ORIGINAL PAPER

Chilling and heat requirements for woody taxa in Tétouan (NW Morocco)

Asmaa Boullayali · Carmen Galán · Moisés Martínez‑Bracero · Hassan Bouziane

Received: 9 August 2022 / Accepted: 29 March 2023 / Published online: 11 April 2023 © The Author(s), under exclusive licence to Springer Nature B.V. 2023

Abstract Impact of climate change affects chilling and heat accumulation that phenological development of plant needs, air temperature being determinant for fowering, pollination and fruit production, but few knowledges are available in the winter and spring climate of Tétouan. The physiological mechanisms of the reproductive cycle that controls pollen emission are related with temperature, and diferent environmental factors regulate strongly the reproductive phases of the plant's life cycle. However, from an empirical point of view, the alternance between endodormancy and ecodormancy is not well detectable. Our work focuses on determining the heat accumulation periods associated with the thermal balance needed to fulfll the chilling and heat required for budbreak and bloom timing. To evaluate *Morus*, *Pistacia, Quercus* and *Olea* response to changes in chill and heat accumulation rates, the Dynamic Model and the Growing Degree-Days Method were used. Regression analyses identifed the chilling and forcing periods for these taxa. Over the past 12 years, chill accumulation

A. Boullayali $(\boxtimes) \cdot H$. Bouziane Laboratory of Applied Botany, Department of Biology, Faculty of Sciences, University Abdelmalek Essaâdi, Mhannech II, 2121 Tétouan, Morocco e-mail: asmaeboullayali@gmail.com

C. Galán · M. Martínez-Bracero Department of Botany, Ecology and Plant Physiology, University of Córdoba, Edifcio Celestino Mutis (C4), Campus de Rabanales, Córdoba, Spain

during tree dormancy increased signifcantly for most of woody taxa studied, while heat accumulation decreased not signifcantly for all taxa. Heat accumulation was the main driver of bloom timing, with efects of variation in chill accumulation.

Keywords Heat requirement · Dynamic model · Chilling requirement · Dormancy · Flowering · Woody taxa · Tétouan

1 Introduction

The physiological behavior of woody plants with winter–spring flowering is subject to constant variations due to the action of diferent bioclimatic parameters (Fuertes-Rodríguez et al., [2007\)](#page-12-0). The impact of meteorological parameters on fowering depends on the bioclimatic conditions in diferent areas (Hoxha, [2007;](#page-12-1) Jato et al., [2004;](#page-12-2) Ščevková et al., [2021\)](#page-13-0). Adaptation of phenology to temperature is a topic that is receiving increasing attention (Menzel et al., [2006,](#page-13-1) [2020;](#page-13-2) Parmesan et al., [2007](#page-13-3)).

Before fowering, temperature is considered as the primary factor infuencing the growth and development of plants, the maturation of reproductive organs and pollen production (Dahl et al., [2013\)](#page-11-0). Secondary factors, such as photoperiod, temperature and relative humidity, affect the opening of anthers and anthesis. Airborne pollen from anemophilous plants is greatly infuenced by meteorological conditions and is dispersed by a tertiary factor, the wind, which acts by its speed and direction (Fuertes-Rodríguez et al., [2007;](#page-12-0) Rojo et al., [2016](#page-13-4); Cianni et al., [2020\)](#page-11-1).

The Mediterranean region is characterized by a changeable climate, especially in spring when temperature varies quickly from one day to another. Moreover, interannual variations affect the onset of flowering, its intensity and then, pollen production. The air temperature is a good meteorological indicator for the pollen season timing forecast (Achmakh et al., [2015\)](#page-10-0). Forcing models based essentially on heat requirements measured as degree hours or degreedays above a threshold are suitable to quantify phenological development (Galán et al., [2005\)](#page-12-3). The works involved in estimating the best threshold temperature for plant development in a range of climates have been analyzed for several years both in agronomy and botany and more recently in reproductive phenology of airborne pollen (Aguilera et al., [2014](#page-10-1), [2015](#page-10-2); Garcia-Mozo et al., [2002\)](#page-12-4). Depending on several factors in both, the plant and the environment, threshold temperatures vary (Galán et al., 2004; Aguilera et al., [2014;](#page-10-1) Achmakh et al., [2015\)](#page-10-0).

In addition, several studies have indicated that warm temperatures during the heat period can advance spring phenology (Guo et al., [2015;](#page-12-5) Horvath et al., [2003;](#page-12-6) Vitra et al., [2017\)](#page-14-0), but is also likely to be influenced by increased $CO₂$ emissions and frost free days (Ziska et al., [2019](#page-14-1)). The exposure to chilling temperatures in winter and early spring is needed to break plant endodormancy (Coville, [1920;](#page-11-2) Schwartz $& Hanes, 2010$ $& Hanes, 2010$. In this period, which is known as the chilling period, high temperatures may have a negative impact on plant phenology (Xu et al., [2020](#page-14-2)). Warmer temperatures in early spring affect flushing by shortening the ecodormancy phase (Dantec et al., [2014\)](#page-11-3). Contrariwise, in temperate regions, warmer temperatures during winter can conduct to later endodormancy release or to insufficient chilling for the full release of endodormancy, increasing the heat accumulated for budburst (Cannell & Smith, [1986](#page-11-4); Murray et al., [1989;](#page-13-6) Sarvas, [1972;](#page-13-7) Wareing, [1953](#page-14-3)). For example, modeling results in North Atlantic Oceanic (NAO) and Mediterranean regions suggest that a later release of dormancy in plants caused by warmer temperatures would lead to a further delay in the flowering date or insufficient chilling (Galán et al., 2016 ; Legave et al., 2013). Thus, the role of chilling may become more important with increasing

air temperature, warmer temperatures therefore leading to a nonlinear advance in tree reproductive phe-nology in the future (Chuine et al., [2010;](#page-11-5) Fu et al., [2012;](#page-11-6) Laube et al., [2013](#page-12-9)). Moreover, a recent study in aerobiology shows that over the last 50 years the pollen season of some tree species have advanced in response to the temperature increase (Gehrig & Clot, [2021\)](#page-12-10).

The relation between heat and chilling requirements difers markedly between species (Cannell, [1997;](#page-11-7) Murray et al., [1989;](#page-13-6) Vitasse & Basler, [2013](#page-14-4)). In the next few decades, the leaf unfolding will apparently occur earlier under conditions of recurrent climate change in woody species with a low chilling requirement, while species that require a highly fulfllment of chilling may show constant or even later leaf unfolding date due to an unsatisfed chilling requirements or a later endodormancy release (Fu et al., [2012;](#page-11-6) Harrington et al., [2010](#page-12-11); Morin et al., [2010;](#page-13-8) Murray et al., [1989](#page-13-6); Polgar & Primack, [2011;](#page-13-9) Vitasse et al., [2010](#page-14-5)). The rate of chilling and forcing temperatures needed to trigger spring plant phenology varies among species and among diferent places (Campoy et al., [2012](#page-11-8); Chuine et al., [2016;](#page-11-9) Dantec et al., [2014;](#page-11-3) Vitasse & Basler, [2013](#page-14-4)). In general, species tending to develop their leaves and bloom earlier might have a lower chilling requirement for spring phenology (Fu et al., [2012](#page-11-6); Murray et al., [1989](#page-13-6)).

For the quantifcation of chill, many approaches were used, and the Dynamic Model being mainly as the most robust chilling model (Campoy et al., [2011;](#page-11-10) Luedeling & Gassner, [2012;](#page-12-12) Luedeling et al., [2009a,](#page-13-10) [2009b;](#page-12-13) Ruiz et al., [2007;](#page-13-11) Zhang & Taylor, [2011](#page-14-6)), while for determining the heat requirement, the method proposed by Ring et al. [\(1983](#page-13-12)) is also a robust model.

In the present study, based on long-term airborne pollen observations in Tétouan, the aim was to determine the timing of chilling and forcing periods, the optimal temperature threshold within the region and to quantify the chilling and heat requirements of *Morus*, *Pistacia, Quercus* and *Olea* in the warm climate of this region.

2 Materials and methods

Tétouan (35°34′N; 5°22′W) is located at 65 ma.s.l. in the northwest of Morocco in the Thermomediterranean belt. It is characterized by a Mediterranean warm subhumid climate (Benabid, [1982](#page-11-11)) with rainy autumns and winters and dry summers. The annual average temperature is 18.7 °C , and mean annual rainfall is 594.7 mm. Depending on the year, December–February are the coldest months and July or August the warmest months (Aboulaich et al., [2013](#page-10-3)). The prevailing wind directions are those blowing from NE and SW (Aboulaich et al., [2011\)](#page-10-4).

A 7-day volumetric spore trap of Hirst type sampler was used for aerobiological sampling (Hirst, [1952\)](#page-12-14) over a 12-year period (2008–2019). It was installed, 15 m above ground level, on the roof of the Department of Biology of the Faculty of Science (Abdelmalek Essaâdi University; 35°34′N; 5°22′W). Sampling and data analysis were carried out according to the protocol drawn up by the Spanish Aerobiology Network (REA) (Galán et al., [2007](#page-12-15)) and the minimum requirements of the European Aerobiology Society (EAS) (Galán et al., [2014](#page-12-16)). The average daily pollen concentrations were expressed as the number of pollen/ $m³$ of air.

The meteorological data were registered by an automatic meteorological station located in our Biology Department of the Faculty of Sciences, where the pollen trap was installed.

The study focused on *Morus*, *Pistacia*, *Quercus* and *Olea* pollen types in Tétouan during 2008–2019. The main pollen season (MPS) was calculated as described by Velasco et al. (2013), but it was modifed given the low pollen concentrations recorded in the Tétouan region, compared to Córdoba, Spain. The threshold daily pollen concentration (pollen/m³) chosen as the start and end of the MPS was as follows:

- *Olea*: 10 pollen/ m^3 +5 days with 10 or more pollen/m³; End = 10 pollen/m³ + 5 days with concentrations below this level.
- *Morus*, *Pistacia*, *Quercus*: 3 pollen/ $m^3 + 5$ days with 3 or more pollen/ m^3 ; End=3 pollen/ $m³ + 5$ days with concentrations below this level.

In order to calculate the chilling requirement, we used the dynamic model proposed by Fishman [\(1987](#page-11-12)); Chilling portions (CP) were calculated from 1st December to the end of chilling considered as 15 February for every taxa. Threshold temperatures from 9 to 12 °C were tested increasing by 0.5 °C.

For determining the heat requirement, we used the method proposed by Ring et al. ([1983](#page-13-12)). In this method, growing degree-days (GDDº) were calculated using the sum of the diference between daily mean temperatures and threshold temperatures: $\mathrm{D} = \sum$ (Tmean—Th); then, D is set equal to 0 when threshold was higher than Tmean. Accumulated Heat Units, starting from the day after the chilling accumulation until seven days before blooming. Seven threshold temperatures from 13 to 16 \degree C were tested increasing by 0.5 \degree C. The most accurate threshold temperature was chosen for each taxa, taking into account the lowest root mean square error (RMSE) of the predicted $(d¹)$ minus the observed (d^2) date daily calculating the sum of GDD for each study year (*n*) (Galán et al., [2005\)](#page-12-3):

$$
RMSE = \sqrt{\left(d^1 - d\right)^2/n}
$$

Three variables in relation to the heat accumulation period were calculated: (1) the length (in days) of the heat accumulation period (length heat period), which was considered as the time diference between the heat accumulation start date and the end date of the heat accumulation (i.e., as the frst day of seven days before the start of fowering); (2) the timing diference 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 fowering date (peak_ch/peak_f). The number of days was calculated from the 1st December of the previous year, taking into account that the chilling portions were calculated from the autumn of the year preceding fowering, and to avoid biasing the calculation in the period between the end of chilling and the end of heat accumulation (seven days before the date of fowering), the DOY of this later was from the 1st December.

To evaluate the efect of heat accumulation period characteristics on the pollen season start in the different studied taxa, Pearson's parametric correlation analysis was performed.

Variance analysis (one-way ANOVA) was performed to determine the diferences in the heat accumulation periods of the diferent studied taxa. When there were signifcant diferences, a post hoc Tukey test was performed. The analyses have been executed by the IBMSPSS 20.0 Statistics Software package.

Linear regression was made to analyze temporal trends of chilling and heat accumulation during respective periods for *Morus*, *Pistacia*, *Quercus* and *Olea* during 2008–2019. The Mann–Kendall test, a tool commonly used for time series analysis, was undertaken for trends statistical signifcance (Tao et al., [2006](#page-13-13)). Linear regression was used to study the interrelation between chilling and heat accumulation and mean temperature variations during the corresponding chilling and forcing periods. Results were evaluated for signifcance using analysis of variance.

3 Results

The dates corresponding to the pollen season start (PSS) are shown in Table [1.](#page-3-0) The most common PSS of *Morus* and *Pistacia* is late March, the mean date being 15 March, 25 March, respectively. For *Quercus* and *Olea*, the mean PSS occurred in the frst fortnight of April (5 April, 17 April), respectively (Table[1\)](#page-3-0).

Similar average peak chilling and end dates were recorded for the studied taxa. The average of the peak chilling dates for all studied taxa was 22 January and the average of the end of chilling dates occurred as 17 February. The chilling accumulation was calculated from the frst December to the end of chilling over 12 years difered between years and registered an average of 18.70 CP for all taxa (Fig. [1](#page-4-0)). As the chilling amounts were similar, the average heat accumulation start dates was also similar for all taxa and recorded on 18 February (81 DOY). When the growing degree-days (GDD) were calculated, GDD values showed an interannual fuctuations, with highest annual values in 2010 for *Morus*, *Pistacia* and *Quercus*, and in 2016 for *Olea*. As regards, cumulated heat between taxa, *Olea* recorded the highest values, whereas *Morus* showed the lowest values (Fig. [1](#page-4-0)). Averages GDD ranged between 4 and 30 GDD for *Morus* and *Olea,* respectively (Table [2\)](#page-5-0).

For the average fowering peak dates, signifcant diferences between these taxa were found $(F=27.882; P<0.001)$. Here, three groups were observed (Fig. [2\)](#page-5-1). The averages peak of fowering dates in Tétouan was on 29 March (119 DOY) for *Morus*, on 03 April for *Pistacia* (124DOY), on 22 April (143 DOY) for *Quercus* and on 9 May (160 DOY) for *Olea* (Table [2\)](#page-5-0). A Significant difference was reported also for the length of the heat accumulation period (*F*=3.756; *P*<0.01) (Fig. [2](#page-5-1)), which *Olea* revealed the highest mean value (49 days), followed by *Quercus* (37 days), *Pistacia* (28 days) and *Morus* (17 days) . Here, two groups were noticed (Table [2,](#page-5-0) Fig. [2](#page-5-1)).

A clear diference was recorded for the time period between the peak of chilling date and the peak of flowering date with three groups listed $(F=12.823)$; *P*<0.001); while the time period from the peak of chilling to the heat period start date, recorded the same value for the taxa studied (Fig. [2](#page-5-1)). For the frst

Table 1 Beginning of the main pollination season of	Study period	Morus		Pistacia		Quercus		Olea	
Morus, Pistacia, Quercus and <i>Olea</i> (day–month), number of days from 1 December of the previous year		Date	DOY	Date	DOY	Date	DOY	Date	DOY
	2007-2008	2 March	93	14 March	105	15 March	106	1 April	123
	2008-2009	8 March	99	13 March	104	28 March	119	5 April	127
	2009-2010	26 March	117	27 March	118	31 March	122	20 April	142
	2010-2011	11 March	102	20 March	111	26 March	117	19 April	141
	2011-2012	16 March	107	18 March	109	15 April	136	23 April	145
	2012-2013	13 March	104	26 March	117	16 April	138	22 April	144
	2013-2014	20 March	111	20 March	111	23 March	114	5 April	127
	2014-2015	11 March	102	26 March	117	25 March	116	22 April	144
	2015-2016	15 March	106	30 March	121	6 April	128	6 May	158
	$2016 - 2017*$	20 March	111			13 April	135	1 April	123
	2017-2018	12 March	103	3 April	125	23 April	145	4 May	156
	2018-2019	17 March	108	4 April	126	10 April	132	31 March	122
*The values were low to calculate the pollen season for <i>Pistacia</i>	Mean value	15 March	105	25 March	115	5 April	126	17 April	138
	SD		6		8		12		13

 V and V and V $\bigcircled{2}$ Springer

yea

Fig. 1 Chilling and Heat accumulation for *Morus*, *Pistacia*, *Quercus* and *Olea* during chilling and forcing periods from 2008 to 2019. *The values were low in 2017 to calculate the pollen season for *Pistacia*

Taxa	End-ch (DOY)	Peak-ch (DOY)	(DOY)	Start-ht Peak-fl (DOY)	Threshold $(^{\circ}C)$	GDD	(Days)	Peak-ch/Start-ht Length heat period Peak-ch/Peak-fl (Days)	(Days)
Morus		$80+12$ $53+10$ $81+11$		$119+5$ 16			$4+5$ $29+11$	$17 + 9$	$66 + 10$
		<i>Pistacia</i> 80 ± 12 53 ± 10	$81 + 11$	$124 + 5$ 16			$9+6$ 29 + 11	$28 + 9$	$71 + 9$
		<i>Quercus</i> 80 ± 12 53 ± 10 81 ± 11		$143+9$ 16			$12+8$ $29+11$	$37 + 9$	$90 + 12$
Olea		$80 + 12$ $53 + 10$	$81 + 11$	$160+10$ 16		$30+20$ $29+11$		$49 + 11$	$108 + 11$

Table 2 Average values of the main characteristics of the heat accumulation period of each taxa studied. End-ch End of chilling date, Peak-ch Peak of chilling date, Start-ht heat accumula-

tion start date, Peak-f peak of fowering date, *GDD* growing degree-days amounts

Fig. 2 Boxplots of the diferent parameters studied. Diferent letters indicate statistically diferent values (*P*<0.05)

parameter, *Olea* showed the highest mean value, followed by *Quercus* and *Pistacia* (108, 90, 71 days, respectively). The time period from the peak of chilling to the peak of fowering showed the lowest value for *Morus*, which was 66 days. For the second parameter, the time period from the peak of chilling to the heat period was identical for all species (29 days) (Table [2\)](#page-5-0).

Correlation analysis was fulflled for the relationships between the heat accumulation period characteristics for all taxa studied. Only the start date of the heat accumulation period correlated signifcantly and positively with the peak chilling date, showing a similar coefficient of correlation $(r=0.694; P<0.05)$. Non-significant coefficients were obtained for the other parameters considered in this analysis.

Chilling accumulation for *Olea* in Tétouan showed a signifcant trend, increasing by 2.54 CP per year (*P*<0.01) during 2008–2019 (Fig. [3](#page-6-0)). However, Chilling accumulation decreased as mean temperatures increased during the chilling period of *Olea*, but the trend was not signifcant during the past 12 years (Fig. [4\)](#page-7-0). Heat accumulation during the forcing period showed a slight and non-signifcant negative trend (Fig. [3\)](#page-6-0), whereas rising mean temperatures during the forcing period increased heat accumulation by 7.66 GDD/ $\rm ^{o}C$ (Fig. [4](#page-7-0)).

Fig. 3 Trends of chilling and heat accumulation for *Morus, Pistacia*, *Quercus* and *Olea* during chilling and forcing periods from 2008 to 2019. Blue dots Chill accumulation, red dots heat

accumulation. Trends are significant with $*P < 0.1$, $**P < 0.05$, ****P*<0.01

Fig. 4 Trends of relationships between chilling and heat accumulation and mean temperature during relevant periods for all taxa studied. Blue dots Chill accumulation, red dots heat accumulation. Trends are signifcant with **P*<0.1, ***P*<0.05

A similar response of chilling and heat accumulation occurred for *Morus*, *Quercus* and *Pistacia* showing a signifcant increasing of chilling accumulation over time by 2.54 CP per year $(P < 0.01)$ was observed (Fig. [3\)](#page-6-0). Chilling accumulation decreased during chilling period when the mean temperatures increased but not signifcantly. Rising mean temperatures during the forcing period increased heat accumulation of *Morus, Pistacia* and *Quercus* by 1.40, 1.63, 3.05 GDD/°C, respectively (Fig. [4\)](#page-7-0). However, the trend decreased not signifcantly for heat accumulation (Fig. [3](#page-6-0)).

4 Discussion

The phenological response of spring-fowering woody species to temperature has been widely approved and correlates very well with the air temperature (Menzel, [2002](#page-13-14); Spano et al., [1999](#page-13-15)). After fower bud break, morphological development requires a certain thermal contribution to continue to develop after their latent phase (Anderson et al., [2005](#page-11-13); Foley et al., [2009](#page-11-14); Orlandi et al., [2002](#page-13-16)). In general, our results confrm a clear relationship between the beginning of pollination and air temperature.

It is commonly accepted that heat is only efective after sufficient chill has been met (Cannell $\&$ Smith, [1983;](#page-11-15) Cesaraccio et al., [2004;](#page-11-16) Fuchigami & Nee, [1987;](#page-12-17) Rea & Eccel, [2006](#page-13-17)). The models to estimate chill accumulation are under disagreement due to their variability among climates and the lack of physiological knowledge involved in their development (Luedeling, [2012](#page-12-12)). The choice of which type of model to use is often made a priori in phenology modeling studies, and models are then ftted to available data (Guo et al., [2013\)](#page-12-18).

The chilling requirement based on "chill portions" has been considered as one of the best models for temperate nuts and fruits (Guo et al., [2013](#page-12-18); Luedeling et al., [2009a,](#page-13-10) [2009b;](#page-12-13) Zhang & Taylor, [2011](#page-14-6)). This Dynamic Model has been found to be efective for other woody species (Xu et al., [2020](#page-14-2)), naming apricot (Benmoussa et al., [2017](#page-11-17); Zhuang et al., [2016](#page-14-7)), olive (Aguilera et al., 2013), apple (Parkes et al., [2020](#page-13-18)), pistachio (Benmoussa et al., [2017](#page-11-17); Zhang & Taylor, [2011](#page-14-6)), walnut (Luedeling et al., [2009a,](#page-13-10) [2009b](#page-12-13)), almond (Benmoussa et al., [2017](#page-11-17)) and cherry (Luedeling et al., [2013a](#page-12-19)). As a result, we kept the same parameter values proposed by Fishman et al. ([1987\)](#page-11-12) to calculate the chill portions of four taxa in this study. The Dynamic Model has often been found to be the most suitable among common chill models, especially in warm regions (Benmoussa et al., [2017\)](#page-11-17).

The biothermic requirements that govern the different phenological development of the woody species in Mediterranean areas and estimated by diferent methodologies and threshold temperatures were the objective of numerous studies (Alba and de la Guardia, [1998](#page-10-5); Galán et al., [2005](#page-12-3); Bonofglio et al., [2008;](#page-11-18) Aguilera et al., [2014](#page-10-1), [2015](#page-10-2); Achmakh et al., [2015\)](#page-10-0). Although numerous methods for calculating GDD have been reported, agreement in estimating the best threshold temperatures has not received widespread acceptance (Achmakh et al., [2015;](#page-10-0) Ruml et al., [2010\)](#page-13-19). The threshold temperature resulting effective in this research difers from those recorded for woody species in previous studies. The base temperatures reported ranged between 5 and 12.5 °C for *Olea* in Andalusia region and Italy (Galán et al., [2005;](#page-12-3) Orlandi et al., [2006\)](#page-13-20), between 0 and 25 °C in Tunis (Aguilera et al., [2014](#page-10-1)) and between 4 and 12 \degree C for *Quercus* in diferent climatic zones in Spain (Garcia-Mozo et al., [2000\)](#page-12-20). Previously in the area of Tétouan, threshold temperatures of 10 and 7 °C performed well at forecasting the initiation of pollen season and full anthesis of *O. europaea*, respectively (Achmakh et al., [2015\)](#page-10-0). This fact can be considered to depend mainly on methodology used both to begin the heat accumulation and to statistically evaluate the best GDD threshold temperatures. Indeed, in the previous study undertaken in Tétouan, Achmakh et al. [\(2015](#page-10-0)) tested a range of base temperatures from 0 to 10 °C. Aguilera et al. [\(2014](#page-10-1)) reported that the thresholds values decrease proportionally; as the latitude increases, diferent threshold was obtained and ranged from 16 \degree C in Perugia to 23 \degree C in Zarzis. These results showed that the lower threshold or base temperature may vary between geographical areas. A relationship may exist between specifc climatic conditions and taxa (Benmoussa et al., [2017](#page-11-17)). However, we have observed that the threshold temperatures are the same for the four taxa studied.

The peak of chilling, i.e., the day of the year with the maximum accumulation of positive chilling portions, has not been considered as the day to begin the heat accumulation in any taxa studied. This later ftted as the day after the end of chilling. This result suggests that, despite arriving at the peak chilling day, the chilling requirements have not been met and the endodormancy phase release would need more days of chilling (Lang, [1987](#page-12-21)).

According to several studies, chilling and heat accumulation appeared discontinuous (Benmoussa et al., [2017;](#page-11-17) Guo et al., [2013](#page-12-18)) due to diferent physiological processes inside the bud that happen during diferent stages within the chilling and forcing periods. Dormancy initiation and release and plants sensitivity to chill are governed by genetical, genomic and physiological mechanisms (Ríos et al., [2014\)](#page-13-21). Other factors such as endogenous signals, temperature, photoperiod and water availability regulate the fowering transition (Benmoussa et al., [2017](#page-11-17)).

Moreover, when buds chilling is met and conditions are favorable for budbreak, the active phenological development starts (De la Rosa et al., [2000](#page-11-19)). In this regard, the results of the present study demonstrate a good approximation. Here, for all studied taxa, the cumulative chilling decline after the peak of chilling provided the best start date to begin the heat accumulation period.

On these terms, a period of approximatively one month between the peak of chilling and the heat accumulation start date was detected for all taxa, accumulating the same amount of chilling. However, different GDD was required for their fowering onset. This fnding might indicate that in woody species fowering in early spring, such as *Morus*, *Pistacia* and *Quercus* species, endodormancy release occurs earlier which is consequently related to their adaptative capacity to the environment concerned. However, for *Olea*, the endodormancy release seems to occur later. Indeed, Aguilera et al. [\(2014](#page-10-1)) suggested that a delay in the peak fowering date of olive observed in the Italian and Spanish areas might be provoked by a long transition between the end of endodormancy and the initiation of ecodormancy. 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](#page-11-20); Pinney & Polito, [1990;](#page-13-22) Rallo & Martin, [1991](#page-13-23)).

Summer temperature, winter chilling units and heat accumulation in woody species have been studied by numerous authors (Arnold, [1959](#page-11-21); Chuine et al., [1999](#page-11-22); Frenguelli & Bricchi, [1998](#page-11-23); Galán et al., [2001;](#page-12-22) Garcia-Mozo et al., [2000](#page-12-20)) in order to clarify their involvement in the settlement and intensity of dormancy as well as cold acclimatization. In the Tingitana peninsula, the coldest temperature is recorded during December–February (Aboulaich et al., [2013](#page-10-3)). Chilling requirements were not completely met under present climate conditions and insufficient in 2009 and 2010 for all populations, due to a warm winter. This result suggests that woody species in the southern of the Mediterranean sea need more heat than chilling showing their natural plasticity. However, the physiological efects of suboptimal chilling/forcing combinations should be investigated by horticultural researchers, which may have implications on crop yield or quality (Luedeling et al., [2013b](#page-12-23)).

The diferent results observed in chilling and heat requirements between fower and vegetative buds may be due to diferent environmental factors during the growing plant 'life cycle' (Rahemi & Pakkish, [2009](#page-13-24)). Thus, chilling and heat requirement amounts vary from year to year depending on photoperiod, plant nutrition (Powell, [1987\)](#page-13-25), temperature (Jacobs et al., [2002\)](#page-12-24) and other environmental factors (Rahemi & Pakkish, [2009](#page-13-24)).

In our analysis, chill accumulation trend showed a signifcant increase for most of taxa studied over the past 12 years. This could be due to the signifcant decreasing trend of annual and monthly minimum temperatures observed in Tétouan in our previous study (Boullayali et al., 2021). Heat accumulation increased signifcantly with rising mean temperatures during the forcing period. However, during 2008–2019, heat accumulation trend of *Morus*, *Olea*, *Pistacia* and *Quercus* decreased by −0.89–−0.19 GDD per year. These tendencies in heat requirements have been related to abundant chill accumulated, and this conclusion was also confrmed by Alburquerque et al. [\(2008](#page-10-6)).

Corresponding with many other studies, heat accumulation is the main driver for fowering dates of woody taxa. Similarly, to this study, Guo et al. [\(2013](#page-12-18)) demonstrated in the cold winter climate of Beijing that forcing efects were much stronger than those of chilling on chestnut and jujube. Alonso et al. ([2005\)](#page-10-7) showed a similar result on almond in the cool climate of Zaragoza in northeast Spain. Sparks [\(1993](#page-13-26)) indicated that bud break of pecan could occur even when no chill is accumulated, and heat requirements are satisfed. In contrast, Egea et al. ([2003\)](#page-11-24) showed that in Spain, the initiation of fowering of almond cultivars was infuenced mostly by chilling requirements, with a little heat requirements contributing. This result was corroborated by other studies concerning namely apricot, almond, pistachio and sweet cherry cultivars

(Alburquerque et al., [2008](#page-10-6); Campoy et al., [2012](#page-11-8); Rahemi & Pakkish, [2009](#page-13-24); Ruiz et al., [2007](#page-13-11)).

Regarding our results, it seems that warming due to increasing mean temperature during some parts of the dormancy season decreased chill accumulation rates, whereas the chill trend increased during the whole period studied. Since chilling requirements of woody taxa are met in all winters under present climate conditions of Tétouan, changes in winter chill may cause delays in spring phases in the near future. In contrast, impacts due to climate change are thus likely to arise from increased rates of heat accumulation rather than from changes in chill (Guo et al., [2013\)](#page-12-18). These two fgures may translate into delayed bud break and partial fowering compromising fruit production and resulting in low yield production.

5 Conclusion

Adaptation of phenology to temperature is the subject of numerous studies. Thermal balance of chilling and heat requirements is necessary for metabolic activation and budbreak time in woody taxa. Based on long-term aerobiological observations in Tétouan, our results determine the timing of chilling and forcing periods, the optimal temperature threshold within the region and quantify the chilling and heat requirements of taxa studied in the warm climate of this region. During the past 12 years, heat accumulation of *Morus, Olea*, *Pistacia* and *Quercus* decreased by −0.56; −0.89; −0.19; −0.30 GDD per year, respectively. Flowering dates of all taxa were determined by heat accumulation, when ecodormancy is met, with chill accumulation contributing a small effect on bloom timing. In woody species fowering in early spring, endodormancy release occurs earlier. However, for late spring specie, it was observed later suggesting a long transition between the end of endodormancy and the onset of ecodormancy. Since chilling requirements of woody taxa were achieved under present climate conditions, changes in winter chill may cause delays in spring phases in the near future.

Acknowledgements We thank Mr. Mohamed Kadiri, Mr. Mestapha Hassoun from Algology-Mycology team, and Mr. Khalil Kadaoui from Bio-Agrodiversity team for helpful, discussions and comments.

Author contribution AB and HB—methodology, formal analysis**,** writing, editing and fnalizing the manuscript. CG and MM-B—methodology, review, provided critical suggestions and editing the manuscript. All authors read and approved the manuscript.

Funding There is no funding for this research.

Declarations

Confict of interest The authors declare no commercial or associative interest that represents a confict of interest with the results submitted.

References

- Aboulaich, N. (2011). Production du pollen à potential allergissant chez les Cupressaceae et les Poaceae, et analyses aérobiologiques de l'atmosphére de Tétouan (NW du maroc) (2008–2010). Faculty Abdelmalek Essaâdi of sciences, Tétouan
- Aboulaich, N., Trigo, M. M., Bouziane, H., Cabezudo, B., Recio, M., Kadiri, M., & Ater, M. (2013). Variations and origin of the atmospheric pollen of Cannabis detected in the province of Tétouan (NW Morocco): 2008–2010. *Science of the Total Environment, 443*, 413–419. [https://doi.](https://doi.org/10.1016/j.scitotenv.2012.10.075) [org/10.1016/j.scitotenv.2012.10.075](https://doi.org/10.1016/j.scitotenv.2012.10.075)
- Achmakh, L., Bouziane, H., Aboulaich, N., Trigo, M. M., Janati, A., & Kadiri, M. (2015). Airborne pollen of Olea europaea L. in Tetouan (NW Morocco): Heat requirements and forecasts. *Aerobiologia, 31*, 191–199. [https://](https://doi.org/10.1007/s10453-014-9356-0) doi.org/10.1007/s10453-014-9356-0
- Aguilera, F., Orlandi, F., Ruiz-Valenzuela, L., Msallem, M., & Fornaciari, M. (2015). Analysis and interpretation of long temporal trends in cumulative temperatures and olive reproductive features using a seasonal trend decomposition procedure. *Agricultural and Forest Meteorology, 203*, 208–216. <https://doi.org/10.1016/j.agrformet.2014.11.019>
- Aguilera, F., Ruiz, L., Fornaciari, M., Romano, B., Galán, C., Oteros, J., Ben Dhiab, A., Msallem, M., & Orlandi, F. (2014). Heat accumulation period in the mediterranean region: Phenological response of the olive in diferent climate areas (Spain, Italy and Tunisia). *International Journal of Biometeorology, 58*, 867–876. [https://doi.org/10.](https://doi.org/10.1007/s00484-013-0666-7) [1007/s00484-013-0666-7](https://doi.org/10.1007/s00484-013-0666-7)
- 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. [https://doi.org/10.1007/](https://doi.org/10.1007/s00484-004-0223-5) [s00484-004-0223-5](https://doi.org/10.1007/s00484-004-0223-5)
- Alburquerque, N., García-Montiel, F., Carrillo, A., & Burgos, L. (2008). Chilling and heat requirements of sweet cherry cultivars and the relationship between altitude and the probability of satisfying the chill requirements. *Environmental and Experimental Botany, 64*, 162–170. [https://](https://doi.org/10.1016/j.envexpbot.2008.01.003) doi.org/10.1016/j.envexpbot.2008.01.003
- Alonso, J. M., Ansón, J. M., Espiau, M. T., & Company, R. S. I. (2005). Determination of endodormancy break in almond fower buds by a correlation model using the

average temperature of diferent day intervals and its application to the estimation of chill and heat requirements and blooming date. *Journal of the American Society for Horticultural Science, 130*, 308–318.

- Anderson, J. V., Gesch, R. W., Jia, Y., Chao, W. S., & Horvath, D. P. (2005). Seasonal shifts in dormancy status, carbohydrate metabolism, and related gene expression in crown buds of leafy spurge. *Plant Cell and Environment, 28*, 1567–1578.
- Arnold, C. Y. (1959). The determination and signifcance of the base temperature in a linear heat unit system Proc. *Journal of the American Society for Horticultural Science, 74*, 430–445.
- Benabid, A. (1982). Etudes phytoécologique, biogéographique et dynamique des associations et séries sylvatiques du Rif occidental (Maroc). Thèse Doctorat Es-Sciences, Faculté Sciences et Techniques St-Jérôme- Marseille. 199
- Benmoussa, H., Ghrab, M., Ben Mimoun, M., & Luedeling, E. (2017). Chilling and heat requirements for local and foreign almond (*Prunusdulcis* Mill.) cultivars in a warm Mediterranean location based on 30 years of phenology records. *Agricultural and Forest Meteorology, 239*, 34–46. <https://doi.org/10.1016/j.agrformet.2017.02.030>
- Bonofglio, T., Orlandi, F., Sgromo, C., Romano, B., & Fornaciari, M. (2008). Infuence of temperature and rainfall on timing of olive (*Olea europaea*) fowering in southern Italy. *New Zealand Journal of Crop and Horticultural Science, 36*, 59–69. [https://doi.org/10.1080/0114067080](https://doi.org/10.1080/01140670809510221) [9510221](https://doi.org/10.1080/01140670809510221)
- Campoy, J. A., Ruiz, D., Allderman, L., Cook, N., & Egea, J. (2012). The fulflment of chilling requirements and the adaptation of apricot (Prunusarmeniaca L.) in warm winter climates: An approach in Murcia (Spain) and the Western Cape (South Africa). *European Journal of Agronomy, 37*(1), 43–55. <https://doi.org/10.1016/j.eja.2011.10.004>
- Campoy, J. A., Ruiz, D., & Egea, J. (2011). Dormancy in temperate fruit trees in a global warming context: A review. *Scientia Horticulturae, 130*, 357–372. [https://doi.org/10.](https://doi.org/10.1016/j.scienta.2011.07.011) [1016/j.scienta.2011.07.011](https://doi.org/10.1016/j.scienta.2011.07.011)
- Cannell, M. G. R. (1997). Spring phenology of trees and frost avoidance. *Weather, 52*, 46–52. [https://doi.org/10.1002/J.](https://doi.org/10.1002/J.1477-8696.1997.TB06268.X) [1477-8696.1997.TB06268.X](https://doi.org/10.1002/J.1477-8696.1997.TB06268.X)
- Cannell, M. G. R., & Smith, R. I. (1983). Thermal time, chill days and prediction of budburst in *Piceasitchensis*. *Journal of Applied Ecology, 20*, 951–963. [https://doi.org/10.](https://doi.org/10.2307/2403139) [2307/2403139](https://doi.org/10.2307/2403139)
- Cannell, M. G. R., & Smith, R. I. (1986). Climatic warming, spring budburst and frost damage on trees. *Journal of Applied Ecology, 23*, 177–191.
- Cesaraccio, C., Spano, D., Snyder, R. L., & Duce, P. (2004). Chilling and forcing model to predict bud-burst of crop and forest species. *Agricultural and Forest Meteorology, 126*, 1–13. [https://doi.org/10.1016/j.agrformet.2004.03.](https://doi.org/10.1016/j.agrformet.2004.03.002) [002](https://doi.org/10.1016/j.agrformet.2004.03.002)
- Chuine, I., Bonhomme, M., Legave, J. M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A., & Améglio, T. (2016). Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology, 22*(10), 3444– 3460.<https://doi.org/10.1111/gcb.13383>
- Chuine, I., Cour, P., & Rousseau, D. D. (1999). Selecting models to predict the timing of fowering of temperate trees: Implications for tree phenology modelling. *Plant Cell and Environenment, 22*, 1–13. [https://doi.org/10.1046/j.1365-](https://doi.org/10.1046/j.1365-3040.1999.00395.x) [3040.1999.00395.x](https://doi.org/10.1046/j.1365-3040.1999.00395.x)
- Chuine, I., Morin, X., & Bugmann, H. (2010). Warming, photoperiods and tree phenology. *Science, 329*, 277–278. <https://doi.org/10.1126/science.329.5989.277-e>
- Ciani, F., Marchi, G., Dell'Olmo, L., Foggi, B., & Mariotti Lippi, M. (2020). Contribution of land cover and wind to the airborne pollen recorded in a South European urban area. *Aerobiologia, 36*, 325–340. [https://doi.org/10.1007/](https://doi.org/10.1007/s10453-020-09634-y) [s10453-020-09634-y](https://doi.org/10.1007/s10453-020-09634-y)
- Coville, F. V. (1920). The infuence of cold in stimulating the growth of plants. *Proceedings of the National Academy of Sciences of United States of America, 6*(7), 434–435. <https://doi.org/10.1073/pnas.6.7.434>
- Dahl, Å., Galán, C., Hajkova, L., Pauling, A., Sikoparija, B., Smith, M., & Vokou, D. (2013). The onset, course and intensity of the pollen season. In M. Sofiev & K.-C. Bergmann (Eds.), *Allergenic Pollen: A Review of the Production, Release, Distribution and Health Impacts* (pp. 29–70). Dordrecht: Springer Netherlands. [https://doi.org/](https://doi.org/10.1007/978-94-007-4881-1_3) [10.1007/978-94-007-4881-1_3](https://doi.org/10.1007/978-94-007-4881-1_3)
- Dantec, C. F., Vitasse, Y., Bonhomme, M., Louvet, J. M., Kremer, A., & Delzon, S. (2014). Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range. *International Journal of Biometeorology, 58*, 1853–1864.<https://doi.org/10.1007/s00484-014-0787-7>
- De la Rosa, R., Rallo, L., & Rapoport, H. F. (2000). Olive foral bud growth and starch content during winter rest and spring budbreak. *HortScience, 35*(7), 1223–1227. [https://](https://doi.org/10.21273/HORTSCI.35.7.1223) doi.org/10.21273/HORTSCI.35.7.1223
- Egea, J., Ortega, E., Martinez-Gomez, P., & Dicenta, F. (2003). Chilling and heat requirements of almond cultivars for fowering. *Environmental and Experimental Botany, 50*, 79–85.
- Fernández-Escobar, R., Benlloch, M., Navarro, C., & Martín, G. C. (1992). The time of foral induction in the olive. *Journal of the American Society for Horticultural Science., 110*, 303–309.
- Fishman, S., Erez, A., & Couvillon, G. A. (1987). The temperature dependence of dormancy breaking in plants: Mathematical analysis of a two-step model involving a cooperative transition. *Journal of Theorotical Biology, 124*, 473–483. [https://doi.org/10.1016/S0022-5193\(87\)80221-7](https://doi.org/10.1016/S0022-5193(87)80221-7)
- Foley, M. E., Anderson, J. V., & Horvath, D. P. (2009). The efects of temperature, photoperiod, and vernalization on regrowth and fowering competence in *Euphorbia esula* (Euphorbiaceae) crown buds. *Botany, 87*, 986–992. <https://doi.org/10.1139/B09-055>
- Frenguelli, G., & Bricchi, E. (1998). The use of the phenoclimatic model for forecasting the pollination of some arboreal taxa. *Aerobiologia, 14*, 39–44. [https://doi.org/10.](https://doi.org/10.1007/BF02694593) [1007/BF02694593](https://doi.org/10.1007/BF02694593)
- Fu, Y. H., Campioli, M., Deckmyn, G., & Janssens, I. A. (2012). The impact of winter and spring temperatures on temperate tree budburst dates: results from an experimental climate manipulation. *PLoS ONE, 7*(10), e47324. <https://doi.org/10.1371/journal.pone.0047324>
- Fuchigami, L. H., & Nee, C. (1987). Degree growth stage model and rest- breaking mechanisms in temperate woody perennials. *HortScience, 22*, 836–845.
- Fuertes-Rodríguez, C. R., González-Parrado, Z., Vega-Maray, A. M., Valencia-Barrera, R. M., & Fernández-González, D. (2007). Effect of air temperature on forecasting the start of *Cupressaceae* pollen type in Ponferrada (Leon, Spain). *Annals of Agricultural and Environmental Medicine, 14*, 237–242.
- Galán, C., Alcázar, P., Oteros, J., García-Mozo, H., Aira, M. J., Belmonte, J., Diaz de la Guardia, C., Fernández-González, D., Gutierrez-Bustillo, M., Moreno-Grau, S., Pérez-Badía, R., Rodríguez-Rajo, J., Ruiz-Valenzuela, L., Tormo, R., Trigo, M. M., & Domínguez-Vilches, E. (2016). Airborne pollen trends in the Iberian Peninsula. *Science of the Total Environment, 550*, 53–59. [https://doi.org/10.1016/j.scito](https://doi.org/10.1016/j.scitotenv.2016.01.069) [tenv.2016.01.069](https://doi.org/10.1016/j.scitotenv.2016.01.069)
- Galán, C., Cariñanos, P., Alcázar, P., & Domínguez-Vilches, E. (2007). *Spanish Aerobiology Network (REA): Management and quality manual* (p. 61). Servicio de publicaciones de la Universidad de Córdoba.
- Galán, C., Garcia-Mozo, H., Cariñanos, P., Alcazar, P., & Dominguez-Vilches, E. (2001). The role of temperature in the onset of the *Olea europaea* L. pollen season in southwestern Spain. *International Journal of Biometeorology, 45*, 8–12.
- Galán, C., García-Mozo, H., Vázquez, L., Ruiz Valenzuela, L., Díaz de la Guardia, C., & Trigo-Pérez, M. M. (2005). Heat requirements for the onset of the *Olea europaea* L. pollen season in several places of Andalusia region and the efect of the expected future climate change. *International Journal of Biometeorology, 49*, 184–188. [https://](https://doi.org/10.1007/s00484-004-0223-5) doi.org/10.1007/s00484-004-0223-5
- Galán, C., Smith, M., Thibaudon, M., Frenguelli, G., Oteros, J., Gehrig, R., Berger, U., Clot, B., Brandao, R., EAS QC Working Group. (2014). Pollen monitoring: minimum requirements and reproducibility of analysis. *Aerobiologia, 30*, 385–395. [https://doi.org/10.1007/](https://doi.org/10.1007/s10453-014-9335-5) [s10453-014-9335-5](https://doi.org/10.1007/s10453-014-9335-5)
- Garcia-Mozo, H., Galán, C., Aira, M. J., Belmonte, J., Diaz de la Guardia, C., Fernández, D., Gutierrez, A. M., Rodriguez, F. J., Trigo, M. M., & Dominguez-Vilches, E. (2002). Modelling start of oak pollen season in diferent climatic zones in Spain. *Agricultural and Forest Meteorology, 110*, 247–257. [https://doi.org/10.1016/S0168-](https://doi.org/10.1016/S0168-1923(02)00003-5) [1923\(02\)00003-5](https://doi.org/10.1016/S0168-1923(02)00003-5)
- Garcia-Mozo, H., Galán, C., Gomez-Casero, M. T., & Dominguez-Vilches, E. (2000). A comparative study of diferent temperature accumulation methods for predicting the start of the *Quercus* pollen season in Córdoba (South West Spain). *Grana, 39*, 149–199. [https://doi.org/10.1080/](https://doi.org/10.1080/00173130051084322) [00173130051084322](https://doi.org/10.1080/00173130051084322)
- Gehrig, R., & Clot, B. (2021). 50 years of pollen monitoring in Basel (Switzerland) demonstrate the infuence of climate change on airborne Pollen. *Frontiers Allergy, 2*, 677159. <https://doi.org/10.3389/falgy.2021.677159>
- Guo, L., Dai, J., Ranjitkar, S., Yu, H., Xu, J., & Luedeling, E. (2013). Chilling and heat requirements for fowering in temperate fruit trees. *International Journal of Biometeorology, 58*(6), 1195–1206. [https://doi.org/10.1007/](https://doi.org/10.1007/s00484-013-0714-3) [s00484-013-0714-3](https://doi.org/10.1007/s00484-013-0714-3)
- Guo, L., Dai, J. H., Wang, M. C., Xu, J. C., & Luedeling, E. (2015). Responses of spring phenology in temperate zone trees to climate warming: A case study of apricot fowering in China. *Agricultural and Forest Meteorology, 201*, 1–7. <https://doi.org/10.1016/j.agrformet.2014.10.016>
- Harrington, C. A., Gould, P. J. S., & Clair, J. B. (2010). Modeling the efects of winter environment on dormancy release of Douglas-fr. *Forest Ecology and Management, 259*, 798–808. [https://doi.org/10.1016/j.foreco.2009.06.](https://doi.org/10.1016/j.foreco.2009.06.018) [018](https://doi.org/10.1016/j.foreco.2009.06.018)
- Hirst, J. M. (1952). An automatic volumetric spore trap. *Annals of Applied Biology, 39*, 257–265.
- Horvath, D. P., Anderson, J. V., Chao, W. S., & Foley, M. E. (2003). Knowing when to grow: Signals regulating bud dormancy. *Trends in Plant Sciences, 8*(11), 534–540. <https://doi.org/10.1016/j.tplants.2003.09.013>
- Hoxha, E. (2007). Forecast models for the main features of the pollen season and daily average counts for allergenic taxa in central Albania. University of Coventry.
- Jacobs, J. N., Jacobs, G., & Cook, N. C. (2002). Chilling period infuences the progression of bud dormancy more than does chilling temperature in apple and pear shoots. *The Journal of Horticultural Science and Biotechnology, 77*, 333–339. [https://doi.org/10.1080/14620316.2002.11511](https://doi.org/10.1080/14620316.2002.11511502) [502](https://doi.org/10.1080/14620316.2002.11511502)
- Jato, V., Rodríguez-Rajo, J., Dacosta, N., & Aira, M. (2004). Heat and chill requirements of *Fraxinus* flowering in Galicia (NW Spain) heat and chill requirements of *Fraxinus* fowering in Galicia. *Grana, 43*(4), 217–223. [https://doi.](https://doi.org/10.1080/00173130410016274) [org/10.1080/00173130410016274](https://doi.org/10.1080/00173130410016274)
- Lang, G. A. (1987). Dormancy: A new universal terminology. *HortScience, 22*, 817–820.
- Laube, J., Sparks, T. H., Estrella, N., Höfers, J., Ankerst, D. P., & Menzel, A. (2013). Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology, 20*(1), 170–182. [https://doi.org/10.1111/](https://doi.org/10.1111/gcb.12360) [gcb.12360](https://doi.org/10.1111/gcb.12360)
- Legave, J. M., Blanke, M., Christen, D., Giovannini, D., Mathieu, V., & Oger, R. (2013). A comprehensive overview of the spatial and temporal variability of apple bud dormancy release and blooming phenology in Western Europe. *International Journal of Biometeorology, 57*, 317–331. <https://doi.org/10.1007/s00484-012-0551-9>
- Luedeling, E., & Gassner, A. (2012). Partial least squares regression for analyzing walnut phenology in California. *Agricultural and Forest Meteorology, 158–159*, 43–52. <https://doi.org/10.1016/j.agrformet.2011.10.020>
- Luedeling, E., Guo, L., Dai, J., Leslie, C., & Blanke, M. M. (2013a). Diferential responses of trees to temperature variation during the chilling and forcing phases. *Agricultural and Forest Meteorology, 181*, 33–42. [https://](https://doi.org/10.1016/j.agrformet.2013.06.018) doi.org/10.1016/j.agrformet.2013.06.018
- Luedeling, E., Kunz, A., & Blanke, M. M. (2013b). Identifcation of chilling and heat requirements of cherry trees-a statistical approach. *International Journal of Biometeorology, 57*, 679–689. [https://doi.org/10.1007/](https://doi.org/10.1007/s00484-012-0594-y) [s00484-012-0594-y](https://doi.org/10.1007/s00484-012-0594-y)
- Luedeling, E., Zhang, M. H., Luedeling, V., & Girvetz, E. H. (2009b). Sensitivity of winter chill models for fruit and nut trees to climatic changes expected in California's central Valley. *Agriculture, Ecosystems & Environment,*

133(1–2), 23–31. [https://doi.org/10.1016/j.agee.2009.](https://doi.org/10.1016/j.agee.2009.04.016) [04.016](https://doi.org/10.1016/j.agee.2009.04.016)

- Luedeling, E., Zhang, M., McGranahan, G., & Leslie, C. (2009a). Validation of winter chill models using historic records of walnut phenology. *Agricultural and Forest Meteorology, 149*, 1854–1864. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.agrformet.2009.06.013) [agrformet.2009.06.013](https://doi.org/10.1016/j.agrformet.2009.06.013)
- Menzel, A. (2002). Phenology: Its importance to the global change community. *Climatic Change, 54*, 379–385. <https://doi.org/10.1023/A:1016125215496>
- Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kubler, K., Bissoli, P., Braslavska, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, A., Defla, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., … Zust, A. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology, 12*, 1–8. [https://doi.](https://doi.org/10.1111/j.1365-2486.2006.01193.x15) [org/10.1111/j.1365-2486.2006.01193.x15](https://doi.org/10.1111/j.1365-2486.2006.01193.x15)
- Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifnger, H., Gehrig, R., & Estrella, N. (2020). Climate change fngerprints in recent European plant phenology. *Global Change Biology, 26*, 2599–2612. [https://doi.org/10.](https://doi.org/10.1111/gcb.15000) [1111/gcb.15000](https://doi.org/10.1111/gcb.15000)
- Morin, X., Roy, J., Sonié, L., & Chuine, I. (2010). Changes in leaf phenology of three European oak species in response to experimental climate change. *New Phytologist, 186*, 900–910. [https://doi.org/10.1111/j.1469-8137.](https://doi.org/10.1111/j.1469-8137.2010.03252.x) [2010.03252.x](https://doi.org/10.1111/j.1469-8137.2010.03252.x)
- Murray, M. B., Cannell, M. G. R., & Smith, R. I. (1989). Date of budburst of ffteen tree species in Britain following climatic warming. *Journal of Applied Ecology, 26*, 693–700.
- 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. *International Journal of Biometeorology, 46*, 2–8. <https://doi.org/10.1007/s00484-001-0108-9>
- Orlandi, F., Lanari, D., Romano, B., & Fornaciari, M. (2006). New model to predict the timing of olive (*Olea europaea*) fowering: A case study in central Italy. *New Zealand Journal of Crop and Horticultural Science, 34*, 93–99. <https://doi.org/10.1080/01140671.2006.9514392>
- Parkes, H., Darbyshire, R., & White, N. (2020). Chilling requirements of apple cultivars grown in mild Australian winter conditions. *Scientia Horticulturae, 260*, 108858. <https://doi.org/10.1016/j.scienta.2019.108858>
- Parmesan, C. (2007). Infuences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology, 13*, 1860–1872. [https://](https://doi.org/10.1111/j.1365-2486.2007.01404.x) doi.org/10.1111/j.1365-2486.2007.01404.x
- Pinney, K., & Polito, V. S. (1990). Olive pollen storage and in vitro germination. *Acta Horticulturae, 286*, 207–210. <https://doi.org/10.17660/ActaHortic.1990.286.42>
- Polgar, C. A., & Primack, R. B. (2011). Leaf-out phenology of temperate woody plants: From trees to ecosystems. *New Phytologist, 191*, 926–941. [https://doi.org/10.1111/j.1469-](https://doi.org/10.1111/j.1469-8137.2011.03803.x) [8137.2011.03803.x](https://doi.org/10.1111/j.1469-8137.2011.03803.x)
- Powell, L. E. (1987). Hormonal aspects of bud and seed dormancy in temperate-zone woody plants. *HortSciences, 22*, 845–850.
- Rahemi, M., & Pakkish, Z. (2009). Determination of chilling and heat requirements of Pistachio (*Pistacia vera* L.) cultivars. *Agricultural Sciences in China, 8*(7), 803–807. [https://doi.org/10.1016/S1671-2927\(08\)60281-3](https://doi.org/10.1016/S1671-2927(08)60281-3)
- Rallo, L., & Martin, G. C. (1991). The role of chilling in releasing olive foral buds from dormancy. *Journal of the American Society for Horticultural Science, 116*(6), 1058–1062.<https://doi.org/10.21273/JASHS.116.6.1058>
- Rea, R., & Eccel, E. (2006). Phenological models for blooming of apple in a mountainous region. *International Journal of Biometeorology, 51*, 1–16. [https://doi.org/10.1007/](https://doi.org/10.1007/s00484-006-0043-x) [s00484-006-0043-x](https://doi.org/10.1007/s00484-006-0043-x)
- Ring, D. R., Harris, M. K., Jackman, J. A., Henson, J. L. (1983). A Fortran computer program for determining start date and base temperature for degree-day models. The Texas Agricultural Experiment Station Bull MP-1537, The Texas University System, College Station, Texas
- Ríos, G., Leida, C., Conejero, A., & Badenes, M. L. (2014). Epigenetic regulation of bud dormancy events in perennial plants. *Frontiers in Plant Science, 5*, 1–6. [https://doi.org/](https://doi.org/10.3389/fpls.2014.00247) [10.3389/fpls.2014.00247](https://doi.org/10.3389/fpls.2014.00247)
- Rojo, J., Orlandi, F., Perez-Badia, R., Aguilera, F., Ben Dhiab, A., Bouziane, H., & Fornaciari, M. (2016). Modeling olive pollen intensity in the Mediterranean region through analysis of emission sources. *Science of Total Environment, 551–552*, 73–82. [https://doi.org/10.1016/j.scitotenv.](https://doi.org/10.1016/j.scitotenv.2016.01.193) [2016.01.193](https://doi.org/10.1016/j.scitotenv.2016.01.193)
- Ruiz, D., Campoy, J. A., & Egea, J. (2007). Chilling and heat requirements of apricot cultivars for fowering. *Environmental and Experimental Botany, 61*, 254–263. [https://](https://doi.org/10.1016/j.envexpbot.2007.06.008) doi.org/10.1016/j.envexpbot.2007.06.008
- Ruml, M., Vuković, A., & Milatović, D. (2010). Evaluation of diferent methods for determining growing degree-day thresholds in apricot cultivars. *International Journal of Biometeorology, 54*, 411–422. [https://doi.org/10.1007/](https://doi.org/10.1007/s00484-009-0292-6) [s00484-009-0292-6](https://doi.org/10.1007/s00484-009-0292-6)
- Sarvas, R. (1972). Investigations on annual cycle of development of forest trees Active Period. *Environmental Science, 76*, 1–110.
- Ščevková, J., Dušička, J., Hrabovský, M., & Vašková, Z. (2021). Trends in pollen season characteristics of Alnus, Poaceae and Artemisia allergenic taxa in Bratislava, central Europe. *Aerobiologia, 37*, 707–717. [https://doi.org/10.](https://doi.org/10.1007/s10453-021-09717-4) [1007/s10453-021-09717-4](https://doi.org/10.1007/s10453-021-09717-4)
- Schwartz, M. D., & Hanes, J. M. (2010). Continental-scale phenology: Warming and chilling. *International Journal of Climatology, 30*(11), 1595–1598. [https://doi.org/10.](https://doi.org/10.1002/joc.2014) [1002/joc.2014](https://doi.org/10.1002/joc.2014)
- Spano, D., Cesaraccio, C., Duce, P., & Snyder, R. L. (1999). Phenological stages of natural species and their use as climate indicators. *International Journal of Biometeorology, 42*, 124–133. <https://doi.org/10.1007/s004840050095>
- Sparks, D. (1993). Chilling and heating model for pecan budbreak. *Journal of the American Society for Horticultural Science, 118*(1), 29–35. [https://doi.org/10.21273/JASHS.](https://doi.org/10.21273/JASHS.118.1.29) [118.1.29](https://doi.org/10.21273/JASHS.118.1.29)
- Tao, F., Yokozawa, M., Xu, Y., Hayashi, Y., & Zhang, Z. (2006). Climate changes and trends in phenology and yields of feld crops in China, 1981–2000. *Agricultural and Forest Meteorology, 138*, 82–92. [https://doi.org/10.](https://doi.org/10.1016/j.agrformet.2006.03.014) [1016/j.agrformet.2006.03.014](https://doi.org/10.1016/j.agrformet.2006.03.014)
- Vitasse, Y., & Basler, D. (2013). What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research, 132*, 1–8. [https://doi.org/10.](https://doi.org/10.1007/s10342-012-0661-2) [1007/s10342-012-0661-2](https://doi.org/10.1007/s10342-012-0661-2)
- Vitasse, Y., Bresson, C. C., Kremer, A., Michalet, R., & Delzon, S. (2010). Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology, 24*, 1211–1218. [https://doi.org/10.1111/j.1365-2435.](https://doi.org/10.1111/j.1365-2435.2010.01748.x) [2010.01748.x](https://doi.org/10.1111/j.1365-2435.2010.01748.x)
- Vitra, A., Lenz, A., & Vitasse, Y. (2017). Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist, 216*(1), 113–123. [https://doi.](https://doi.org/10.1111/nph.14698) [org/10.1111/nph.14698](https://doi.org/10.1111/nph.14698)
- Wareing, P. F. (1953). Growth studies in woody species. V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiologia Plantarum, 6*, 692–706. [https://doi.org/10.](https://doi.org/10.1111/j.1399-3054.1953.tb08442.x) [1111/j.1399-3054.1953.tb08442.x](https://doi.org/10.1111/j.1399-3054.1953.tb08442.x)
- Xu, Y., Dai, J., Ge, Q., Wang, H., & Tao, Z. (2020). Comparison of chilling and heat requirements for leaf unfolding in deciduous woody species in temperate and subtropical China. *International Journal of Biometeorology*. [https://](https://doi.org/10.1007/s00484-020-02007-7) doi.org/10.1007/s00484-020-02007-7
- Zhang, J., & Taylor, C. (2011). The dynamic model provides the best description of the chill process on "Sirora"

Pistachio trees in Australia. *HortScience, 46*, 420–425. <https://doi.org/10.21273/HORTSCI.46.3.420>

- Zhuang, W. B., Cai, B. H., Gao, Z. H., & Zhang, Z. (2016). Determination of chilling and heat requirements of 69 Japanese apricot cultivars. *European Journal of Agronomy, 74*, 68–74.<https://doi.org/10.1016/j.eja.2015.10.006>
- Ziska, L. H., Makra, L., Harry, S. K., Brufaerts, N., Hendrickx, M., Coates, F., Annika, S., Thibaudon, M., Oliver, G., Damialis, A., Charalampopoulos, A., Vokou, D., Heiđmarsson, S., Guđjohnsen, E., Bonini, M., Oh, J.-W., Sullivan, K., Ford, L., Brooks, G. D., … Crimmins, A. R. (2019). Temperature-related changes in airborne allergenic pollen abundance and seasonality across the northern hemisphere: A retrospective data analysis. *Lancet Planet Health, 3*, e124–e131. [https://doi.org/10.1016/](https://doi.org/10.1016/S2542-5196(19)30015-4) [S2542-5196\(19\)30015-4](https://doi.org/10.1016/S2542-5196(19)30015-4)

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.