

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/236206146>

Heat accumulation period in the Mediterranean region: Phenological response of the olive in different climate areas (Spain, Italy and Tunisia)

Article in *International Journal of Biometeorology* · April 2013

DOI: 10.1007/s00484-013-0666-7 · Source: PubMed

CITATIONS

84

READS

759

9 authors, including:



F. Aguilera

University of Jaén

50 PUBLICATIONS 639 CITATIONS

[SEE PROFILE](#)



Luisa Ruiz

University of Jaén

7 PUBLICATIONS 419 CITATIONS

[SEE PROFILE](#)



Bruno Romano

University of Perugia

103 PUBLICATIONS 2,638 CITATIONS

[SEE PROFILE](#)



Carmen Galán

University of Córdoba

304 PUBLICATIONS 12,657 CITATIONS

[SEE PROFILE](#)

Heat accumulation period in the Mediterranean region: phenological response of the olive in different climate areas (Spain, Italy and Tunisia)

Fátima Aguilera · Luis Ruiz · Marco Fornaciari ·
Bruno Romano · Carmen Galán · Jose Oteros ·
Ali Ben Dhiab · Monji Msallem · Fabio Orlandi

Received: 17 December 2012 / Revised: 20 March 2013 / Accepted: 23 March 2013 / Published online: 17 April 2013
© ISB 2013

Abstract The main characteristics of the heat accumulation period and the possible existence of different types of biological response to the environment in different populations of olive through the Mediterranean region have been evaluated. Chilling curves to determine the start date of the heat accumulation period were constructed and evaluated. The results allow us to conclude that the northern olive populations have the greatest heat requirements for the development of their floral buds, and they need a period of time longer than olives in others areas to completely satisfy their biothermic requirements. The olive trees located in the warmest winter areas have a faster transition from endogenous to exogenous inhibition once the peak of chilling is met, and they show more rapid floral development. The lower heat requirements are due to better adaptation to warmer regions. Both the threshold temperature and the peak of flowering date are closely related to latitude. Different types of biological responses of olives to the environment were found. The adaptive capacity shown by

the olive tree should be considered as a useful tool with which to study the effects of global climatic change on agro-ecosystems.

Keywords Chilling · Flowering · Heat requirements · Olive · Plasticity · Threshold temperature

Introduction

In the Mediterranean basin, the olive tree (*Olea europaea* L.) is one of the most widespread cultivated arboreal species. In this area, olive growing has a social and economic role that is of paramount importance, with olive fruit and oil being among the oldest and the most important of products.

The Mediterranean region accounts for approximately 98 % of the world production and 82 % of the world consumption of olive oil. Spain is the largest olive oil producing country, with 41.9 % of world production, followed by Italy (18.3 %), Greece (12.2 %) and Tunisia (5.9 %) (International Olive Council 2011). Together, these countries produce about 2,178,000 tonnes of olive oil, which represents 78 % of the world total olive oil production.

This region lies in a transition zone between the arid climate of North Africa and the temperate and rainy climate of central Europe. It is thus affected by interactions between mid-latitude and tropical processes, and is an area that is potentially vulnerable to the effects of climate change (Giorgi and Lionello 2008). Indeed, the Mediterranean region has been identified as one of the most prominent ‘hot spots’ in future climate-change projections (Giorgi 2006).

Climate affects practically all of the physiological processes throughout the life cycle of plants (Barranco et al. 2008; Osborne et al. 2000). Of all of the biological phases, flowering

F. Aguilera (✉) · M. Fornaciari · B. Romano · F. Orlandi
Department of Applied Biology, University of Perugia, Borgo XX
Giugno 74, 06121 Perugia, Italy
e-mail: faguiler@ujaen.es

L. Ruiz
Department of Animal Biology, Plant Biology and Ecology,
Agrifood Campus of International Excellence (CeiA3), University of
Jaén, Campus of the Lagunillas s/n, 23071 Jaén, Spain

C. Galán · J. Oteros
Department of Botany, Ecology and Plant Physiology, Agrifood
Campus of International Excellence (CeiA3), University of
Córdoba, Campus of Rabanales, 14071 Córdoba, Spain

A. Ben Dhiab · M. Msallem
Institut de l'Olivier, BP 208, 1082 Tunis, Tunisia

is the most critical for every fructiferous plant. Olive floral phenology is characterised by bud formation during summer, dormancy during autumn, budburst in late winter, and flowering in late spring (Fernández-Escobar et al. 1992; Galán et al. 2005). The release of floral bud dormancy occurs when olive trees have been exposed to a long enough period of chilling temperatures (Fernández-Escobar et al. 1992; Pinney and Polito 1990; Rallo and Martin 1991). Indeed, incomplete chilling can delay the release of floral bud dormancy, and thus delay the first flowering, which can result in an expanded flowering period (Barranco et al. 2008).

After budbreak, certain biothermic units are required for the development of the inflorescences (Chuine et al. 1998). Determination of the exact start date for olive heat accumulation has proven difficult, and remains lacking to date. Both the onset of the heat accumulation period and the temperature threshold for the amount of positive heat units might vary according to the climate of a determined geographical area. Changes in the temperature requirements might negatively affect the correct development of flower buds and the timing of olive flowering and, consequently, the evolution of the olive pollen season.

Many authors have used a combination of aerobiological and phenological information to analyse the flowering phase in anemophilous species, with pollen emission data being widely used as a well-proven tool for indirect evaluation of the flowering period (Galán et al. 2008; Jato et al. 2002; Orlandi et al. 2005, 2010). Nevertheless, the location of pollen monitoring stations, as well as both the topographical and the meteorological conditions should be considered (Aguilera and Ruiz Valenzuela 2009; Dimou 2012; Osborne et al. 2000).

Phenotypic plasticity is the ability of an individual organism to alter its physiology and/or morphology in response to changes in environmental conditions. This is particularly important in plants, where a sessile life-style requires them to deal with ambient conditions (Schlichting 1986). Moreover, Bradshaw (1965) reported that perennial species are more plastic than annual species, as the most obvious environmental changes that can affect a perennial species will be those connected with the seasons.

The climate of the Mediterranean region is characterised by a great diversity of features, which results in a variety of climate types and great spatial variability (Lionello et al. 2006). On this basis, the role of biothermic requirements related to the olive flowering period needs further evaluation.

The aim of the present study was to determine the start date of the period of heat accumulation and the optimal temperature threshold within the Mediterranean region across the large latitudinal gradient of Tunisia, Spain and Italy. At the same time, we evaluated the possible different types of plastic responses to the environment in these different populations of olive trees.

Materials and methods

Study area

The main characteristics of the olive growing areas considered in the present study are shown in Table 1. The latitudinal gradient through this Mediterranean region covers a large geographical area, from 43°05'N in Perugia, Italy, to 33°35'N in Zarzis, Tunisia. In terms of longitude, the study areas cover from 09°50'E in Menzel, Tunisia, to 04°45'W in Córdoba, Spain. The range of altitude is from 17 m a.s.l. in Zarzis, Tunisia, to 528 m a.s.l. in Jaén, Spain. The study period comprises from 13 years (1999–2011) to 20 years (1992–2001), depending on the year of onset of aerobiological monitoring in each area.

Bioclimatic data

To determine the optimal date for the onset of the heat accumulation period, chilling curves were constructed and evaluated for each year and study area on the base of daily chilling values. The chilling units were calculated by the Utah method (Richardson et al. 1974). This model assumes the presence of an optimum curve of the chilling effect, and it assigns a weighted value to each temperature data. A maximum chilling value at 5.2 °C was assigned, while a temperature below 0 °C and above the maximum threshold produces negative values (Orlandi et al. 2006). Of note, the function used to calculate the chilling units takes into account a threshold maximum temperature, which is more realistic for adaptation to the climate characteristics of each study area (Orlandi et al. 2006).

A maximum threshold temperature of 16 °C was used. If the temperature goes above this, then it is too warm for the olive to accumulate chilling. As soon as the temperature drops below this threshold temperature of 16 °C, different chilling values can be calculated on the base of the hourly temperatures considered by the Utah model. The 16 °C threshold was chosen because, considering all the study areas, it was the best temperature base for obtaining positive chilling units. Indeed, this was the lowest threshold temperature that allowed obtaining positive chilling units also in the southern Tunisian areas.

The chilling curves, derived by daily chilling values, were constructed as polynomial equations and were used for estimation of the heat accumulation start date (*start_ht*) for each year and study area. Eight heat accumulation start dates were tested: the peak of chilling (*peak_ch*) as the day of the year with the maximum accumulation of positive chilling units, and the following days with the decline in the cumulative chilling percentages of 1 %, 3 %, 5 %, 10 %, 15 %, 20 % and 25 % (relative to the peak of chilling).

The heat amounts are expressed as growing degree days (GDDs, °C-day). The GDD values were calculated using the

Table 1 Biogeographical characteristics of the olive growing study areas in Italy, Spain and Tunisia

Site	Coordinates	Altitude (m a.s.l.)	Mean annual temperature (°C)	Annual total precipitation (mm)	Studied period
Italy					
Perugia (PG)	43°05'N,12°30'E	450	13.6	850	1992–2011
Brindisi (BR)	40°55'N,17°01'E	230	16.6	573	1999–2011
Spain					
Córdoba (CO)	37°50'N,04°45'W	123	18.0	674	1992–2011
Jaén (JN)	37°47'N,03°46'W	528	16.9	578	1993–2011
Tunisia					
Menzel (ME)	35°25'N,09°50'E	160	20.9	317	1993–2011
Zarzis (ZR)	33°35'N,11°01'E	17	21.0	192	1993–2011

method proposed by Arnold (1960), based on the maximum and minimum daily temperatures. This model assumes a temperature base below which biothermic accumulation stops or is reduced to the lowest terms. To determine the most appropriate temperature base for the heat accumulation for each area, a wide range of 25 threshold temperatures from 1 °C to 25 °C were tested.

To interpret the relationship between the heat accumulation period and the olive flowering phase, aerobiological databases were used (International Association for Aerobiology Newsletter 2011). Sampling was carried out by the volumetric method, which is based on the possibility of capturing pollen and other biological particles present in the atmosphere using the principle of depression impact. Aerobiological sampling techniques provide data on daily pollen content in the air that reflect the process of flower opening in the olive growing areas around a monitoring station. Moreover, this kind of sampling reduces the subjectivity in interpretation of the flowering period. Considering that the monitoring traps were located inside or very near to the olive groves, the peak day of the pollen season, that is, the day with the maximum olive pollen concentration, was used as the full flowering date (peak of flowering; peak_fl) (Galán et al. 2008; Orlandi et al. 2010; Osborne et al. 2000).

The different GDD amounts were calculated from the start dates above to the peak of flowering, for each year and study site. The root mean square errors (RMSEs) were calculated and plotted. The most accurate start heat accumulation date and the best threshold temperature were selected for each area, which took into account the lowest RMSE mean value over the study period.

Three variables related to the heat accumulation period were calculated: (1) the length (in days) of the heat accumulation period (length ht period), which was calculated as the time difference between the best heat accumulation start date and the peak of flowering date; (2) the time period between the peak of chilling date and the heat period start date (peak_ch/start_ht); and (3) the duration of the period between the peak of chilling date and the peak of flowering date (peak_ch/peak_fl).

Maximum and minimum daily temperatures were obtained from the weather stations nearest to the study monitoring units, i.e. Network stations of the National Council of Agricultural Research (CRA-Cma) for Italy, the Agroclimatic Station Network of the Andalusian *Consejería de Agricultura y Pesca* for Spain and the National Meteorological Centre for Tunisia.

Statistical analysis

To define the degree of the relationship between heat accumulation period characteristics and olive reproductive phase, Pearson's parametric correlation analysis was performed, in relation to data normality. A 95 % confidence level was used. Only significant absolute coefficient values ≥ 0.50 were considered. Similarly, the correlation coefficients between inter-related variables were not considered; i.e. a variable calculated by the combination of the other two variables (e.g. the length of the heat accumulation period is the difference between the peak of flowering date and the start heat date).

Linear regression analyses were also performed according to the latitude, altitude and bioclimatic parameters, to establish the highest statistical relationship of dependence for olive flowering.

Variance analysis (one-way ANOVA) was carried out to determine whether the differences in the heat accumulation periods were induced by variable geographic environmental conditions. When there were significant differences, a post-hoc Tukey test was performed. This comparative analysis between the study areas allowed evaluation of the possible different types of biological response of the olive trees to the environment.

Statistica 7.0 software was used for all statistical analyses.

Results

The mean RMSE values obtained relating to both the different heat accumulation start dates and all of the threshold temperatures tested for each study area are shown in Fig. 1.

The best start date for the onset of the heat accumulation period in the olive growing areas of Perugia and Brindisi

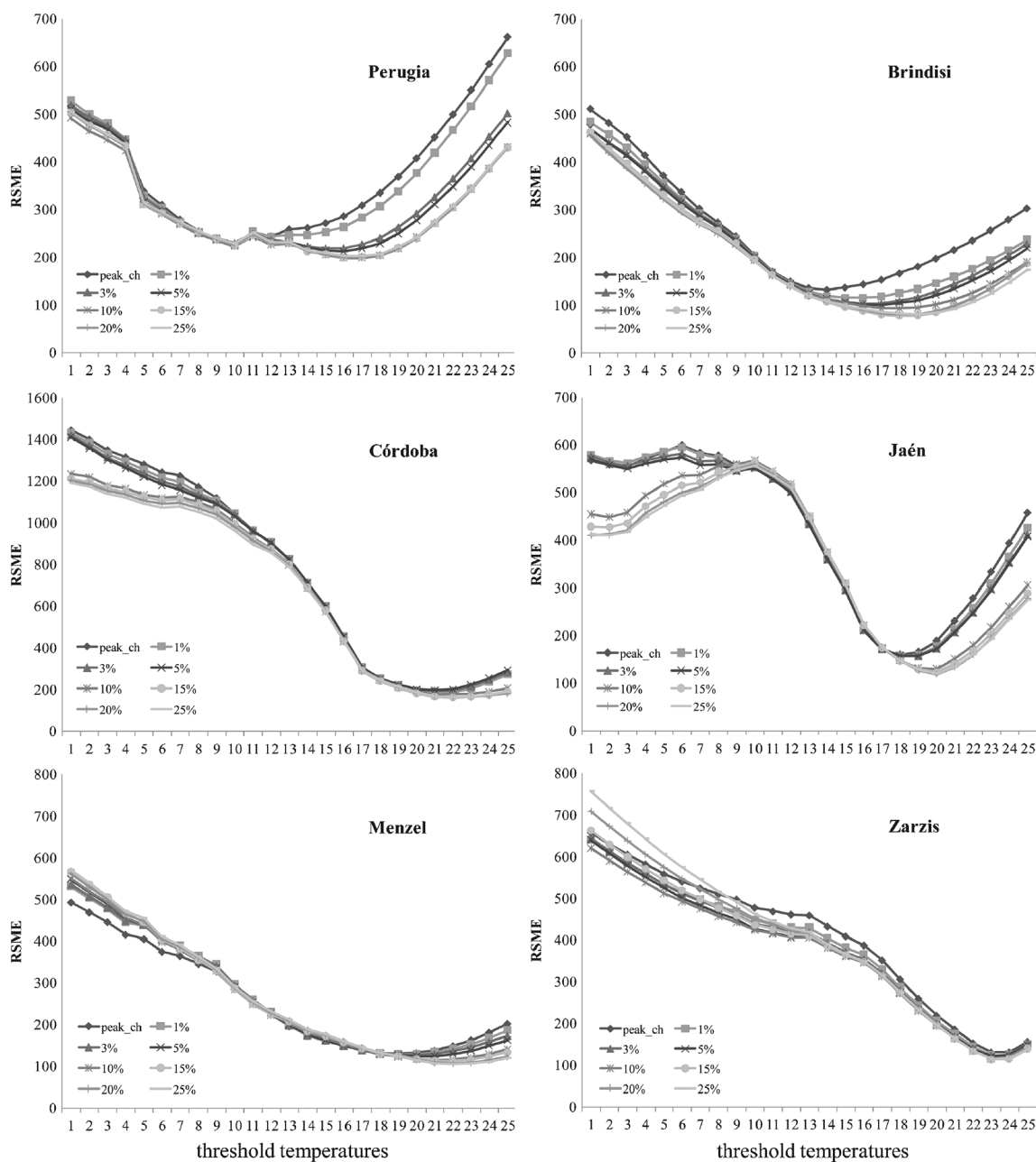


Fig. 1 Mean root mean square error (RMSE) values for the different heat accumulation start dates and the different threshold temperatures evaluated for each study site. *Peak_ch* Peak of chilling date

was the day with a 10 % cumulative chilling percentage decline in comparison to the peak of chilling. In Córdoba, 15 % was obtained as the best heat accumulation start date, while 20 % was obtained for the Jaén site. In this latter area, a 20 % cumulative chilling percentage decline in comparison to the peak of chilling was the best heat accumulation start date for both the Menzel and Zarzis olive-growing areas.

Different threshold temperatures were obtained across the study areas, with values that ranged from 16 °C in Perugia to 23 °C in Zarzis (Table 2). Two simple linear regression analyses that tested for relationships between the threshold

temperature and the main geographical characteristics are shown in Fig. 2. A significant and strong negative relationship ($R^2=0.91$) was found between latitude and threshold temperature. This relationship was lowest in terms of the altitude ($R^2=0.49$).

The average dates of peak of chilling for each of the study areas are given in Table 2. This parameter varied geographically ($F=10.777$; $P<0.001$). The average peak of chilling in the Perugia, Brindisi, Menzel and Zarzis olive growing areas was between 18 and 22 January, while in Córdoba and Jaén, this average date occurred as 11 January.

Table 2 Average values of the main characteristics of the heat accumulation period in each study area. *Peak_ch* Peak of chilling date, *Start_ht* heat accumulation start date, *Peak_fl* peak of flowering date, *GDD* growing degree days amounts

Study area	Peak_ch	Start_ht	Peak_fl	Threshold	GDD	Peak_ch/ Start_ht	Length heat period	Peak_ch/ Peak_fl
Perugia	18±7	46±10	158±6	16	200±47	28	112	140
Brindisi	20±6	41±8	141±4	18	123±30	21	100	121
Córdoba	11±6	37±8	133±13	22	119±38	26	96	122
Jaén	11±9	39±9	134±7	20	114±28	28	95	123
Menzel	22±7	36±7	119±8	22	81±25	14	83	97
Zarzis	22±6	32±8	114±9	23	83±27	10	82	92

It is noteworthy that, although similar peak chilling dates were recorded in the Italian and Tunisian areas, the chilling amounts were clearly different. The average chilling accumulation from the first day in which positive chilling units were detected to the peak of chilling date was 1,246 chilling units in Perugia and 1,034 chilling units in Brindisi, which are notably higher than the 130 and 27 chilling units recorded in Menzel and Zarzis, respectively. In the Spanish areas, this accumulation value was 606 chilling units for Córdoba and 767 chilling units for Jaén.

The heat accumulation start dates were significantly different between these olive growing areas ($F=5.825$; $P=0.001$). Two groups were differentiated (Fig. 3). The average heat start

date in Perugia was 15 February (Julian day 46). However, in Brindisi, Córdoba, Jaén, Menzel and Zarzis, the average heat accumulation start date was from 1 to 10 February (Julian days 32 to 41).

For the average flowering peak date, significant differences between these sites were found ($F=62.030$; $P=0.001$). Here, three groups were observed. The average peak of flowering date in the olive growing areas of Menzel and Zarzis were 24 and 29 April (Julian days 114 and 119), respectively, followed by the average flowering peak dates recorded in Brindisi, Córdoba and Jaén, which were between 14 and 21 May (Julian days 134 to 141). For the Perugia site, the average peak of flowering was 7 June (Julian day 158). The linear regression analysis between the peak of flowering date and the latitude is shown in Fig. 4. A highly significant positive relationship between latitude and peak of flowering was obtained ($R^2=0.97$). The same type of relationship was seen for the altitude, although with a lower R^2 (0.47).

Significant differences between study areas were recorded for both the length of the heat accumulation period ($F=23.630$; $P<0.001$) and the GDD amounts ($F=31.998$; $P=0.001$) and, as above, three groups were observed. Perugia showed the highest length of heat accumulation period and the highest GDD amounts recorded, with means of 112 days and 200 GDD (threshold temperature, 16 °C), respectively. In the Brindisi, Córdoba and Jaén olive growing areas, the length of the heat accumulation period was from 95 to 100 days, and a mean of 119 GDD (threshold temperature, 18 °C–22 °C) was recorded. Menzel and Zarzis showed the lowest values, with a mean length of heat accumulation period of 83 days, and a mean of 82 GDD (threshold temperature, 22 °C–23 °C). The correlation analysis carried out to test the relationship between latitude, altitude and GDD amounts showed a highly significant positive relationship between latitude and GDD amount ($r=0.71$). However, this relationship was lower regard to the altitude ($r=0.50$).

The time periods between the peak of chilling date and both the heat period start date and the peak of flowering date were also analysed. For the first of these, two groups with clear differences were recorded ($F=47.710$; $P=0.001$). The study areas of Perugia, Brindisi, Córdoba and Jaén showed

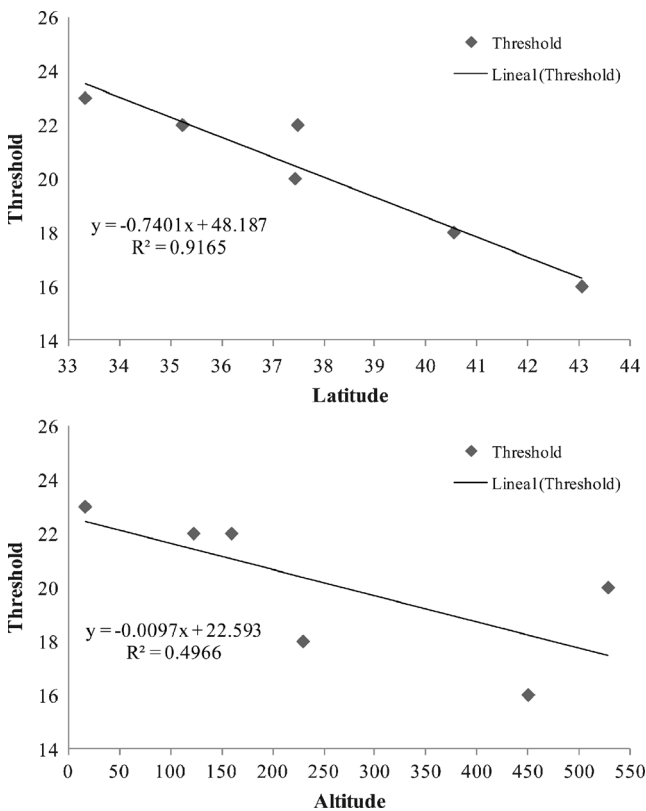
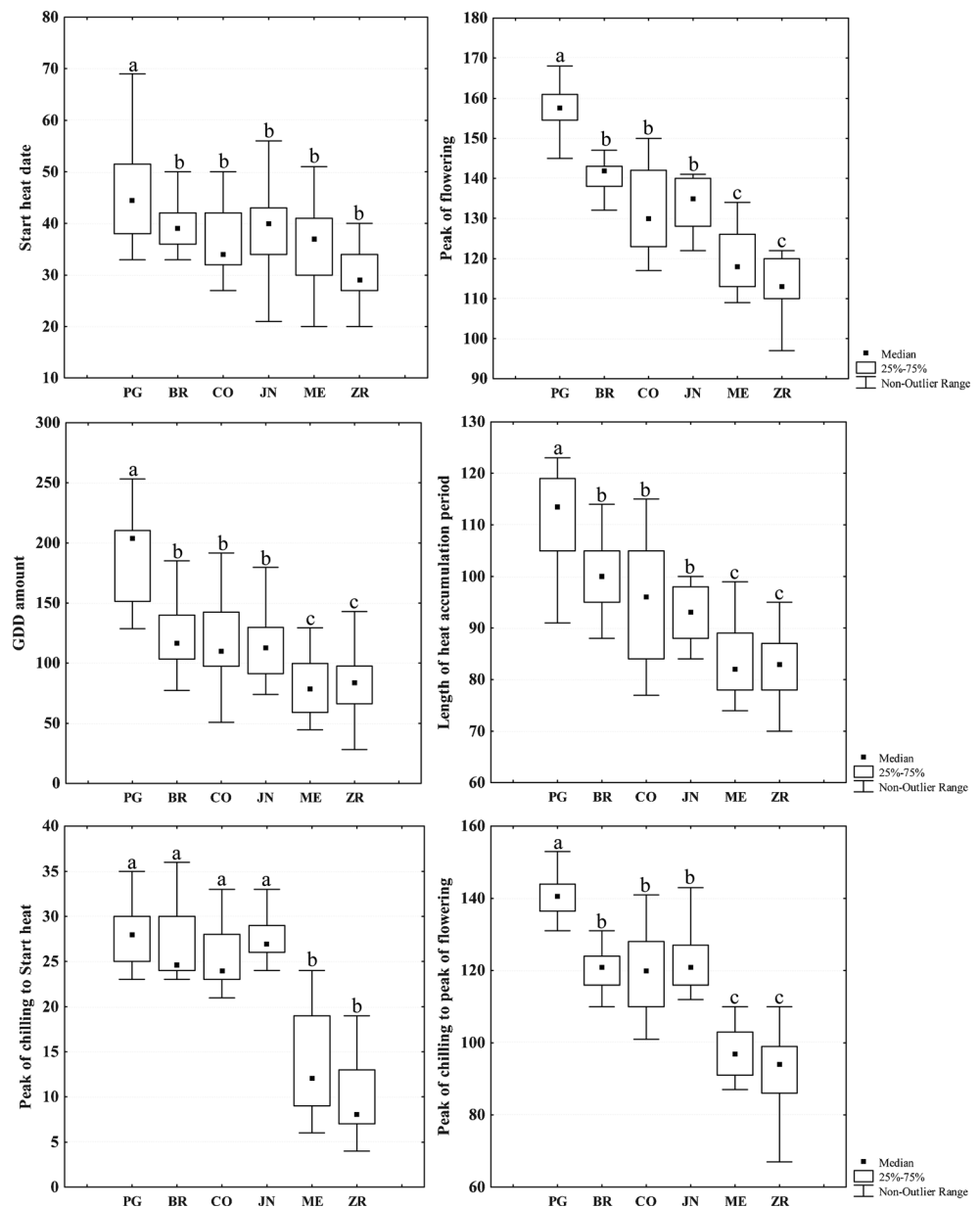


Fig. 2 Linear equations and fitting of the regression analyses between latitude, altitude and threshold temperatures

Fig. 3 Box-plots of the different parameters studied. *PG* Perugia, *BR* Brindisi, *CO* Córdoba, *JN* Jaén, *ME* Menzel, *ZR* Zarzis. Different letters indicate statistically different values ($P \leq 0.05$)



the highest mean values, from 21 to 28 days, whereas in the Menzel and Zarzis olive areas these were 14 days and 10 days, respectively. For the second parameter, as the time period from the peak of chilling to the peak of flowering, three significantly different groups were observed ($F=58.060$; $P=0.001$). The mean length of this time period in Menzel and Zarzis was 95 days, follow by 122 days in Brindisi, Córdoba and Jaén. The highest value was observed in Perugia, at 140 days.

Correlation analysis was performed for the relationships between the heat accumulation period characteristics in each study area. In general terms, the start date of the heat accumulation period correlated significantly and positively with the peak chilling date (Perugia $r=0.96$; Brindisi $r=0.99$; Jaén $r=0.93$;

Menzel $r=0.76$; Zarzis $r=0.84$). Non-significant coefficients were obtained for the other parameters considered in this analysis. The GDD amounts showed significant and positive correlation coefficients in some areas. The time period between the peak of chilling and the start heat accumulation date had a positive influence on the GDD amounts in the olive groves of Perugia ($r=0.51$) and Jaén ($r=0.70$). Moreover, the peak of flowering in Córdoba correlated significantly, although with a lower coefficient, with the GDD amounts ($r=0.51$). The time period between the peak of chilling and the start heat accumulation date also had a positive influence on the peak of flowering. This variable correlated significantly in the Perugia ($r=0.53$), Córdoba ($r=0.55$) and Jaén ($r=0.59$) olive-growing areas. The peak of chilling

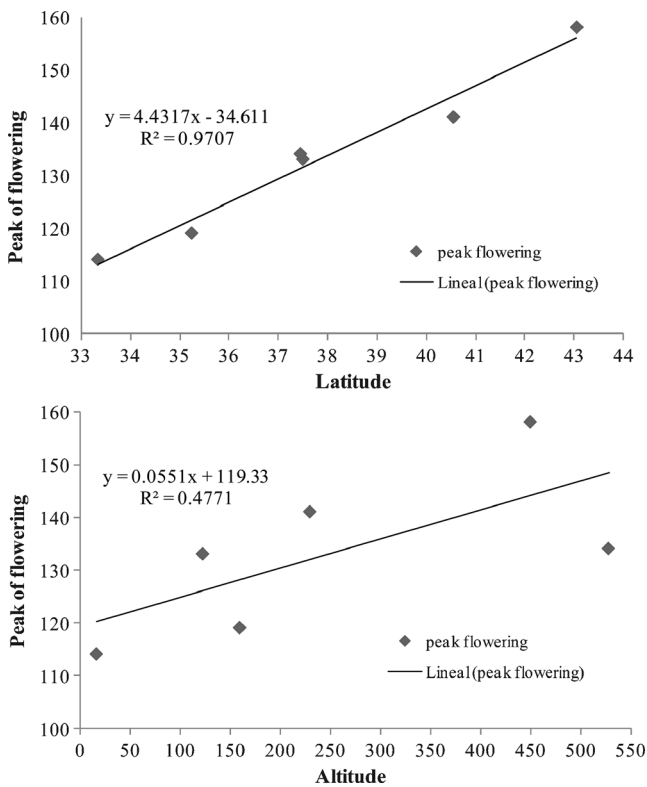


Fig. 4 Linear equations and fitting of the regression analyses between latitude, altitude and average peak of flowering dates

date correlated positively with the peak of flowering in the Menzel area ($r=0.62$).

Discussion

The specific moment for the onset of the olive heat accumulation period is difficult to determine and has essentially remained unknown. Flower buds that are ready to begin the first phase of morphological development require a certain thermal contribution to continue to develop after their latent phase (Anderson et al. 2005; Foley et al. 2009; Orlandi et al. 2002). Numerous studies, adopting methodologies and threshold temperatures of great heterogeneity, have investigated the biothermic requirements regarding the biological development of the olive in different areas (Alba and de la Guardia 1998; Bonofiglio et al. 2008; Galán et al. 2005). The GDD is a commonly used thermal time method of widespread acceptance, but agreement in the method for evaluating the best threshold temperatures is currently lacking (Ruml et al. 2010; Snyder et al. 1999; Yang et al. 1995).

The threshold temperatures obtained in this research field differ from those provided for the olive tree in previous studies (Galán et al. 2005; Martins et al. 2012; Orlandi et al. 2006). The base temperatures reported by these authors ranged between 5 °C and 12.5 °C, values lower than those are shown

here. This fact can be considered to depend mainly on methodology used both to determine the onset of the heat amount and to statistically evaluate the best GDD threshold temperatures. Moreover, there are other factors that should be considered. On the one hand, the lower threshold or base temperature may vary between geographical areas (Črepinšek et al. 2006). In this sense we have observed that the threshold temperatures are related closely to latitude. Threshold values decrease proportionally as the latitude increases, as these values are lower in olive groves at higher latitudes. The same relationship was seen for altitude, although at a lower intensity. Furthermore, and according to several studies, it should not be surprising that the temperature affects both the dormancy induction and flowering time, and that, in the northern cooler areas, the olive trees consider as heat lower temperatures than in the southern areas (Edwards et al. 2006; Foley et al. 2009; Ramos et al. 2005). On the other hand, threshold temperatures could differ between species and also between cultivars within a species (Martins et al. 2012; Ruml et al. 2010). It would be interesting to take this point of view into account in future studies in the Mediterranean region considering different olive cultivars located at the same latitude to avoid geographical variability.

The construction and evaluation of chilling curves to determine the start date of the heat accumulation period was successful. The peak of chilling, i.e. the day of the year with the maximum accumulation of positive chilling units, has not been considered as the start date of the heat accumulation in any olive growing area. This result is particularly important because it could indicate that, upon arriving at the peak chilling day, the chilling requirements may have not been met, and more days of chilling would be needed to break the endodormancy phase (Lang 1987).

Once the chilling requirements are met, crown buds remain in temporary suspension, with their visible growth state being controlled by environmental factors (ecodormancy) (Lang 1987). We have observed that, from the peak of chilling, a certain number of days are needed to begin the heat accumulation period, which, as seen above, might be related closely to the transition from endodormancy to ecodormancy. According to Doorenbos (1953), the transition from one phase of dormancy to another does not show morphological evidence that would allow an unequivocal classification. Moreover, De la Rosa et al. (2000) reported that active growth and development starts as soon as buds that have completed chilling are placed under favourable conditions for budbreak. In this sense, the results of the present study provide a good approximation. Here, in all study areas, the range from 10 % to 20 % cumulative chilling percentage decline in comparison to the peak of chilling provided the best start date for the onset of the heat accumulation period.

On this basis, two types of biological responses of olives to the environment were seen. In the Italian and Spanish olive-growing areas, the time period between the peak of chilling

and the heat accumulation start date was 2 weeks longer than in the Tunisian areas. This finding might indicate that olive trees located in the warmest winter areas have a faster transition from endogenous to exogenous inhibition once the peak of chilling is met, which is consequently related to their adaptive capacity to the environment concerned. Several studies have reported that, for the olive, low temperatures are needed only to break dormancy in previously initiated buds, as occurs in other fruit-tree species (Fernández-Escobar et al. 1992; Pinney and Polito 1990; Rallo and Martin 1991). However, our data indicate that a delay in the peak of the olive flowering date can be caused by a long transition between the end of internal dormancy and the onset of ecodormancy. This was observed in the Italian and Spanish areas, but not in the Tunisian areas, where there is a more rapid transition between the dormancy phases.

In the different study areas from the coldest to the warmest, the chilling requirements for successive flowering development can be considered as adequately fulfilled even if the differences were elevated in areas of central Italy in comparison with those in south Tunisia. Until now, the lowest winter chilling amounts recorded in north African areas were also sufficient to regulate the olive dormancy phenomenon but in the future these might no longer be adequate. In this sense, genetic selection to obtain new olive cultivars with commercial quality and low chilling requirement, which is a heritable character (Barranco et al. 2008), could be a convenient agronomical practice, as could the applications of rest-breaking agents, developed to avoid or reduce the negative consequences of an insufficient chilling accumulation.

The onset of the heat accumulation period usually occurs in the first two weeks of February, although in Perugia there was a delay of 9 days compared to the other areas studied. This date is positively related to the occurrence of the peak of chilling. It is noteworthy that, once the heat accumulation period begins, different biological responses can be observed with respect to subsequent floral development.

The olive groves located in the northern areas (e.g. the Perugia site) need a longer period of time than the other areas to completely satisfy their biothermic requirements, with these being notably higher than those in the warmer areas. The lowest heat requirements were observed in the southern areas (e.g. the Tunisian sites), where there was a mean difference of 59 % with respect to the biothermic requirements in the northern olive-growing areas. These low heat requirements are due to better adaptation to warmer regions.

The same phenomenon was seen for the peak of flowering. The day on which most of the tree canopy flowers are open, and consequently the main flowering date, is influenced strongly by latitude. Thus, olive trees located in the Tunisian areas were the first to complete flower development and to begin their flowering period. Both the GDD amounts and the peak of flowering date increase progressively with latitude.

This is in agreement with Bonofiglio et al. (2008), who reported homogeneity in plant behaviour as a function of latitude.

Another particularly interesting result is that the period of time between the day with the maximum accumulation of chilling and the day with the maximum olive pollen emission to the atmosphere was notably shorter in the southern areas than in olive groves situated at intermediate and high latitudes. It is important to consider that both the metabolic activity and the photosynthetic activity of the olive are maximal across an optimal range of temperature between 15 °C and 30 °C (Krueger 1994). According to this latter author, respiration is catalysed by enzymes that are temperature sensitive. In the temperature range of 10 °C–30 °C, respiration shows a positive trend line, doubling for each 10 °C increase in temperature. However, at higher temperatures, the enzymes can be denatured. In addition, excessive temperatures of around 30 °C–35 °C can be a limiting factor for olive reproductive success (Barranco et al. 2008; Cuevas et al. 1994; Martin et al. 1994). High temperatures when olive flower buds are developing, especially if these temperatures are accompanied by dry, windy conditions, can have a detrimental effect on subsequent flowering, pollination and fruit set (Martin et al. 1994). Moreover, the olive pollen tube growth is maximal at 25 °C, while temperatures higher than this value show a negative influence (Cuevas et al. 1994; Koubouris et al. 2009). Hence, and according to these authors, excessive temperatures can negatively influence several reproductive parameters such as flower development, pollen tube growth, pollen viability or the pollination process, and, consequently, subsequent fertilisation and production yield.

For this reason, olive trees situated in southern areas develop all of this process in a shorter time, through adapting their physiology in response to the very high temperatures, probably as a defence mechanism. On the other hand, the olive has also developed environmental control in more northern olive-production areas, in this case to avoid injury due to the potential occurrence of freezing during the first spring weeks (i.e. end of March to beginning of April). In these areas, the higher heat requirement to completely develop floral buds assures that plants reach their flowering period during the second half of May to the beginning of June, when the warmer season is definitely established, and before very high temperatures can stress the flower apparatus and pollen viability during the fertilisation processes (Aguilera and Ruiz Valenzuela 2012; Bonofiglio et al. 2008).

In the future, a substantial drying and warming of the Mediterranean region is expected, with a decrease in precipitation of around 25 % to 30 %, and warming that might exceed 4 °C–5 °C (Giorgi and Lionello 2008). In this regard, a decrease in the biothermic requirements and a more rapid transition from endodormancy to ecodormancy can be hypothesized in future scenarios, and consequently, the more

rapid development of the floral buds, which will lead to earlier flowering peak dates in the southern areas in particular. Therefore, the adaptive capacity shown by the olive tree can be considered as a useful tool with which to study the effects of global climatic change on agro-ecosystems located in this especially vulnerable region.

Conclusions

The data presented herein allow us to conclude that northern olive populations have the greatest heat requirements for development of their floral buds, and that they need a longer period of time than olives in other areas to completely satisfy their biothermic requirements. The olive trees located in the warmest winter areas have a faster transition from endogenous to exogenous inhibition once the peak of chilling is met, and they show more rapid floral development. Different types of biological response by different populations of olive trees occur over this large Mediterranean area. These differences can be shown to arise from the adaptive biological responses of the olive to the environment. The present study provides us with interesting conclusions and a basis for further investigations that will make it possible to interpret the biological responses of the olive to future climate change.

Acknowledgements F.A. is grateful to the Fundación Ramón Areces (Madrid, Spain) for a post-doctoral grant. The authors are grateful to the Italian Network stations of the National Council of Agricultural Research, the Agroclimatic Stations Network of the Andalusian *Consejería de Agricultura y Pesca*, and the Tunisian Network stations of the National Meteorological Centre for the meteorological data.

References

- Aguilera F, Ruiz Valenzuela L (2009) Study of the floral phenology of *Olea europaea* L. in Jaen province (SE Spain) and its relation with pollen emission. *Aerobiologia* 25:217–225
- Aguilera F, Ruiz Valenzuela L (2012) Time trend in the viability of pollen grains in the ‘Picual’ olive (*Olea europaea* L.). *Palynology*. doi:10.1080/01916122.2012.662920
- Alba F, Díaz de la Guardia C (1998) The effect of air temperature on the starting dates of the *Ulmus*, *Platanus* and *Olea* pollen seasons in the SE Iberian Peninsula. *Aerobiologia* 14:191–194
- Anderson JV, Gesch RW, Jia Y, Chao WS, Horvath DP (2005) Seasonal shifts in dormancy status, carbohydrate metabolism, and related gene expression in crown buds of leafy spurge. *Plant Cell Environ* 28:1567–1578
- Arnold CY (1960) Maximum-minimum temperature as a basis for computing heat units. *J Am Soc Hortic Sci* 76:682–692
- Barranco D, Fernández-Escobar R, Rallo L (eds) (2008) *El Cultivo del Olivo*, 8th edn. Junta de Andalucía y Ediciones Mundi-Prensa, Sevilla
- Bonofiglio T, Orlandi F, Sgromo C, Romano B, Fornaciari M (2008) Influence of temperature and rainfall on timing of olive (*Olea europaea*) flowering in southern Italy. *N Z J Crop Hortic Sci* 36:59–69
- Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115–155
- Chuine I, Cour P, Rousseau DD (1998) Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell Environ* 21:455–466
- Črepiňšek Z, Kajfež-Bogataj L, Bergant K (2006) Modelling of weather variability effect on fitophenology. *Ecol Model* 194:256–265
- Cuevas J, Rallo L, Rapoport HF (1994) Staining procedure for the observation of olive pollen tube behaviour. *Acta Hort* 356:264–267
- De la Rosa R, Rallo L, Rapoport H (2000) Olive floral bud growth and starch content during winter rest and spring budbreak. *Hortscience* 35:1223–1227
- Dimou M (2012) Comparison of phenological, aerobiological and melissopalynological patterns of *Olea europaea*. *Apidologie* 43:103–112
- Doorenbos J (1953) Review of the literature on dormancy in buds of woody plants. *Meded. Landbouwhogeschool Wagening* 53:1–24
- Edwards KD, Anderson PE, Hall A, Salathia NS, Locker JCW, Lynn JR, Straume M, Smith JQ, Millar AJ (2006) FLOWERING LOCUS C mediates natural variation in the high-temperature response of the *Arabidopsis* circadian clock. *Plant Cell* 18:639–650
- Fernández-Escobar R, Benlloch M, Navarro C, Martín GC (1992) The time of floral induction in the olive. *J Am Soc Hortic Sci* 110:303–309
- Foley ME, Anderson JV, Horvath DP (2009) The effects of temperature, photoperiod, and vernalization on regrowth and flowering competence in *Euphorbia esula* (Euphorbiaceae) crown buds. *Botany* 87:986–992
- Galán C, García Mozo H, Vázquez L, Ruiz Valenzuela L, Díaz de la Guardia C, Trigo-Pérez MM (2005) Heat requirements for the onset of the *Olea europaea* L. pollen season in several places of Andalusia region and the effect of the expected future climate change. *Int J Biometeorol* 49:184–188
- Galán C, García-Mozo H, Vázquez L, Ruiz Valenzuela L, Díaz de la Guardia C, Domínguez Vilches E (2008) Modeling olive crop yield in Andalucía, Spain. *Agron J* 100:98–104
- Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. *Global Planet Change* 63:90–104
- Giorgi F (2006) Climate change hot-spots. *Geophys Res Lett* 33:L08707
- International Association of Aerobiology (2011) *International Aerobiology Newsletter* 72. <https://sites.google.com/site/aerobiologyinternational/iaa-newsletter>
- International Olive Council (2011) November 2011 report. <http://www.internationaloliveoil.org>. Accessed 5 November 2012
- Jato V, Rodríguez-Rajo FJ, Méndez J, Aira MJ (2002) Phenological behaviour of *Quercus* in Ourense (NW Spain) and its relationship with the atmospheric pollen season. *Int J Biometeorol* 46:176–184
- Koubouris GC, Metzidakis IT, Vasilakakis MD (2009) Impact of temperature on olive (*Olea europaea* L.) pollen performance in relation to relative humidity and genotype. *Environ Exp Bot* 67:209–214
- Krueger WH (1994) Carbohydrate and nitrogen assimilation. In: Ferguson L et al (eds) *Olive production manual*, 2nd edn. Division of Agriculture and Natural Resources, University of California. Publication 3353, pp 35–38
- Lang GA (1987) Dormancy: a new universal terminology. *Hortscience* 22:817–820
- Lionello P et al (2006) The Mediterranean climate: an overview of the main characteristics and issues. In: Lionello P, Malanotte-Rizzoli P, Boscolo R (eds) *Mediterranean climate variability*. Elsevier, Amsterdam, pp 1–26
- Martin GC, Ferguson L, Sibbett GS (1994) Flowering, pollination, fruiting, alternate bearing, and abscission. In: Ferguson L et al (eds) *Olive production manual*, 2nd edn. University of California. Division of Agriculture and Natural Resources. Publication 3353, pp 49–54
- Martins FB, Reis DF, Pinheiro MVM (2012) Base temperature and phyllochron in two olive cultivars. *Cien Rural* 42:1975–1981

- Orlandi F, Fornaciari M, Romano B (2002) The use of phenological data to calculate chilling units in *Olea europaea* L. in relation to the onset of reproduction. *Int J Biometeorol* 46:2–8
- Orlandi F, Ruga L, Romano B, Fornaciari M (2005) An integrated use of aerobiological and phenological data to analyse flowering in olive groves. *Grana* 44:51–56
- Orlandi F, Lanari D, Romano B, Fornaciari M (2006) New model to predict the timing of olive (*Olea europaea*) flowering: a case study in central Italy. *N Z J Crop Hortic Sci* 34:93–99
- Orlandi F, Sgromo C, Bonofiglio T, Ruga L, Romano B, Fornaciari M (2010) Yield modelling in a Mediterranean species utilizing cause-effect relationships between temperature forcing and biological processes. *Sci Hortic* 123:412–417
- Osborne CP, Chuine I, Viner D, Woodward FI (2000) Olive phenology as a sensitive indicator of future climatic warming in the Mediterranean. *Plant Cell Environ* 23:701–710
- Pinney K, Polito VS (1990) Olive pollen storage and in vitro germination. *Acta Hortic* 286:207–210
- Rallo L, Martin GC (1991) The role of chilling in releasing olive floral buds from dormancy. *J Am Soc Hortic Sci* 116:1058–1062
- Ramos A, Pérez-Solis E, Ibañez C, Casado R, Collada C, Gómez L, Aragoncillo C, Allona I (2005) Winter disruption of the circadian clock in chesnut. *Proc Natl Acad Sci USA* 102:7037–7042
- Richardson EA, Seeley SD, Walter DR (1974) A model for estimating the completion of rest for Redhaven and Elberta peach trees. *Hortscience* 82:302–306
- Ruml M, Vuković A, Milatović D (2010) Evaluation of different methods for determining growing degree-day thresholds in apricot cultivars. *Int J Biometeorol* 54:411–422
- Schlichting CD (1986) The evolution of phenotypic plasticity in plants. *Annu Rev Ecol Syst* 17:667–693
- Snyder R, Spano D, Cesaraccio C, Duce P (1999) Determining degree-day thresholds from field observations. *Int J Biometeorol* 42:177–182
- Yang S, Logan J, Coffey DL (1995) Mathematical formulae for calculating the base temperature for growing degree days. *Agric For Meteorol* 75:61–74