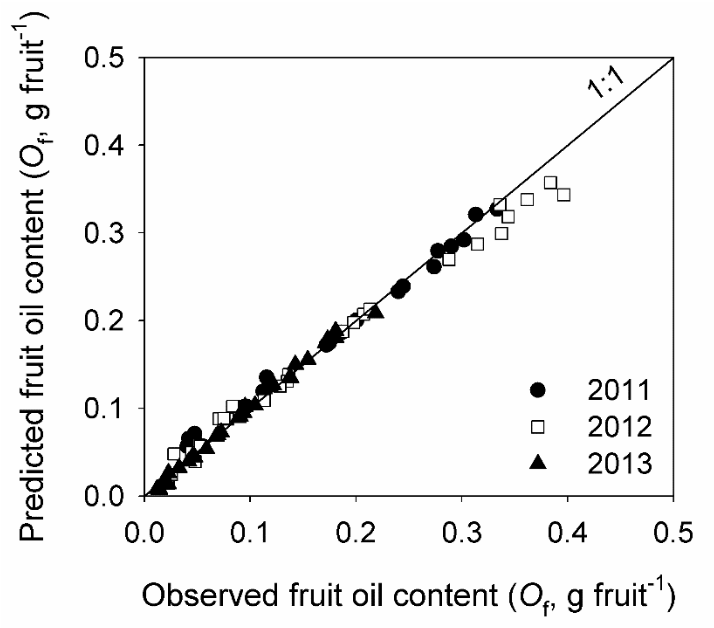

Fig. 6. Validation of Approach A for the olive cultivar 'Arbequina' on the dataset of Experiment II. Predicted versus observed plots of fruit oil content (O_f) in relation to the 1:1 line. Data are grouped in years (circles, squares and triangles for 2011, 2012 and 2013, respectively).

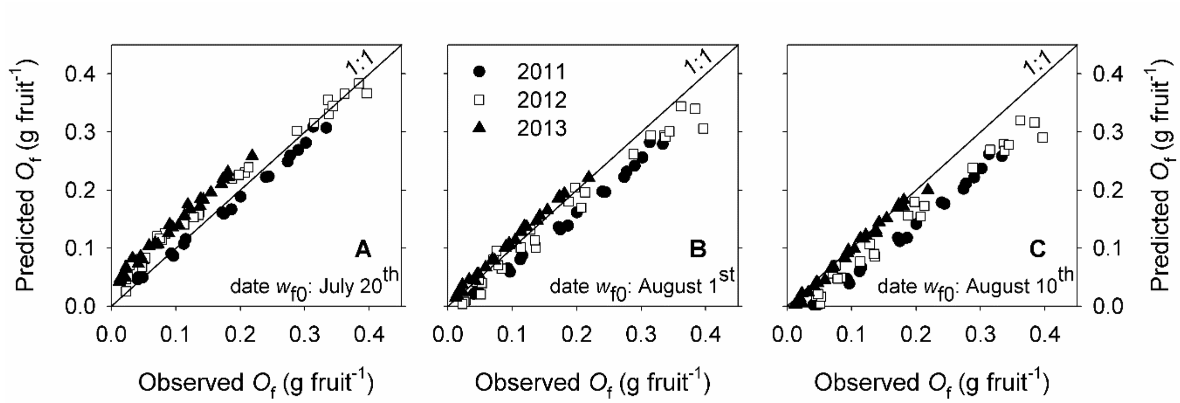

Fig. 7. Validation of Approach B for the olive cultivar 'Arbequina' on the dataset of Experiment II using three scenarios for the onset of oil accumulation: July 20th (A), August 1st (B) and August 10th (C). Predicted versus observed plots of fruit oil content (O_f) in relation to the 1:1 line. Data are grouped in years (circles, squares and triangles for 2011, 2012 and 2013, respectively).