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RESEARCH ARTICLE

# Phenological response of olive cultivars to inter-annual temperature variability in Morocco

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## Abstract

Climatic factors strongly influence the phenology of olive trees, with flowering time responding sensitively to temperature variations. This study investigated the effects of inter-annual temperature variability on olive phenology in a mountainous Mediterranean region of Morocco. Experiments were conducted over two contrasting seasons (2020–2021 and 2021–2022) on four cultivars (Picholine Marocaine, Haouzia, Dahbia and Arbequina) in Khenifra. Forcing tests were performed to determine endodormancy release dates and to estimate chill and heat requirements. Throughout the dormancy period, fresh flower bud weights were recorded before and after a 7-day forcing period at weekly intervals and bud water content was monitored. The climatic requirements of each cultivar represent a major determinant of adaptability under variable seasonal conditions. The results revealed clear inter-cultivar differences in endodormancy and ecodormancy durations, thermal requirements and flowering dates. Arbequina exhibited the earliest dormancy release with relatively low chill requirements, whereas Picholine Marocaine and Dahbia flowered later and required higher chill accumulation. In all cultivars, bud growth activity increased near the time of dormancy release, indicated by water content exceeding 30 %, with only minor genotypic variation in the transition between dormancy phases. Across both seasons, flowering occurred after heat accumulation ranging from 6774 to 8051 Growing Degree Hours (GDH). These findings suggest that co-planting Picholine Marocaine and Dahbia may improve cross-pollination and enhance yield potential due to their similar flowering responses to seasonal temperature patterns. Overall, this research provides valuable insights for cultivar selection and orchard management under variable climatic conditions in Mediterranean environments.

**Keywords:** chill and heat requirements; dormancy; flowering; inter-annual variability; olive tree

## Introduction

*The* olive (*Olea europaea* L.) is the predominant fruit tree cultivated in Morocco, covering more than 1.2 million ha and representing more than 55 % of countries' current fruit tree orchards. Although olive trees are found across Morocco along a transect of more than 700 km under diverse ecological and climatic conditions, the geographical distribution of olive cultivation highlights two contrasting production systems, rainfed and irrigated systems. These systems differ considerably in the varieties cultivated and in respective growing environments. Despite the crops' importance in Morocco, the varietal spectrum is dominated by a single major variety, Picholine Marocaine (locally called "Zeitoun" or "Zeitoun Beldi"), which occupies approximately 95 % of the total olive growing area in traditional olive orchards (1, 2).

Olive varieties are highly sensitive to climatic conditions and cultural practices, which influence the growth and development of olive trees and therefore, fruit and olive oil yields (3). Optimal climatic conditions for successful flowering and fruit set are characterized by cold and rainy winters, with temperatures rarely dropping below 0 °C and warm, sunny summers that favour both flowering and fruiting. Phenological stages are highly impacted by variation in climatic conditions, as their timing largely depends on environmental factors such as temperature (4). Olive varieties can be classified according to their flowering dates into early, intermediate and late flowering cultivars, with flowering behavior shaped by the specific climatic environment where each variety was selected. In the Mediterranean area, floral buds of olives enter their dormancy phase in autumn, during which their physiological and metabolic activities decline. After dormancy has been released, buds sprout and continue their development until they reach advanced flowering stages in April or May. The flowering duration may extend beyond three weeks, depending on location and prevailing seasonal conditions. Following successful pollination, olive fruit set occurs, followed by fruit development until fruits reach a specific size and color during summer. After reaching the final stage of maturation in autumn, fruits can be harvested, completing the annual cycle.

The physiological phenomenon of floral induction initiates flowering and depends largely on intrinsic factors of the tree, notably its nutritional level and genetic characteristics. These genetic traits determine the seasonal hormonal balance that influences primordium development, flower induction and differentiation and length of inflorescence, while external factors such as temperature, rainfall and photoperiod exert only limited effects (5, 6). In olive trees of Morocco, floral induction occurs in June-July in buds borne on the current years' twigs (5, 6). The processes of floral induction and flowering, both of which are dependent on thermal conditions, generally take place after bud endodormancy has been released. Bud dormancy is a reversible physiological state found in the buds of many tree species, especially temperate deciduous fruits of the Rosaceae and is characterized by reduced metabolic activities and diminished interaction with the external environment (7). The dormancy period is commonly divided into three phases: (i) paradormancy, during which bud growth is inhibited by endogenous physiological factors outside the bud; (ii) endodormancy, characterized by growth inhibition caused by internal factors within the bud; and (iii) ecodormancy, during which bud development is constrained by environmental conditions, particularly temperature (8).

The transition from endodormancy to ecodormancy is triggered by exposure to low temperatures that satisfy the buds' chill requirements, which varies among species and varieties. Meeting this requirement restores the ability of buds to grow but it does not directly promote growth (9). During the subsequent ecodormancy phase, warmer temperatures may initiate budburst. Whether all aspects of winter dormancy observed in deciduous trees can be directly applied to evergreen species such as olive remains under debate. Major uncertainties relate to the period of flower differentiation, the effect of alternate bearing (ON/OFF years) and the underlying physiological mechanisms governing dormancy.

A number of studies have examined the temperature responses of dormant olive buds. For instance, temperatures of 4 °C or below can satisfy a substantial portion of the chill requirement, whereas temperatures between 10–13 °C appears to be more effective toward the end of chill accumulation (3). Subsequent research confirmed that olive trees, despite their evergreen habit, require a certain amount of winter chill for proper floral development (10). Other studies reported that olive bud development may be inhibited when temperatures persist above 16 °C and that at least one month with temperatures below 11–12 °C is necessary to meet chill requirements (11).

Exposure to low temperatures during winter plays an important role in floral induction and subsequent differentiation, with more effective flower bud differentiation reported in colder years than in warmer ones (12). This difference has been attributed to the inhibitory effect of high temperatures on induction and subsequent flower formation (13, 14). Once chill accumulation is complete, olive trees begin to accumulate heat necessary for bud development and flowering. Understanding heat requirements provides a basis for predicting the flowering period. Although olive trees are relatively tolerant to drought (15), severe drought can nevertheless reduce profitability and suppress vegetative growth (16). Chill and heat requirements for endodormancy release and flowering (accumulated during winter and spring) vary among variety (5, 6, 17). Regardless of cultivar-specific variation in climatic requirements, areas that are suitable for olive cultivation are generally characterized by mild-winter with very limited frost occurrence. Olive leaves can suffer severe damage at temperatures below -6 or -7 °C, while temperatures below -3 or -4 °C may damage fruits with high water content that have not yet been harvested, ultimately affecting oil quality (11).

Although many studies have examined olive dormancy, key features, including chill and heat requirements, phenology and flowering processes, remain poorly understood, particularly in Morocco. Previous work has largely involved annual assessments and has focused on a single development stage, such as flowering. The present study aims to investigate olive phenology by comparing the flowering and dormancy behavior of four olive varieties in Morocco. The overall objective is to evaluate the resilience of olive flowering to temperature variation in the context of global warming. Drawing on experiments and field observations, we identify dormancy periods and estimate chill and heat requirements for cultivars widely grown across the country.

## Materials and Methods

### Site and plant material

Experiments were carried out on olive trees located in Khenifra, Morocco, at an altitude of 837 m a.s.l. (32°56′22″ N, 5°40′03″ W). The experimental work was conducted during the 2020–2021 and 2021–2022 seasons (Fig. 1). These two seasons were selected because they exhibited contrasting winter temperature regimes typical of Mediterranean mountain environments. The winter of 2020–2021 recorded markedly lower minimum temperatures and a prolonged period of cold exposure, whereas 2021–2022 was characterized by comparatively mild winter conditions. Such inter-annual thermal contrast is widely recognized as sufficient to reveal cultivar-specific patterns of chill accumulation, dormancy release and flowering responses in perennial fruit species (18–20).

The Khenifra region has a Mediterranean continental mountain climate with cold and relatively rainy winter and hot, dry summers. Mean annual rainfall ranges from 400 to 700 mm, with most precipitation occurring between November and April. The average daily minimum, maximum and mean temperatures recorded during 2020 and 2021 were 10.14 °C, 23.82 °C and 16.98 °C respectively.

The experiment included four olive cultivars, Picholine Marocaine, Haouzia, Dahbia and Arbequina, which were grown in a commercial production orchard. The three Moroccan cultivars were selected due to their widespread cultivation, while Arbequina, a

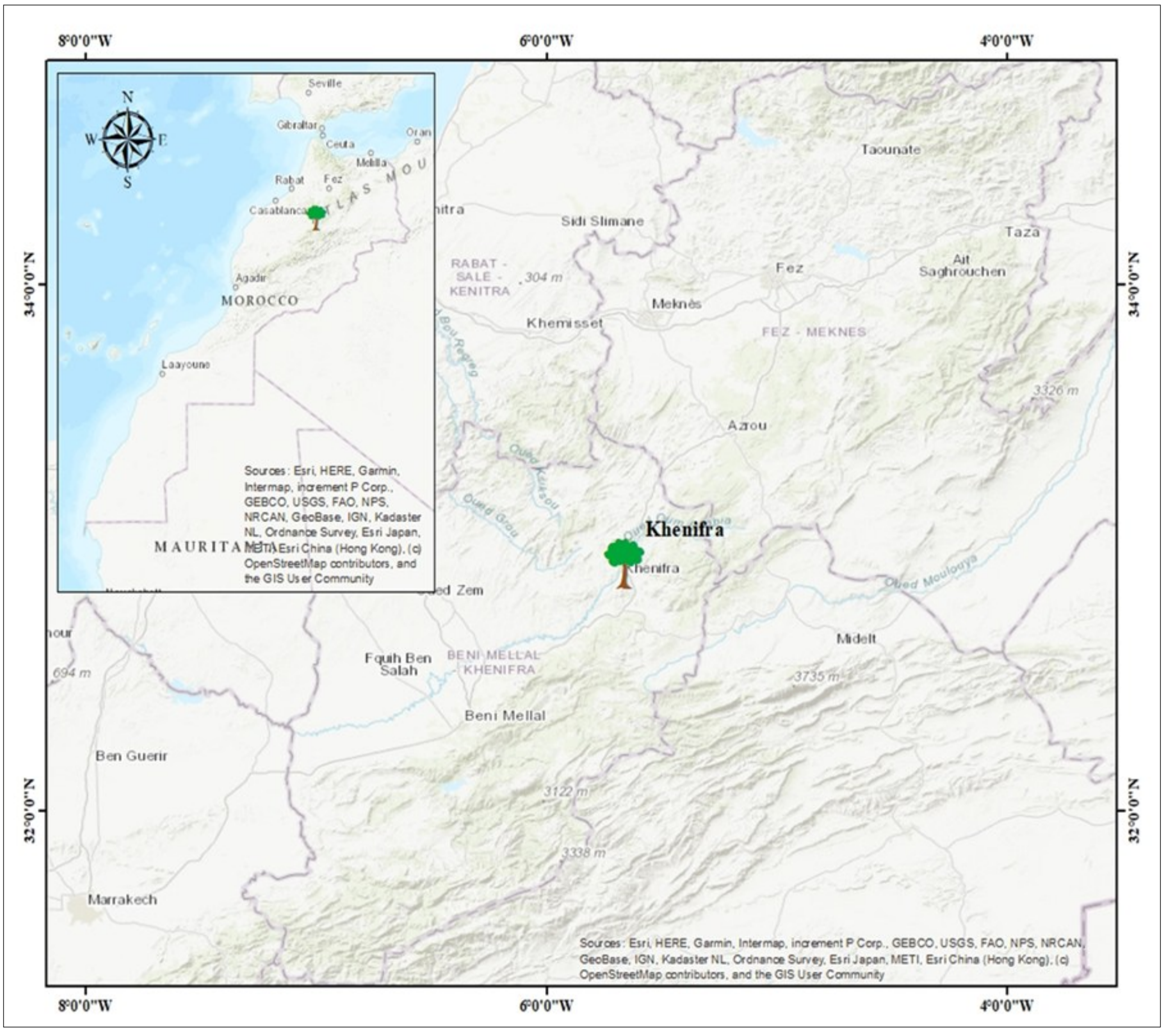

Fig. 1. Location of the study site in Khenifra, Morocco.

foreign cultivar was included because of its introduction and increasing use in intensive systems. Trees were about 25 years old and managed under standard horticultural practices, including annual pruning, drip irrigation, fertilization and plant protection. All cultivars were maintained under the same orchard management practices, with uniform pruning, fertilization, drip irrigation scheduling and plant protection were applied consistently across trees. This uniformity ensured that observed differences in dormancy release and flowering responses reflected cultivar-specific physiological traits rather than variations in cultural practices.

## Collection of temperature data and flowering observations

Daily temperature data (maximum and minimum) were obtained from the automatic weather stations of the National Office of Agriculture Advisory (ONCA), located at Khenifra city, close to the sampling and observational site where trees were planted (about 8 km away and at a similar elevation). The daily temperature dataset was subjected to quality checks to avoid any missing data or erroneous readings.

Flowering dates were monitored over two years, with observations focused on the full flowering stage, defined as the point at which approximately 50 % of flowers are open, with the first petals falling). This corresponds to stage 65 of the international Biologische Bundesanstalt, Bundessortenamt and Chemical industry code (BBCH) (21). Flowering observations were conducted on a weekly basis throughout the blooming period. The flowering observations were assessed on at least 10 adult trees, with mean flowering dates were calculated across the sampled trees.

## Endodormancy, dormancy release and ecodormancy of floral buds

A forcing test was employed to determine the date of endodormancy release and to delineate the endo- and ecodormancy phases. Floral bud development (weight) was observed and measured immediately after collection from the orchard, as well as under controlled forcing conditions following a 7-day incubation period in a growth chamber. The date of endodormancy release was determined as the first sampling date on which floral bud weight under artificial forcing conditions became significantly greater than the weight of unforced buds collected directly from the field.

The dates of endodormancy release were subsequently used to define the endodormancy and ecodormancy phases. The endodormancy period was considered to extend from the beginning of November corresponding to the onset of chill accumulation and the post-growth transition phase in olive buds under Mediterranean conditions (7, 8, 22, 23), until the release date determined by the forcing test.

Short olive shoots were randomly collected from around the trees at weekly intervals and transferred to the laboratory. To facilitate comparisons across seasons, the same sampling schedule was followed in both study years. Two sets of three shoots (about 0.4 cm in diameter and 30–40 cm in length) were collected from three trees on each sampling date. For the first set (unforced shoots), floral buds were immediately excised from the shoot base using a scalpel and weighed both before and after dehydration at ~75 °C for

48 hrs in a drying oven. The second set (forced shoots) was placed in pots containing water in a climate-controlled growth chamber at 24 ± 1 °C, under a 16/8 h light/dark cycle and 70 % relative humidity for 7 days. Shoots were freshly cut at the base every two days to ensure water transport across the shoot. The forced shots were then used to measure fresh and dry weight of buds using a precision balance in the same way as for unforced samples.

Each sample (cultivar × year × sampling date × unforced/ forced) included three replications, each consisting of five buds. In total, 15 floral buds were collected per sampling date for both forced and unforced treatments. In early sampling dates, when buds were very small, dissections were performed using binocular magnification.

Confidence intervals were computed as t-based 95 % CIs (n = 3 replicates × 5 buds). A non-overlap between the confidence intervals of forced and unforced CIs was used as a conservative indicator of significant difference. Endodormancy released was considered to have occurred when two conditions were met: i) the upper bound of the confidence interval of unforced bud weight and the lower bound of forced bud weight continuously (on the following sampling dates) showed no overlap and ii) forced floral buds showed 30–40 % increase in weights compared to unforced buds.

### Bud water content

To assess water dynamics in floral buds during the endodormancy and ecodormancy phases, water content of buds was determined using the fresh and dry weight (FW and DW respectively) measured in the forcing test. The water content (WC) of floral buds was calculated as:

$$\text{WC (\%)} = \frac{\text{FW - DW}}{\text{FW}} \text{ X 100} \qquad \text{(Eq. 1)}$$

### Chill and heat requirements

We estimated chill and heat requirements based on the assumption that bud endodormancy release results from the sequential fulfillment of chilling followed by heat accumulation. Although this approach simplifies the underlying physiological processes, it offers a useful approximation of cultivar-specific climatic requirements. Chill accumulation was quantified using three commonly applied models in fruit tree phenology: the Chilling Hours model (CH), the Utah model (CU) and the Dynamic model (CP) (24–28).

- Chilling Hours model (CH)

CH was computed as the total number of hrs with temperatures between 0 °C and 7.2 °C:

$$CH_t = \sum_{i=1}^{t} T_{7.2} \qquad \text{(Eq. 2)}$$

where $T_{7.2} = 1$ when $0\,°C \leq T \leq 7.2\,°C$ and 0 otherwise.

- Utah model (CU)

Chill Units were accumulated following the temperature-efficiency weighting system (26):

$$CU = \sum_{i=1}^{t} w(T_i) \qquad \text{(Eq. 3)}$$

where w(T) is a temperature-dependent weighting function defined as follows:

+1 for 2.5–9.1 °C, +0.5 for 1.5–2.4 °C or 9.2–12.4 °C, 0 for 12.5–15.9 °C, -0.5 for 16–18 °C and -1 when temperatures exceed 18 °C.

- Dynamic model (CP)

Chill accumulation was also quantified using the CP (27, 28), in which chill results from the formation of a temperature-dependent intermediate product that is irreversibly converted into stable Chill Portions (CP):

$$CP_t = CP_{t-1} + \Delta_t \qquad \text{(Eq. 4)}$$

where $\Delta_t$ represents the temperature-dependent conversion rate of the intermediate product.

- Heat accumulation (GDH)

Heat accumulation during ecodormancy was quantified as GDH, using a base temperature of 4.5 °C and an upper threshold of 25 °C (26):

$$GDH = \sum_{i=1}^{t} (T_i - 4.5°C) \qquad \text{(Eq. 5)}$$

Only temperatures between 4.5 °C and 25 °C contributed to GDH; values outside this range were set to zero.

### Statistical analysis

Comparisons of endodormancy release dates, chill and heat accumulations and bud water content among cultivars and between years were assessed using a one-way Analysis of Variance (ANOVA). When ANOVA indicated significant effects ($p < 0.05$), mean separations were performed using Tukey's Honest Significant Difference (HSD) post-hoc test. The normality and homoscedasticity of residuals were verified prior to analysis. For estimating endodormancy release, we retained the non-overlapping 95 % confidence interval criterion between forced and unforced bud fresh weights as a conservative, biologically grounded indicator. This interpretation was combined with ANOVA/Tukey results and temperature-accumulation trends. All statistical analyses were conducted using R software version 4.3.1 and graphical outputs were generated using the ggplot2 package.

## Results

### Climatic characteristics of the site

Temperature patterns from October to April exhibited considerable differences between the two experimental seasons, 2020-2021 and 2021-2022 (Fig. 2a). Compared with 2021-2022, the 2020-2021 season was characterized by a warmer autumn (mainly in November), colder winter (December-February) and warmer spring (March and April) (Fig. 2a). Mean temperature during November, December-February and March-April in 2020-2021 were 13.54 °C, 8.28 °C and 12.35 °C respectively, compared with 9.90 °C, 10.21 °C and 10.95 °C in 2021-2022. According to all three chill models used in this study (CH, CU and CP), chill accumulation began earlier in 2020-2021 (early November) and resulted in slightly higher seasonal totals than in 2021-2022 (Fig. 2b).

With respect to heat accumulation, higher values were recorded during 2021-2022 up to the end of March. By the end of April, accumulated heat had reached similar levels in both years (Fig. 2c).

### Bud dormancy dynamics and flowering

Across all cultivars, the endodormancy release dynamics of floral buds exhibited similar behavior in the two seasons (Fig. 3). In both forced and unforced shoots, floral buds started off with low weights, which slowly increased throughout January and February. This was followed by a marked increase in bud weight beginning, depending on the cultivar, between mid-February and mid-March. During this phase, forced buds gained weight more rapidly than unforced buds, with values surpassing those of unforced buds by 30 % or more (Fig. 3).

The estimated dates of endodormancy release for Picholine Marocaine and Arbequina occurred earlier in 2020-2021 than in 2021-2022. In contrast, Haouzia showed the opposite trend and Dahbia exhibited the same endodormancy release date in both years (March 6th) (Fig. 3 and Table 1). On average, Arbequina was the earliest cultivar to release endodormancy (February 20th), followed by Picholine Marocaine (February 27th) whereas the latest dates were observed for Dahbia and Haouzia (March 6th) (Table 1). Annual variability was highest in Picholine Marocaine (range of 29 days),

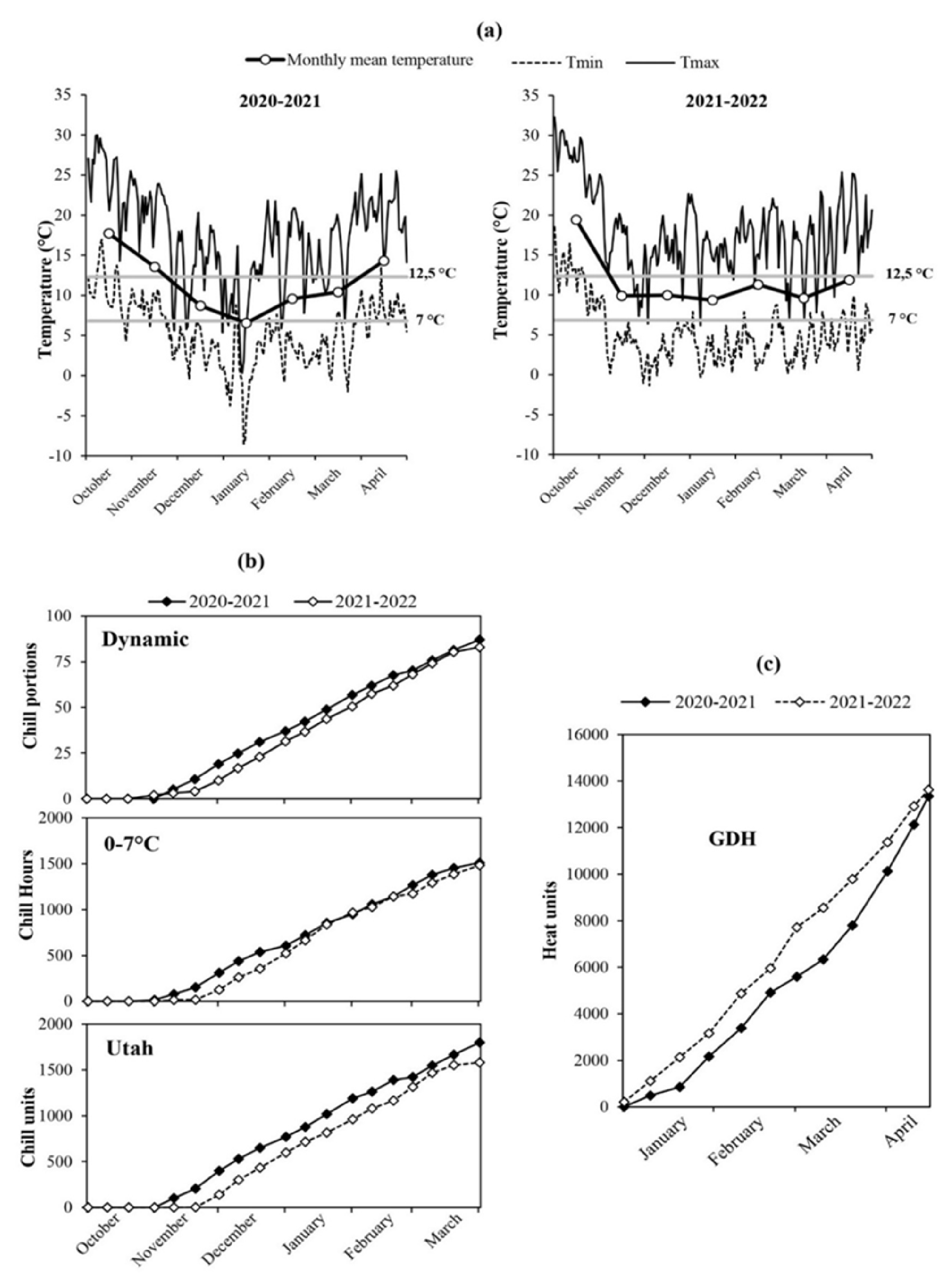

**Fig. 2.** Daily minimum and maximum temperatures and average of monthly mean tempera-tures (a) as well as chill and heat accumulations recorded according to Chilling Hours, Utah, Dynamic (b) and GDH (c) models from October to April during the two years of experimentation in Khenifra, Morocco.

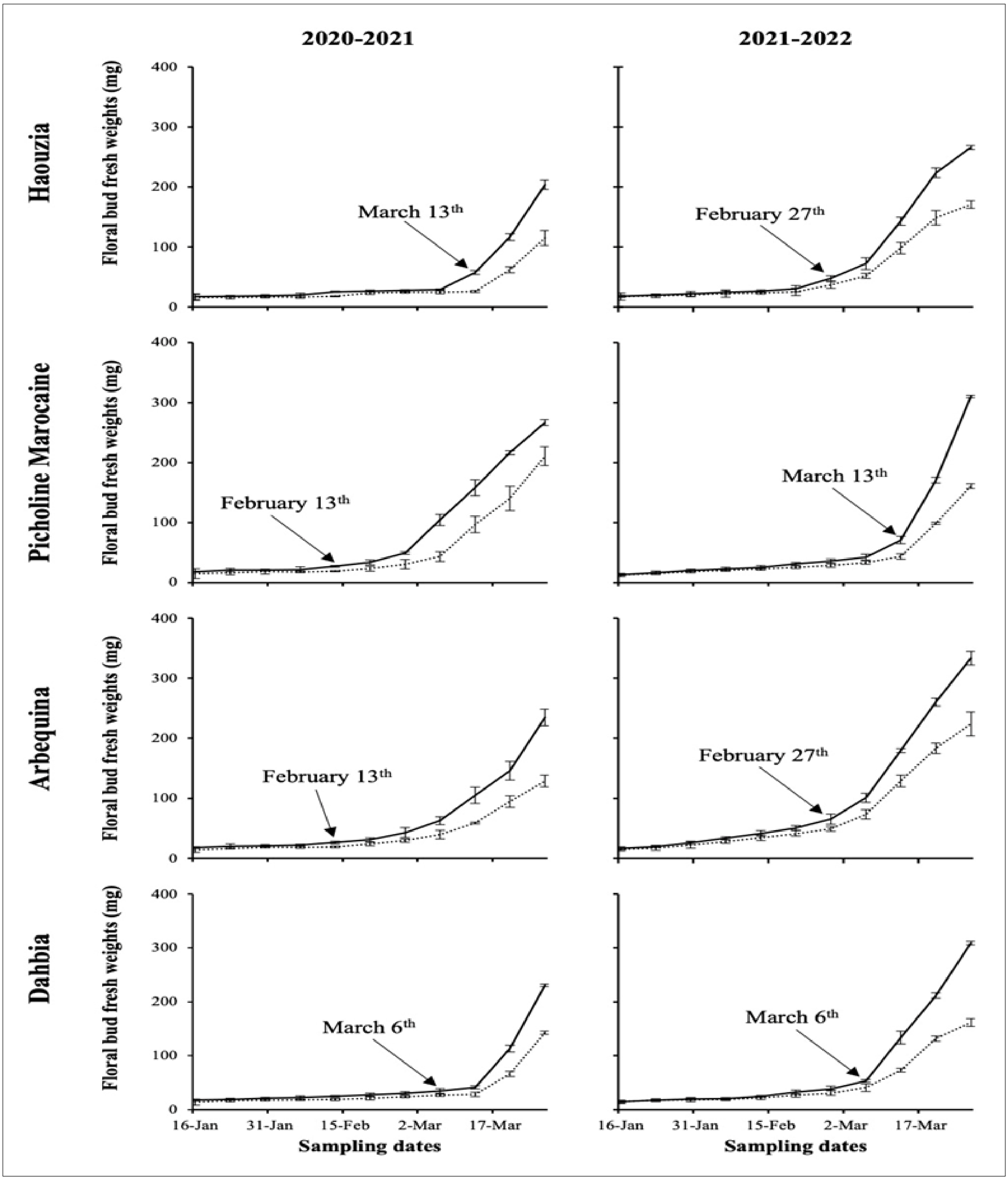

**Fig. 3.** Mean fresh weights of forced (solid lines) and unforced (dashed lines) floral buds of four olive cultivars studied during two years of experimentation in Khenifra, Morocco. The dates indicated by arrows are the derived dates of endodormancy release.

intermediate in Haouzia and Arbequina (15 days) and absent in Dahbia.

Regarding flowering, all cultivars reached full bloom later in 2020-2021 than in 2021-2022 (Table 1). BBCH stage 65 occurred in late April in 2020-2021 and about one month earlier in 2021-2022 (Table 1). The early-flowering cultivars Haouzia and Arbequina reached this stage earlier than the late-flowering Picholine Marocaine and Dahbia. Statistical comparison of flowering dates confirmed significant differences among cultivars ($p < 0.05$), as well as between years, indicating a strong influence of inter-annual temperature variability on flowering time.

## Dormancy phases and chill and heat requirements

We defined the endodormancy period as extending from November 1st (the approximate date when chill accumulation begins) to the endodormancy release date determined by the forcing test. Ecodormancy was considered to begin on the day following endodormancy release and to continue until the full flowering date observed in the orchard under natural conditions. Arbequina exhibited the shortest endodormancy for, with an average duration of 112 days across both seasons and accumulated the lowest amount of chill (an average of 1,116 CH, 1,292.0 CU and 65.4 CP). For Picholine Marocaine, endodormancy lasted an average of 119 days, during which 1,190 CH, 1,397.5 CU and 70 CP were accumulated (Table 1). Dahbia and Haouzia had the longest endodormancy durations, averaging 126 days and showing the highest chill

**Table 1**. Phenological stages and chill/heat requirements of four olive cultivars grown under Moroccan climate conditions during two years of experimentation. Chill requirements are expressed in Chilling Hours (CH), Utah Chill Units (CU) and Dynamic Chill Portions (CP); heat requirement is expressed in Growing Degree Hours (GDH, base 4.5 °C)

| **Cultivar** | **Year** | **Endodormancy release date** | **Full flowering** (stage 65) | **Chill requirement** | | | **Heat requirement** | **Endodormancy duration** (days) | **Ecodormancy duration** (days) |
|---|---|---|---|---|---|---|---|---|---|
| | | | | **Chilling Hours** (CH) | **Utah** (CU) | **Dynamic** (Portions) | **GDH** (Base 4.5°C) | | |
| *Picholine Marocaine* | 2020-2021 | February 13th | April 25th | 1,097 | 1,308.0 | 63.9 | 11,914.8 | 105 | 71 |
| | 2021-2022 | March 13th | April 10th | 1,283 | 1,487.0 | 76.0 | 3,931.7 | 133 | 28 |
| | **Average** | **February 27th** | **April 17th** | **1,190** | **1,397.5** | **70.0** | **7,923.2** | **119** | **50** |
| *Haouzia* | 2020-2021 | March 13th | April 25th | 1,422 | 1,578.0 | 76.7 | 9,009.1 | 133 | 43 |
| | 2021-2022 | February 27th | April 5th | 1,135 | 1,276.0 | 66.8 | 4,537.7 | 119 | 37 |
| | **Average** | **March 6th** | **April 10th** | **1,279** | **1,427.0** | **71.8** | **6,773.4** | **126** | **40** |
| *Dahbia* | 2020-2021 | March 6th | April 30th | 1,341 | 1,499.5 | 72.8 | 10,681.5 | 126 | 55 |
| | 2021-2022 | March 6th | April 5th | 1,216 | 1,396.0 | 70.9 | 3,790.5 | 126 | 30 |
| | **Average** | **March 6th** | **April 17th** | **1,279** | **1,447.8** | **71.9** | **7,236.0** | **126** | **43** |
| *Arbequina* | 2020-2021 | February 13th | April 27th | 1,097 | 1,308.0 | 63.9 | 12,324.6 | 105 | 73 |
| | 2021-2022 | February 27th | March 30th | 1,135 | 1,276.0 | 66.8 | 3,776.2 | 119 | 31 |
| | **Average** | **February 20th** | **April 13th** | **1,116** | **1,292.0** | **65.4** | **8,050.4** | **112** | **52** |

accumulation (Table 1).

For all cultivars, chill accumulation during endodormancy varied between the two seasons. This may indicate differences in chill requirements across years, but it may also reflect limitations in the chill models used, none of which were specifically developed or rigorously validated for olives. The mean duration of ecodormancy was similar across cultivars: 45 days for Arbequina (with 8051 GDH accumulated), 43 days for Dahbia (7236 GDH), 42 days for Picholine Marocaine (7924 GDH) and 40 days for Haouzia (6774 GDH).

ANOVA results showed significant cultivar effects on chill accumulation (CH, CU and CP) and on heat accumulation (GDH) required to reach flowering ($p < 0.05$), confirming true physiological differences rather than year-specific environmental variability.

### Bud water content

The purpose of measuring bud water content was to link endodormancy release with the onset of growth activity in floral bud cells, a process strongly related to water mobilization. Our results highlighted temporal variation in bud water content, with notable differences between the endodormancy and ecodormancy periods in both experimental seasons (Fig. 4). For all olive cultivars, floral bud water content remained relatively stable at approximately 10–30 % during endodormancy, followed by a progressive increase that coincided with a significant rise in fresh bud weight. Water content exceeded 30 % around the date of endodormancy release or 1–2 weeks later (except for Haouzia in 2020-2021, where this occurred roughly 2 weeks before the date of endodormancy release), after the accumulation of 1116–1279 CH, 1292–1448 CU and 65.4–71.9 CP. This threshold aligns with previous work showing that the transition from bound to free water in dormant buds corresponds to the resumption of metabolic activity and growth potential (29, 30).

The increase in water content between the endodormancy and ecodormancy phases was statistically significant across cultivars ($p < 0.05$), supporting its relevance as a physiological indicator of dormancy transition. By the end of ecodormancy, water content reached 50–55 % in all cultivars. In general, the water content in forced buds was slightly higher than unforced buds across all cultivars and in both years (Fig. 4). This pattern was supported by statistical comparison, which showed a significant increase in water content from endodormancy to ecodormancy for all cultivars ($p < 0.05$).

## Discussion

The phenological responses of olive cultivars to climatic variability arise from a complex interplay between genotypic traits and environmental cues. In this section, we discuss our findings in the context of previous research on dormancy mechanisms, chill and heat requirements and physiological indicators of bud development. Particular attention is given to the suitability of existing chill models, cultivar-specific differences in phenological behavior and the potential use of bud water content as a biological marker for dormancy transitions. To enhance clarity and provide actionable insights, the discussion is structured into four thematic subsections that integrate theoretical considerations with guidance for phenological modelling and cultivar management under changing climate scenarios.

### Revisiting dormancy in olives under inter-annual climate variability

The limited studies available on olive dormancy and the chill and heat requirements of this species have largely relied on long-term phenological datasets analysed using statistical and modelling approaches originally developed for deciduous fruit and nut species (18, 31–37). Tree dormancy has also been addressed experimentally, but such studies have mostly focused on temperate deciduous fruit species such as apple, apricot and almond (38, 39). Many of these studies have employed the forcing test approach, which has proven effective for determining the timing of endodormancy release and for inferring chill and heat requirements across fruit tree species. Collectively, these investigations have provided substantial evidence of the importance of winter chill for dormancy release in deciduous fruit trees (40), as well as the necessity of subsequent heat accumulation for the completion of bud development (8, 22).

In this study, we applied the same experimental setup to olive trees to assess their phenological responses to inter-annual temperature variability, particularly the effects of seasonal thermal patterns. According to previous controlled climate conditions, temperatures below 12.5 °C, with an optimum around 7 °C, are effective for fulfilling chill requirements in floral buds of olives (5, 19). In our case study, winter mean temperatures were generally below the threshold of 12.5 °C, with significantly lower temperatures recorded in 2020–2021. These colder winter conditions led to an

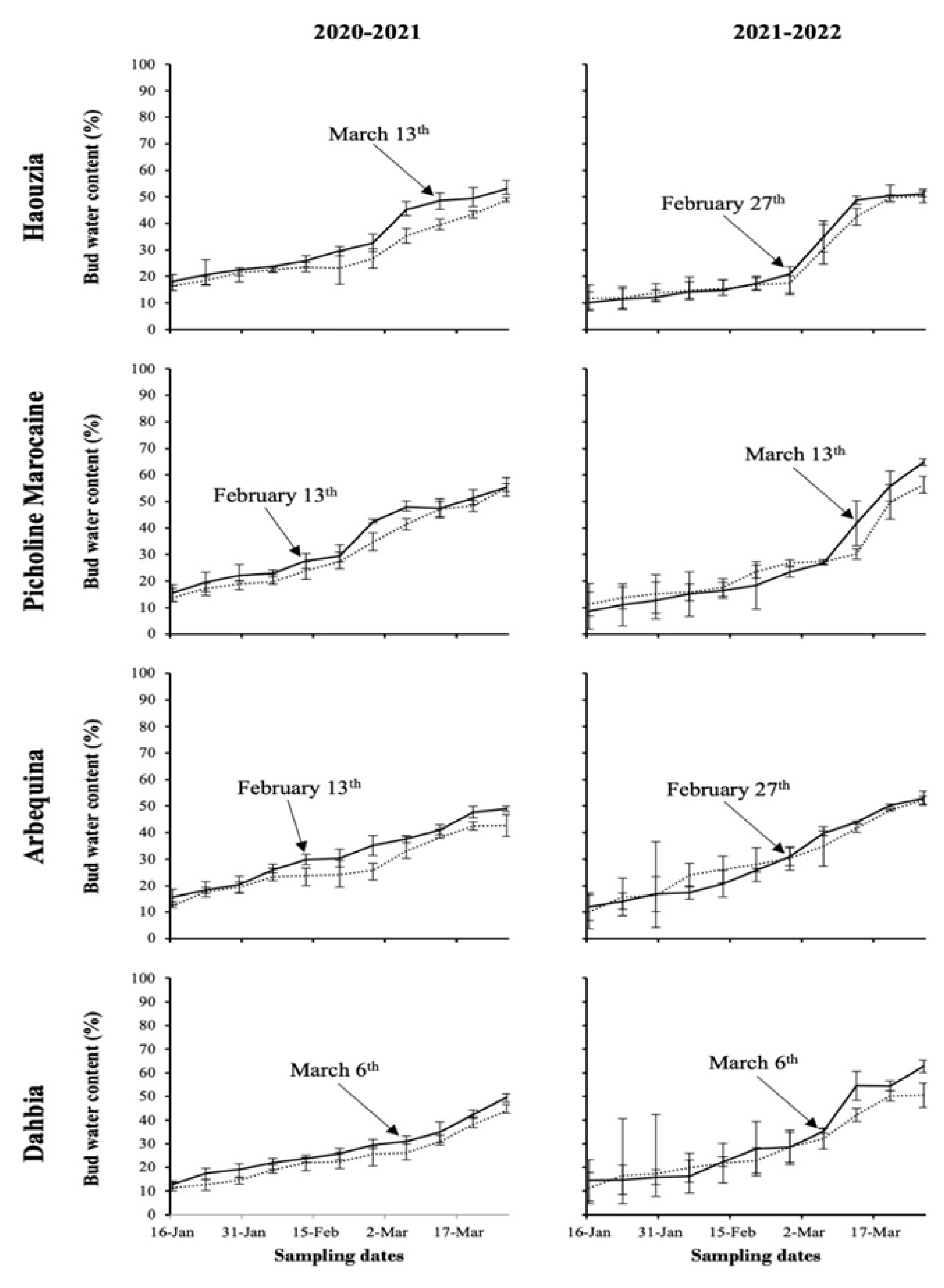

**Fig. 4.** Mean water content measured in forced (solid lines) and unforced (dashed lines) floral buds of four olive cultivars studied during two years of experimentation in Khenifra, Morocco. The dates indicated by arrows are the derived dates of endodormancy release.

earlier release of endodormancy and subsequently, later flowering across all cultivars, especially Picholine Marocaine and Arbequina.

This apparent paradox highlights the two-phase thermal control of olive phenology. While chill accumulation facilities release from endodormancy, the progression of floral buds toward flowering depends largely on the accumulation of heat post-dormancy. In 2020–2021, the cold winter conditions accelerated chill fulfillment and led to early endodormancy release; however, the colder spring slowed heat accumulation, prolonging the ecodormancy phase and delaying flowering. Thus, flowering phenology is not determined solely by the timing of chill completion but by the interaction between chill fulfillment and subsequent heat availability.

Effective chill accumulation at temperatures up to 12.5 °C was also inferred from controlled-temperature experiments reported previously (23). These two olive cultivars showed similar patterns of early endodormancy release, which can be explained by early fulfillment of chill requirements during the cold 2020–2021 winter months (December, January and February). In addition, late endodormancy release recorded in 2021–2022 was probably explained by the lower chill accumulated during this warmer season compared to 2020–2021, highlighting the clear inter-annual variability in dormancy response. As Picholine Marocaine is a high-chill cultivar, the date of endodormancy release was earlier during the cooler season (2020–2021) and later during the warmer season (2021–2022).

## Genotypic response to chill and heat: Insights from a two-year trial

Our findings demonstrated that a significant increase of floral bud weight in shoots following the accumulation of winter chill , as previously reported (5). Olive chill requirements registered in our study showed some contrast with those obtained in warm regions such as Tunisia, where a considerably lower chill requirements have been reported for Arbequina (20). Similarly, a comparative study conducted in Spain and Italy showed considerably differences in chill requirements between the two countries, with notably lower values in Italy (997 CH) compared to Spain (1848 CH) (37, 38).

It is worth noting, however, that these earlier studies relied primarily on the CH, which only provides a crude approximation of chill accumulation and may lead to misleading results in warm climates (41, 42). In our study, estimated chill requirements were intermediate, falling between those reported for Tunisia and Italy. Such differences should be interpreted with caution, as they may arise from multiple interacting factors. First, climatic conditions differ substantially among Tunisia, Italy and Morocco, particularly with respect to winter minimum temperatures and seasonal temperature variability. Second, some studies estimated chill requirements from field-phenology, whereas others (including the present study) used forcing tests, which typically provide more accurate dormancy transition estimates. Third, the CH, used in several of these investigations, can oversimplify chill accumulation in warm environments and may underestimate or overestimate effective chill where temperatures fluctuate widely. Therefore, the contrasts in chill requirements reported across studies are likely shaped by both genuine physiological differences among cultivars and methodological and climatic variations.

We observed clear differences in dormancy release dynamics across cultivars, revealing intra-specific variability consistent with prior findings. Overall, Arbequina (a low-chill cultivar) showed early and intermediate flowering dates. This result is well aligned with what was reported in Tunisia and Argentina (20, 43). Haouzia (an early-flowering cultivar) showed high chill and low heat requirements. The late-flowering cultivars Picholine Marocaine and Dahbia differed notably in their chill and heat responses. In Picholine Marocaine, flowering was advanced by substantial chill accumulation during endodormancy combined with heat accumulation during ecodormancy. In contrast, Dahbia, which showed the same endodormancy release date in both years, had its flowering time primarily driven by heat accumulation. Across the two seasons, the average duration of endodormancy was shortest for Arbequina (112 days), longest for Haouzia and Dahbia (126 days) and intermediate for Picholine Marocaine (119 days).

## Modeling gaps and physiological complexities: Beyond peach -based frameworks

The use of chill models originally developed for peach and apricot to estimate chill requirements in olive trees raises significant questions because of major differences in the physiology and dormancy dynamics among these species. Chill models such as CH or CU were designed and presumably optimized for the thermal responses of peach and their underlying assumptions may not align with the climatic needs of olive trees. Olives, which are well-adapted to warmer Mediterranean climates, likely exhibit greater tolerance to high temperatures and typically have much lower chill requirements. In contrast to peaches, olive trees exhibit a relatively superficial form of dormancy, allowing them to resume growth after limited chill accumulation. Consequently, peach-derived models may overestimate olive chill requirements and lead to inaccurate projections of phenological stages.

Similar limitations arise when the CP is applied using the original parameter set derived from peach (27). Because the CPs' was parameterized using data from temperate deciduous species, its direct transfer to olive may not adequately reflect the dormancy physiology of this crop. For this reason, we recommend calibrating the CP parameters using olive-specific phenological datasets (ideally combining forcing-test–based estimates of dormancy release with multi-year field observations to ensure transferability across Mediterranean environments. To better represent the dormancy behavior of olives, it would be valuable to calibrate these models using olive-specific parameter sets, as recently proposed (44).

With increasing inter-annual temperature variability and more frequent weather anomalies, accurate quantifications of chill requirements is becoming increasingly critical.

## Bud water content: A promising physiological marker for dormancy transitions

Our investigation also sought to clarify the relationship between the fulfillment of chill requirements, endodormancy release dates obtained through forcing tests and bud water content. We found that the rehydration of floral buds started to increase at, or shortly after, the date of endodormancy release. The rise in fresh weight observed in floral buds likely reflects the onset of rehydration, marked by water content exceeding 30 %. This rehydration is facilitated through cell-to-cell water transport, once the vascular system becomes sufficiently differentiated to support renewed metabolic activity. During endodormancy, water is largely bound to macromolecules as a protective mechanism against freezing (29, 30). This bound water is then converted to free water during the ecodormancy phase, as temperatures become favorable for growth. The speed of this transition depends strongly on winter and spring temperature conditions; it proceeds more slowly under cold temperatures, requiring additional time to convert water from its bound to free form.

Although water mobility in cells varied slightly among cultivars, our findings suggest that bud water content may serve as a physiological indicator of the ecodormancy status. The coordinated increase in bud fresh weight and water content around endodormancy release supports the use of integrated frameworks that jointly account for chilling and heat accumulation. In this context, PhenoFlex offers a coherent conceptual structure for linking physiological signals (e.g., water status) with temperature-driven dormancy transitions, with potential to improve olive flowering predictions under variable climatic conditions (45). In particular, stabilization of bud water content around 50–55 % may represent a reliable biological marker for the effective establishment of the ecodormancy phase in olive trees.

In light of these insights and considering the complexity of dormancy mechanisms in olives, future research would benefit from integrated approaches that combine chill and heat accumulation models. One promising path is the PhenoFlex framework (45), which enables simultaneous modeling of chilling and heat processes and can be adapted to diverse climatic environments, representing a promising avenue. Developing olive-specific calibrations of such models could significantly improve phenological predictions and guide better orchard management strategies under future climate conditions.

Although this study provides valuable insights into the dormancy dynamics of olive cultivars under Moroccan climate conditions, certain limitations should be acknowledged. The experiments were conducted over only two consecutive seasons at a single location, which may not capture the full extent of climatic variability across the Mediterranean basin. Moreover, while the forcing test is a robust method for estimating chill and heat requirements, further validation through physiological, molecular and multi-site approaches would help strengthen the generalizability of the results. Future research should therefore extend observations over longer periods and assess cultivar responses across a wider range of agro-climatic zones.

## Conclusion

This study determined the dates of endodormancy release and quantified the chill and heat requirements of four olive cultivars under the mountainous Mediterranean climate of Khenifra. Based on floral bud weight development and water content analysis, clear genotypic differences were observed. Arbequina exhibited early endodormancy release and lower chill requirements, while Haouzia and Dahbia required longer exposure to winter cold and greater heat accumulation to achieve flowering. Picholine Marocaine showed an intermediate response, though with greater inter-annual variability linked to seasonal temperature conditions. The contrasting patterns observed between the two study years highlight the high sensitivity of olive phenology to inter-annual temperature variability.

These findings underscore the importance of aligning cultivar selection with local thermal profiles and anticipating shifts in flowering time under ongoing climatic change. From a practical standpoint, selecting and co-planting cultivars with compatible flowering periods may improve pollination efficiency and yield stability in Mediterranean orchards. Future research should extend observation across additional years and agro-climatic zones and further calibrate phenological models specifically for olive trees to support adaptive orchard management strategies increasing climate uncertainty.

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## Authors' contributions

Conceptualization of the study was carried out by HB, OK and ME. The methodology was developed by HB. Formal analysis and investigation were performed by HB, ME and HH. Data curation was conducted by HB, ME and HH. The original draft of the manuscript was prepared by HB. Manuscript review and editing were undertaken by HB, OK, ME, EL, MBM, MG, AEB, HH, HO, JC, TA and AEY. Visualization was completed by HB and OK. Funding acquisition was secured by OK and AEY. Supervision of the study was provided by OK and AEY. All authors have read and approved the final version of manuscript. .

## Compliance with ethical standards

**Conflict of interest:** The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this manuscript.

**Ethical issues:** None

## References

1. Boulouha B, Loussert R, Saadi R. Phenotypic variation of the ‘Picholine Marocaine’ olive cultivar in the Haouz region. Olivæ. 1992;30–3.
2. Khadari B, Charafi J, Abdelmajid M, Ater M. Substantial genetic diversity in cultivated Moroccan olive despite a single major cultivar: A paradoxical situation evidenced by the use of SSR loci. Tree Genet Genomes. 2008;4:213–21. https://doi.org/10.1007/s11295-007-0102-4
3. Hackett WP, Hartmann HT. The influence of temperature on floral initiation in the olive. Physiol Plant. 1967;20:430–6. https://doi.org/10.1111/j.1399-3054.1967.tb07183.x
4. Colbrant P, Fabre P. Reference developmental stages of the olive tree. Olivæ. Paris: INVUFLEC, R Maillard; 1975. p. 24–5.
5. Rallo L, Martin GC. The role of chilling in releasing olive floral buds from dormancy. J Am Soc Hortic Sci. 1991;116:1058–62. https://doi.org/10.21273/JASHS.116.6.1058
6. Fernandez-Escobar R, Benlloch M, Navarro C, Martin GC. The time of floral induction in the olive. J Am Soc Hortic Sci. 1992;117:304–7. https://doi.org/10.21273/JASHS.117.2.304
7. Dennis FG. Dormancy-what we know (and don’t know). HortScience. 1994;29:1249–55. https://doi.org/10.21273/HORTSCI.29.11.1249
8. Lang GA. Dormancy: A new universal terminology. HortScience. 1987;22:817–20. https://doi.org/10.21273/HORTSCI.22.5.817

9. Rohde A, Bhalerao R. Plant dormancy in the perennial context. Trends Plant Sci. 2007;12:217–23. https://doi.org/10.1016/j.tplants.2007.03.012
10. Badr SA, Hartmann HT. Effect of diurnally fluctuating vs constant temperatures on flower induction and sex expression in the olive (*Olea europaea*). Physiol Plant. 1971;24:40–5. https://doi.org/10.1111/j.1399-3054.1971.tb06712.x
11. Belguerri H. Effect of irrigation and nitrogen/potassium fertilization on productivity and fruit quality in super-intensive olive orchards [PhD thesis]. Lleida: Univ. de Lleida; 2016. https://www.tdx.cat/handle/10803/385736
12. Lavee S. Biology and physiology of the olive tree. In: World encyclopedia of the olive. Barcelona: Plaza & Janés; 1996. p. 59–110.
13. Ouksili A. Floral biology of olive (*Olea europaea* L.) from flower initiation to effective pollination. Montpellier: Univ. des Sciences et Technologies du Languedoc; 1983.
14. Malik NSA, Bradford JM. Changes in oleuropein levels during differentiation and development of floral buds in 'Arbequina' olives. Sci Hortic. 2006;110:274–8. https://doi.org/10.1016/j.scienta.2006.07.016
15. Mataix J, Barbancho FJ. Olive oil in Mediterranean food. In: Quiles JL, Ramírez-Tortosa MC, Yaqoob P, editors. Olive oil and health. Wallingford: CABI; 2006. p. 1–44. https://doi.org/10.1079/9781845930684.0001
16. Loussert R, Brousse G. The olive tree. Paris: Techniques Agricoles; 1978.
17. Maracchi G, Pittalis F, Bindi M, Sillari B. Olive production and meteorological factors: A preliminary study. Olivæ. 1994;30–7.
18. Garcia-Mozo H, Orlandi F, Galan C, Fornaciari M, Romano B, Ruiz L, et al. Olive flowering phenology variation between different cultivars in Spain and Italy: Modeling analysis. Theor Appl Climatol. 2009;95:385–95. https://doi.org/10.1007/s00704-008-0016-6
19. De Melo-Abreu J. Modelling olive flowering date using chilling for dormancy release and thermal time. Agric For Meteorol. 2004;125:117–27. https://doi.org/10.1016/j.agrformet.2004.02.009
20. Elloumi O, Ghrab M, Chatti A, Chaari A, Ben Mimoun M. Phenological performance of olive tree in a warm production area of central Tunisia. Sci Hortic. 2020;259:108759. https://doi.org/10.1016/j.scienta.2019.108759
21. Meier U. Growth stages of mono- and dicotyledonous plants: BBCH monograph. 2018. https://doi.org/10.5073/20180906-074619
22. Campoy JA, Ruiz D, Egea J. Dormancy in temperate fruit trees in a global warming context: A review. Sci Hortic. 2011;130:357–72. https://doi.org/10.1016/j.scienta.2011.07.011
23. Ramos A, Rapoport HF, Cabello D, Rallo L. Chilling accumulation, dormancy release temperature and the role of leaves in olive reproductive budburst. Sci Hortic. 2018;231:241–52. https://doi.org/10.1016/j.scienta.2017.11.003
24. Hutchins L. Influence of winter temperature on olive flowering. Paper presented at: Am Soc Hortic Sci Annual Meeting; 1932.
25. Weinberger JH. Chilling requirements of peach varieties. Proc Am Soc Hortic Sci. 1950;56.
26. Richardson E, Seeley S, Walker D. A model for estimating the completion of rest for 'Redhaven' and 'Elberta' peach trees. HortScience. 1974;9. https://doi.org/10.21273/HORTSCI.9.4.331
27. Fishman S, Erez A, Couvillon GA. Temperature dependence of dormancy breaking in plants. J Theor Biol. 1987;124:473–83. https://doi.org/10.1016/S0022-5193(87)80221-7
28. Erez A, Fishman S, Linsley-Noakes G, Allan P. The dynamic model for rest completion in peach buds. Acta Hortic. 1990;174.
29. Faust M, Liu D, Millard M, Stutte G. Bound versus free water in dormant apple buds. HortScience. 1991;26. https://doi.org/10.21273/HORTSCI.26.7.887
30. Faust M, Liu D, Line MJ, Stutte GW. Conversion of bound to free water in endodormant buds of apple. Acta Hortic. 1995;395:113–8. https://doi.org/10.17660/ActaHortic.1995.395.10
31. Luedeling E, Gassner A. Partial least squares regression for analyzing walnut phenology in California. Agric For Meteorol. 2012;158–159:43–52. https://doi.org/10.1016/j.agrformet.2011.10.020
32. Moriondo M, Ferrise R, Trombi G, Brilli L, Dibari C, Bindi M. Modelling olive trees and grapevines in a changing climate. Environ Model Softw. 2015;72:387–401. https://doi.org/10.1016/j.envsoft.2014.12.016
33. El Yaacoubi A, Oukabli A, Legave JM, Ainane T, Mouhajir A, Zouhair R, et al. Response of almond flowering and dormancy to Mediterranean temperature conditions. Sci Hortic. 2019;257:108687. https://doi.org/10.1016/j.scienta.2019.108687
34. El Yaacoubi A, Oukabli A, Hafidi M, Farrera I, Ainane T, Cherkaoui SI, et al. Validated model for apple flowering prediction in the Mediterranean area. Sci Hortic. 2019;249:59–64. https://doi.org/10.1016/j.scienta.2019.01.036
35. El Yaacoubi A, El Jaouhari N, Bourioug M, El Youssfi L, Cherroud S, Bouabid R, et al. Vulnerability of Moroccan apple orchards to climate-change-induced phenological perturbations. Int J Biometeorol. 2019;64:377–87. https://doi.org/10.1007/s00484-019-01821-y
36. Rojo J, Orlandi F, Ben Dhiab A, Lara B, Picornell A, Oteros J, et al. Estimation of chilling and heat accumulation periods based on olive pollination timing. Forests. 2020;11:835. https://doi.org/10.3390/f11080835
37. Delgado A, Egea JA, Luedeling E, Dapena E. Agroclimatic requirements of local apple cultivars in NW Spain. Sci Hortic. 2021;283:110093. https://doi.org/10.1016/j.scienta.2021.110093
38. Viti R, Andreini L, Ruiz D, Egea J, Bartolini S, Iacona C, et al. Dormancy overcoming in apricot flower buds under Mediterranean climates. Sci Hortic. 2010;124:217–24. https://doi.org/10.1016/j.scienta.2010.01.001
39. El Yaacoubi A, Malagi G, Oukabli A, Citadin I, Hafidi M, Bonhomme M, et al. Bud dormancy dynamics in temperate fruit trees. Int J Biometeorol. 2016;60:1695–710. https://doi.org/10.1007/s00484-016-1160-9
40. Faust M, Erez A, Rowland LJ, Wang SY, Norman HA. Bud dormancy in perennial fruit trees. HortScience. 1997;32:623–9. https://doi.org/10.21273/HORTSCI.32.4.623
41. Fernandez E, Whitney C, Luedeling E. Importance of chill model selection. Eur J Agron. 2020;119:126103. https://doi.org/10.1016/j.eja.2020.126103
42. Luedeling E, Brown PH. Global analysis of winter chill models. Int J Biometeorol. 2011;55:411–21. https://doi.org/10.1007/s00484-010-0352-y
43. Aybar VE, De Melo-Abreu JP, Searles PS, Matias AC, Del Rio C, Caballero JM, et al. Olive flowering at low latitude sites in Argentina. Span J Agric Res. 2015;13:e0901. https://doi.org/10.5424/sjar/2015131-6375
44. Picornell A, Abreu I, Ribeiro H. Trends and projections of *Olea* flowering in western Mediterranean. Agric For Meteorol. 2023;339:109559. https://doi.org/10.1016/j.agrformet.2023.109559
45. Luedeling E, Schiffers K, Fohrmann T, Urbach C. PhenoFlex: An integrated model for spring phenology prediction. Agric For Meteorol. 2021;307:108491. https://doi.org/10.1016/j.agrformet.2021.108491

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