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Estimating Heat Requirement for Flowering in Peach Germplasm

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Abstract: Bloom date (BD) in peach is determined by the dynamic relationship between chilling (CR) and heat requirement (HR) fulfillment during dormancy. Understanding these thermal requirements would enable breeders to adapt new cultivars to variable climates. Among the three traits, HR is the least investigated, with the genetic variability in peach germplasm and interaction between HR, CR and BD still mostly unknown. Therefore, we investigated the HR of 136 peach cultivars over 8 growing seasons (2014–2021) by calculating the growing degree hours (GDH) from the moment their CR was satisfied until full bloom. The HR ranged from 1362 to 10,348 GDH across years and cultivars, with cultivar HR eight-year having the best linear unbiased prediction (BLUP) values from 4808 to 7721 GDH. In addition, a high positive correlation between BD and CR, a negative correlation between CR and HR and a seasonal effect on the correlation between BD and HR were observed. Moreover, simulating HR with different threshold base temperatures (Tb) revealed different trends of GDH accumulation, suggesting that genotype-specific Tb should be determined to allow precise discrimination of this requirement. Peach germplasm showed high variation in HR that could be used in breeding for bloom delay to adapt to different environments and climate change.

Keywords: Prunus persica (L.) Batsch; bloom date; growing degree hour; climate change; dormancy; breeding

1. Introduction

Temperate fruit trees are adapted to climate zones that experience four well-defined seasons, which is required for dormancy and the growth and fruiting periods [1]. Prunus crops all share a common adaptation to temperate climates. Trees have evolved to lose their leaves and go dormant during the winter. Then, once the trees have experienced sufficient chilling temperatures, they are released from dormancy and start growing and flowering in response to warm temperatures [2]. Increasingly warmer winters, as well as weather patterns with more severe winter and spring temperature fluctuations, disrupt this normal pattern. Warmer winters can cause trees to bloom prematurely and expose their flowers or fruitlets to lethal freezing temperatures. Bloom date (BD) is an important agronomic trait in peach (Prunus persica (L.) Batsch) that takes place after a dormant period during the late autumn and winter, in which meristem growth is inhibited to ensure flowering under favorable environmental conditions [3]. This period, named dormancy, is divided into two main stages, endodormancy and ecodormancy, and describes the temporary suspension in the apparent development of any plant tissue having meristem to prevent damages caused by freezing temperatures [4]. The first stage, endodormancy, also called true dormancy, refers to meristem growth inhibition and exposure to low temperatures to resume growth [5]. The last stage of dormancy, ecodormancy, leads to flowering after exposure to mild or warm temperatures. These periods of cold and warm temperature accumulation are the denominated chilling (CR) and heat (HR) requirements, respectively,
and are essential for dormancy release [6], as the timing of flowering in *Prunus* species is defined by the successful sequential fulfillment of both thermal requirements and have been observed to be controlled by environmental conditions, mainly temperatures, and genetic factors [7–11]. Even though both CR and HR are critical for flowering, and negative correlations were reported between them [12–15], several studies on *Prunus* crops revealed CR as major determinant of BD [14,16,17]. However, in some almond and peach genotypes from warm regions of Spain and Mexico, respectively, the BD was more influenced by HR than CR [18,19].

Even though both CR and HR are reported to have an impact on BD variations [2,7,9,10,20,21], most of the studies in peach have focused on CR investigation rather than HR [21–26]. In fact, only one model to calculate HR [27] is available in comparison to numerous models available for CR calculation [28–30]. The method developed by Richardson et al. [27] and further improved by Anderson et al. [31] is based on a linear model that counts the daily heat unit accumulation from a threshold base temperature (Tb) that must be accumulated from the point chilling fulfillment is satisfied until reaching the developmental degree of bud break [27]. This requirement is expressed as growing degree hours (GDH), and it is described as 1 hour at a temperature of 1 °C above the Tb of 4.4 °C, in which all temperatures above 25 °C are assumed to be equal to 25 °C, with 20.5 GDH as the largest 1-hour accumulation [27]. This model was initially used to estimate phenological stages and later to predict BD based on CR [32,33]. It also assumes that all peach cultivars start counting heat at the same Tb of 4.4 °C. However, due to the lack of an easy and straightforward method to distinguish between endo- and ecodormancy stages, the absence of weather data in target environments, difficulty in methodological implementation and lower influence of HR over BD than CR caused this model to receive less attention than CR models from field experiments [34]. Nevertheless, this model was used in various *Prunus* species to calculate HR. In peach, a wide range of HR was reported (2000–16,500 GDH), with nectarine cultivars displaying values between 5800 and 9300 GDH [12,35–41]. In other *Prunus* species, a narrower interval of HR than peach has been observed with GDH ranging from 2900–10,200 in almond [17,42–44], 485–6000 in apricot [45–47], 1000–1700 in Japanese apricot [48] and 3500–16,000 in sweet cherry [49,50]. In addition, differences in location and environmental conditions affecting the HR have also been observed [51].

Climate fluctuation and warming trends [52] pose a threat to the peach production, as crop losses up to 50% can be experienced when temperatures fall below −3 °C (27 °F) for 30 min during bud development, but the temperature threshold can decrease to −2 °C (28 °F) during petal fall [53]. Therefore, global warming has been identified as an important factor threatening the sustainability of peach production in the upcoming decades, as several studies suggested rising temperatures having critical effect on transitions between dormancy stages and thus BD [54–56]. Under this new climatic scenario, early blooming genotypes are more vulnerable to late frost damage [57,58], while late-blooming cultivars may experience uneven floral growth and poor fruit set due to the lack of amount and quality of chill accumulation [59,60]. Peach breeders need to address both thermal traits (CR and HR) simultaneously to ensure CR will be satisfied and bloom delayed to avoid detrimental low temperatures in late spring [12]. Thus, diversity in these two temperature requirements in peach germplasm is needed for breeding to successfully address adaptation to climate change. When peach cultivar is released/patented in its description CR and bloom time is reported [61] (www.uspto.gov (accessed on 3 February 2022)), it will potentially allow an estimation of the HR. A wide range of CRs exist in peach germplasm, (>150–1390 chill hours (CHs)) [22,62,63], with a trend towards moderate chilling in the cultivars released within the last decade [64]. The HR, however, remains unknown. Nevertheless, recently, Bielenberg and Gasic [12] reported large differences in thermal time requirement in bi-parental peach progeny and suggested that breeding for increased thermal time is a viable strategy for bloom delay and avoiding exposure to potential crop-destroying frosts. Thus, we investigated the HR in peach germplasm, the interaction of CR and HR in relation to BD
and the influence of different climatic conditions to these traits in the U.S. peach germplasm over eight years (2014–2021).

2. Materials and Methods

2.1. Plant Material

A total of 123 peach cultivars from the U.S. peach breeding germplasm reference set [65] and 13 advanced selections from Clemson University peach breeding program were included in this study (Table S1). All this material was grown at the Clemson University Musser Fruit Research Center (Latitude: 34.639038, Longitude: −82.935244) under warm, humid, temperate climate and standard commercial practices for irrigation, fertilization and pest and disease control. The trees were at least five years old, grafted on Guardian® rootstock, grown in triplicate, with 2 × 6 m spacing and either ‘perpendicular V’ (germplasm) or ‘open center’ (advanced selections) training systems.

2.2. Phenotyping

Bloom date (BD) was collected during eight consecutive years (2014 to 2021). The BD was recorded when 90% of flowers buds were fully open [38], and data were expressed as Julian Days (JD; days from 1 January). The available record for 90% BD ranged from 2–8 years per accession, or 15–79% per year. Based on the BD of the germplasm included in this study, we grouped accessions to 5 BD groups: very early (60 to 65 JD; 1–6 March), early (66 to 70 JD; 7–11 March), mid-season (71 to 75 JD; 12–16 March), late (76 and 78 JD; 17–19 March), and very late (79 to 80 JD; 20–21 March).

Chilling requirement (CR) from each accession was obtained from literature [9,21,62,66,67], and the day of the year that each accession completed its CR were estimated by calculating the sum of chill hours (CHs) using the model developed by Weinberger [30]:

\[ CH = \sum CHs (T > 7.2 \, ^\circ C, \, CHs = 0, \, T \leq 7.2 \, ^\circ C, \, CHs = 1), \]  

where \( T = \) temperature; \( CH = \) chill hour; \( ^\circ C = \) degree Celsius. This method was chosen because it was assumed that the chilling requirement reported for peach material used in this study is estimated as simple chill hour accumulation below 7.2 °C. CH accumulation was recorded from 1 November, as one CH under 7.2 °C in 1 h, until the fulfilment of CR. The hourly historical temperature data between 1 November and 1 April from 2014 to 2021 was obtained from the weather station at Musser Fruit Research Center, and missing data were replaced using linear regression imputation from the Weather Underground Website (https://www.wunderground.com/ (accessed on 5 May 2021)).

The CR for peach cultivars reported in the literature and cultivar descriptions as chill hours is determined using the simplest model [30] either by forcing shoots in the greenhouse or comparison of the bloom date with the cultivar with known CR and bloom date [66]. Based on the CR of the germplasm included in this study, we classified peach accessions into 6 different CR groups: low (501–650 CH), low-medium (651–700 CH), medium (701–800 CH), medium-high (801–850 CH), high (851–1000 CH) and very high (>1000 CH) (Tables S1 and S5).

Heat requirement (HR) was calculated for each accession and year (2014 to 2021) as the accumulation of GDH from the day of CR fulfilment until 90% full bloom using the model described by Richardson et al. [27]. In addition to the base temperature (Tb) of 4.5 °C estimated for tart cherry cultivar Montmorency by Richardson et al. [27] and used as a standard in GDH calculations, we calculated GDH using 2 additional Tbs, 2 degrees lower (2.5) and higher (6.5) than the standard. Temperatures above 25 °C were marked as 20.5 GDH for the 3 Tb models, and no GDH accumulation were considered when temperatures were below the Tb of each model.

2.3. Statistical Analyses

Descriptive statistical analyses were conducted to estimate yearly mean, minimum, maximum and standard deviation for BD and HR. The best linear unbiased prediction
(BLUP) values of BD, HR and CR satisfaction point (in Julian Days) per accession were obtained using a mixed effect model. The BLUP was chosen instead of a standard arithmetic mean because of unbalanced annual BD and consequently HR data available for the study. In our case, the annual mean (BD, HR) was used as a random effect to adjust the overall mean of the trait of each accession across all years. For subsequent further studies, the distribution of BD and HR values was evaluated for normality with the Shapiro–Wilk test. The Pearson correlation coefficient ($p < 0.001$) was calculated to identify linear association among traits, years and BLUP values.

The effect of CR and HR on BD were evaluated based on the following multiple regression model:

$$BD = \beta_0 + \beta_1 CR + \beta_2 HR,$$

where $\beta_0$ = intercept; $\beta_1$ = CR effect on BD; $\beta_2$ = HR effect on BD. Analysis of variance (ANOVA) was used to test the significance of the CR and HR coefficients. To assess differences between the coefficients of CR and HR for BD, all data were transformed into standard deviation units ($z$-scores) from their original scale/metric, and a $t$-test was used to compare the coefficients.

All statistical calculations were performed using JMP 16 Pro (https://www.jmp.com/; accessed on 4 June 2021)) and SPSS 27.0 (Armonk, NY, USA; IBM Corp.), and $p$-values $< 0.05$ were considered evidence of statistical significance.

3. Results
3.1. Bloom Date and Chilling Requirement

Phenotyping data for BD and CR, evaluated in the peach germplasm across eight years (2014 to 2021), per accession and across whole germplasm are shown in Tables S1 and S2, respectively. Overall, across experimental years, peach germplasm BD BLUP values ranged from 62–80 Julian Days (JD), with an average BD of 73 JD and a difference between the start and end of bloom of about 3 weeks (Figure 1, Table S2). Two advanced selections, SC-2 and SC-10, had the earliest BD (62 JD), whereas ‘Sweet September’ and ‘Tra-Zee’ were the latest with BLUP BDs of 80 JD (Table S1). A clear skewness to mid-season and late-season blooming was observed in this material, with only 4 (3%) and 22 (16%) accessions showing very early (60 to 65 JD; 1–6 March) and early blooming (66 to 70 JD; 7–11 March), respectively. Moreover, 85 (62.5%) accessions exhibited mid-season flowering (71 to 75 JD; 12–16 March), while 19 (14%) bloomed late (76 and 78 JD; 17–19 March), and only 6 (4.5%) had very late BDs (79 to 80 JD; 20–21 March) (Figure 1; Table S1). A similar accession bloom order within years of the study was observed in this germplasm, although inter-annual differences in the beginning and at the end of the bloom season were noted (Table S2). Analyzing BD across all years of the study, revealed the earliest mean BD (62 JD) in 2018, which was 10–11 days earlier than the 8-year average BD, and only 4 and 3 days earlier than the BDs observed in 2017 and 2019, respectively (Figure 1; Table S2). However, the latest mean BD of 80 JD (Table S2), observed in 2015, was 7 days later than the 8-year mean BLUP BD and only 5 and 2 days delayed from bloom in 2014 and 2021, respectively (Figure 1; Table S2). In addition, variation in the BD intervals between years was also observed, with BD intervals larger than 20 days and not exceeding 11 days recorded in 4 (2014, 2017, 2018 and 2020) and 2 years (2015 and 2021), respectively (Figure 1; Table S2).
BLUP BD distribution exhibited a unimodal non-normal distribution based on the Shapiro–Wilk test (Prob < W: 0.9748–0.0129) and a clear skewed distribution towards medium and late blooming (Figure S1), where only a few cultivars had extra-early or early blooming (60 to 70 JD). Similarly, non-normal distributions were observed for the individual years (Figure S1), with 2017, 2018 and 2019 following a bi-modal distribution and a shift towards early blooming, while 2015, 2016 and 2021 showed a slight transition towards late BD (Figure S1).

The CR of the peach germplasm included in the study ranged from 516 to 1116 CHs (Table S1), with 18 accessions considered low chill, 6 low-medium, 57 medium, 24 medium-high, 24 high and 7 very high chill (Tables S1 and S5). Using CR to establish an accurate starting point for estimating GDH accumulation for each accession revealed the earliest starting point of the eight-year BLUP GDH accumulation on 2 January (SC-10 and SC-13) and the latest on 21 February (SC-6) (Figure 2). However, annual differences in the fulfilment of CR and beginning of HR were also observed (Figure S2). In 3 seasons (2015/16, 2016/17 and 2019/20), low chilling accumulation occurred with less than 1000 CH fulfilment by 15 February, while in 5 seasons (2013/14, 2014/15, 2017/18, 2018/19 and 2020/21), a 1000 CH was accumulated 2 weeks in advance (1 February; Figure S2).

**Figure 1.** Bloom date (blue), expressed in Julian days (JD), and heat requirement (orange), expressed in growing degree hours (GDH), in the U.S. peach germplasm across eight years (2014–2021). Best Linear Unbiased Prediction (BLUP) values (A) and annual (B) data were calculated using standard base temperature of 4.5 °C. The bold line within the boxplot indicates the median value. The whiskers designate variability outside the 25th and 75th percentile, respectively. Dots indicate outliers.
Figure 2. Chilling (Blue; from 1 November) and heat requirement (Orange; from the day of chilling fulfillment until 90% of full bloom) intervals observed in the U.S. peach germplasm. Ranges of chilling requirements (CR) are indicated on the left. Heat requirement (HR) is expressed in growing degree hours (GDH) calculated using standard base temperature of 4.5 °C. Data represent the best linear unbiased prediction (BLUP) values for CR and HR across eight years (2014–2021).

3.2. Heat Requirement

The year-specific HR for each accession, calculated from the point when their individual CR was satisfied for each experimental year using three different Tb (2.5, 4.5 and 6.5 °C), and eight-year BLUP GDH accumulation are shown in Table S1. Overall, under the standard Tb of 4.5 °C, the HR (from CR fulfillment to 90% of full bloom) ranged from 4808 (SC-7) to 7721 GDH (‘Glowingstar’), with an average value of 6444 GDH (Table S1; Figure 1). Most accessions (N = 104) accumulated from 6000–7000 GDH (Figure 1), and only breeding line SC-7 exhibited a BLUP HR below 5000 GDH (Table S1). Low to medium GDH accumulation (5000–6000) was observed in 18 accessions, and 15 accumulated between 7000 and 8000 GDH (Figure 1; Table S1).

Differences among annual GDH accumulation were present, with seasons with only 1362 (2020; SC-07) and 1547 (2017; ‘Augustprince’) GDH needed to fulfill the HR, which
contrasted the minimum HR of 5414 GDH observed in 2015 for ‘Galaxy’ (Table S1). The analysis of HR accumulation intervals revealed similar values between years, especially in 2014, 2015, 2016, 2018 and 2021 (~5000–8500 GDH; Table S2, Figure 1B). Interestingly, a wide interval between cultivars with the lowest and highest HR was observed in 2017 (from 1547–9670 GDH; Table S2, Figure 1B). A similar trend was detected in 2020, where the broadest interval of HR accumulation was observed (1362 to 9761 GDH) and was mostly due to three accessions (SC-7, SC-4 and SC-3; Table S1) from the Clemson University breeding program that had HR lower than 4000 GDH this year, while in the majority of accessions, HR ranged from 6000–10,000 GDH (Figure 1B).

The normality test showed eight-year BLUP HR values (Shapiro–Wilk test; Prob W: 0.9858–0.1738) and annual HR values in three years, 2015, 2018 and 2019, (Shapiro–Wilk test; Prob W: 0.9911–0.7148; Prob W: 0.9357–0.1616; Prob W: 0.9707–0.7493, respectively) following a normal distribution (Figure S3). In 2020 and 2021, a non-normal distribution with a clear shift to high GDH was observed, while a skewed distribution towards low GDH accumulation was detected in 2016 (Figure S3).

3.3. Trait Correlations and CR and HR Effect on BD

Different patterns of interaction between BD, CR and HR were observed in the evaluated plant material (Table S3). When eight-year BLUP values were used, no significant correlation between HR and BD (r = 0.018; Figure 3), moderate correlation between BD and CR (r = 0.564; Figure 3) and a significant negative correlation between HR and CR (r = −0.664; Figure 3) were observed in this plant material.

![Figure 3](https://example.com/figure3.png)

**Figure 3.** Correlation between bloom date (BD), heat requirement (HR) and chill requirement (CR) in the U.S. peach germplasm using the best linear unbiased prediction (BLUP) values of eight analyzed years (2014–2021). Asterisks indicate Pearson correlation coefficient at significance level of p < 0.01 (**).

Moderate to high significant correlations between annual BD (r = 0.454 to 0.846) was observed among all years except 2018 and 2019 (Table S3). Similarly for HR, low to moderate positive correlations (r = 0.317 to 0.778) were observed between annual HR, with the exception of 2018 and 2019. Regarding the annual interaction between traits, significant positive correlation was observed between BD and CR (r = 0.476 to 0.720; Table S3) and a negative correlation was observed between HR and CR across eight years (r = −0.195.
to −0.787; Table S3), with exception for the HR/CR correlation in 2014. For HR and BD, different patterns of correlations were reported with significant positive correlations observed in four years, 2014–2016 and 2021, and no correlation in the 2017–2020 seasons (Table S3).

Additionally, the analysis of significance and differences in the mean phenotypic effects of CR and HR on BD (Table S4) revealed that HR and CR significantly affected BD in all years (p < 0.0001; Table S4), except in 2017, when only HR had a significant statistical effect on BD (p-value: 0.0032; Table S4). Moreover, the transformed BD, CR and HR data (z-scores) manifested a lack of statistical evidence to support either CR or HR having a higher effect on BD (Table S4). However, there is statistical evidence that the mean phenotypic effect of CR was more important for BD than HR in 2016 (p-value = 0.0099; Table S4).

3.4. Simulating HR Using Different Base Temperatures

Influence of Tb on the overall HR accumulation, estimated using Tb two degrees lower (2.5) and higher (6.5) than standard (4.5) (Tables S1 and S2), revealed a shift in the eight-year BLUP HR range from 4808 to 7721 GDH, with Tb = 4.5 °C, to wider (5811–9891 GDH) and narrower (3814–5539 GDH) intervals obtained with a Tb of 2.5 and 6.5 °C, respectively (Tables S1 and S2; Figure 4). On average, 1670 GDH increases or reductions in HR were predicted when Tbs of 2.5 and 6.5 °C were used, respectively (Tables S1 and S2). However, the rate of change in GDH was not the same in the low and high HR accessions. Low HR accessions needed more than 1000 additional GDH to bloom when a Tb of 2.5 °C was assumed, while cultivars with high HR needed up to 2170 GDH (Table S1). The opposite trend was observed for a Tb of 6.5 °C, with low HR cultivars requiring 1000 and high HR cultivars 2180 fewer GDH for bloom than under the standard model (Table S1; Figure 4).

Figure 4. Heat requirement distribution [histogram (A) and dot plot (B)] in the U.S. peach germplasm under 2.5 (orange), 4.5 (black) and 6.5 (blue) °C base temperature (Tb) in Richardson’s model. Data represent the best linear unbiased prediction (BLUP) values for growing degree hours (GDH) across eight years (2014–2021).
Similarly, differences in annual HR (GDH) mean values were observed under different Tb, especially for those accessions with low BLUP HR (Tables S1 and S2). Interestingly, in the seasons with warm winters, such as 2016/17 and 2019/20 (Figure S2), the accumulation of GDH in low HR accessions was remarkably similar under all three Tb (1100–1900 GDH; Table S2). However, noticeable differences were observed in cold winters, such as 2015 (Table S2), with the 5221 and 2386 GDH needed for bloom in low HR accessions under 2.5 and 6.5 °C Tb, respectively (Table S2). Accessions with high HR had these annual differences less pronounced (Tables S1 and S2).

4. Discussion

4.1. Heat Requirement Variation in the Germplasm

In this study, we estimated HR diversity in a large set of U.S. peach germplasm with a goal to determine the best approach and if observed diversity could be used in breeding to counter climate change. The observed HR interval of 1362 to 10,348 GDH is considerably wider than previously reported in studies evaluating fewer peach cultivars (3476 to 7463 GDH) [35,36,38–41] and is within the range (2000 to 16,500 GDH) reported when a larger number of cultivars were considered [12,37]. However, discrepancies in the HRs observed in this study and those previously reported for the same accessions were observed. For example, Richardson et al. [29] estimated 5110 and 4922 GDH for ‘Elberta’ and ‘Redhaven’, respectively, while our results suggested 6687 and 5941 GDH for these same cultivars. Similarly, Maulión et al. [37] reported 8488 and 7415 GDH for ‘Fireprince’ and ‘Gala’, respectively, that, in our study, were estimated to have ~2000 GDH less HR. Some of these discrepancies could be explained by the use of different models to determine the fulfillment of CR in different studies, as a variation of up to 1800 GDH was observed for the same cultivar and year when chilling hours, chilling units, positive chilling units and dynamic models were used to determine CR fulfillment [37]. Thus, despite the moderate correlation of HR between years (r = 0.317 to 0.778), variation of up to 5500 GDH for the same accessions (e.g., ‘Redglobe’, ‘September Sun’, ‘Sunprince’ and ‘Julyprince’) in different environmental years was observed. This observation supports the complexity of temperature-associated traits where the dynamics between CR, HR and BD is influenced by the temperature in addition to other factors such as location, agroclimatic requirement or the accuracy of the chill model [34,37,68].

4.2. Correlations between Dormancy-Related Traits

BD depends on CR and HR accumulation during dormancy period [5], so understanding the interaction between these three traits is essential to address breeding goals related to flowering. However, the impact of HR on BD is not uniform within germplasm, which complicates the implementation of common breeding strategies. In this study, HR was not correlated with BD, as was also observed in an F2 peach population [9] and 54 peach accessions [12]. Nevertheless, positive correlation between HR and BD was reported for 15 peach cultivars, including 10 Korean and 5 North American cultivars [36]. This same positive correlation was also observed in other species such as almond [8,42,43], sweet cherry [20] and apricot [10], suggesting a complex interaction between plant materials and environmental conditions affecting the correlation of these traits. However, it is interesting that the lack of correlation between HR and BD was only found in peach from three independent studies that included different plant material grown in the same experimental area (Seneca, SC, USA) [9,12] and this study. Moreover, Ruiz, et al. [14] and Alonso, et al. [42] concluded that the relationship between BD and HR might be determined by local climatic conditions and how cultivars accumulate chilling during winter and spring, which could explain absence of correlation between BD and HR in this study. In addition, the method used to determine the individual accessions CR might also influence results in this study. The CR data obtained from the literature are obtained either by (i) forcing bloom after a known quantities of chilling by periodically bringing shoots inside and observing percentage of open flowers after two weeks or (ii) simply by comparing an accession’s
bloom date with the bloom date of an accession with a known CR [66]. We have no way of knowing how the reported CR in the literature and cultivar registrations (e.g., patenting) is obtained, which might introduce error, as an estimation by comparison does not take into the account heat accumulation differences between the accessions. In our study, the CR of the breeding material from the Clemson University peach breeding program is obtained by forcing. This further emphasizes the need to require breeders to report CR as chill portions when registering new cultivars, as previously suggested [12].

In case of BD and CR, our study revealed positive correlation between these two traits as previously reported in peach [9,36,37] and other Prunus species such as sweet cherry, almond and apricot [7,10,11], which supports the significant influence of CR over BD [7,9,16,69]. However, the negative correlation between CR and HR observed in our study, which is also reported in apricot, Asian plum and ornamental peach [12–15], agrees with the fact that low CR cultivars need higher amounts of HR to reach BD and vice versa. However, the report in which this pattern of correlation was less pronounced or absent and genetic analyses of CR and HR where different genetic controls for these traits were found for some individuals [9,70,71] shows the potential for breeding for HR independently of CR. This was evident in certain cultivars analyzed in this study that have similar CR but large differences in HR accumulations, such as ‘Goldcrest’ and ‘Snow Queen’ (650 CR) or ‘SC-1’ and ‘Tra-Zee’ (800 CR), exhibiting differences of up to two weeks in the BLUP HR (Figure 2).

4.3. HR and BD in Response to Annual Environmental Conditions

Currently, global warming has proven to alter BD, affecting fruit crop productions [72]. Thus, the investigation of HR and CR variability in the peach germplasm and understanding variations in these traits as consequences of diverse trends in registered temperature within years is necessary to adapt flowering times to the rising temperatures. In peach, a narrow interval of BD was reported, between 10 to 18 days depending on locations and climatic years, with a clear trend towards late BD, which was also observed in this study of the U.S. peach breeding germplasm [66,70,71,73,74]. This is also in agreement with the skewed distribution to high CR observed by Demirel, et al. [22] and explained by the dominant effect of late blooming alleles, as observed in almond and sweet cherry cultivars [75,76]. Furthermore, most of the newly released cultivars over the past decades originated from breeding programs in which late flowering was considered a key breeding trait to avoid late frosts [70,77]. However, we observed different patterns of BD segregation across years in this study, with cold and warmer years having different effect on flowering distribution. Similarly, Guo, et al. [78] proposed that the chill period in warmer years strongly influences the bloom time while in colder years the heat period is the main factor in determining flowering. Thus, the statistical significance of CR and HR on BD found in the eight years of this study further supports importance of these periods on BD in this study. For example, although the earliest satisfaction of CR was fulfilled in 2014, this year had a late start of flowering because cold temperatures during heat accumulation delayed flowering, whereas, in 2016, the year in which cultivars needed more time to fulfill their CR, the flowering start was only delayed for four days. This suggests that despite the lack of correlation between HR and BD and the high correlation between BD and CR, the quality and manner of both CR and HR accumulation are essential to modulate BD.

The eight-year BLUP HR accumulation, as observed in this study, tended to be skewed to high GDH, as was earlier reported in peach [36,37]. The influence of chilling accumulation on the amount of heat accumulation required for bloom was noticed almost 100 years ago [79], and the exponential curvilinear relationship between chilling and heat requirement and differences in CR among the buds on a tree can explain bloom start and duration manifested in different climates. This effect was observed in the 2016/17 and 2019/20 seasons that corresponded to warm temperatures during the period of chilling accumulation (Figure S2), which increased the HR accumulation (around 10,000 GDH) needed for bud break. In contrast, in the 2013/14 and 2014/15, seasons with normal
winter temperatures, a lower HR (around 7500 GDH) was observed. Several other studies observed this strong relationship and noted the effect of the different timing of chilling fulfilment on heat accumulation [78,80,81]. Therefore, although BD was not significantly correlated with HR in this study, an interaction between HR and CR periods, reported before [69] was observed. Thus, in warm years, the heat accumulation starts before the fulfilment of CR, as cultivars with only 50% of chilling fulfilment were observed to reach flowering [82,83], which highlights the importance of HR during warm seasons such as 2016/17 and reinforces the higher influence of HR than CR on BD in warm climates [18,19] or years with warm winters, as observed in this study (Table S4). Okie and Blackburn [34] suggested that "bloom time is a function of the chilling status of the bud and the amount and timing of heat accumulated", and that once the critical chill has been accumulated, bud break timing will depend on the relative proportions of chilling and heat that occur.

4.4. Modeling Heat Requirement

In the current model for estimating heat accumulation, a base temperature threshold (Tb) of 4.4 °C, determined in 1980s for tart cherry ‘Montmorency’, is assumed for the start of heat accumulation [27,31]. However, the Tb at which each individual accession starts to accumulate heat remains unclear [12,84] and questions the appropriateness of this Tb for all crops and weather conditions. For example, Bielenberg and Gasic [12] reported base temperatures of −1.85, −0.5, 0.9 and 4.34 °C in 4 peach cultivars, Elberta, Hakuho, Junegold and UFGold, respectively, as well as Tb ranging from −1.15 to 8.68 °C in segregating progeny. Therefore, we estimated the heat accumulation variation in peach germplasm over eight years using a Tb two degrees lower or higher than the standard. The lower Tb (2.5 °C) resulted in a wider range of eight-year BLUP GDH, allowing a better discrimination of HR, especially in those cultivars with intermediate values of heat accumulation (Figure 4). In addition, the overall increase or reduction in the GDH needed to bloom under different Tbs in low vs. high HR accessions was observed. The increase or decrease in GDH in high-HR accessions was around twice the value of the difference observed in low-HR accessions, under the lower and higher Tb, respectively. Thus, additional studies are needed to determine if the standard Tb should be revisited in different crops [12].

HR modeling has assumed a linear relationship between the development rate and temperature, even though the studies showed curvilinear relationship on temperature-driven plant development [85,86]. Because of the causal relationship among dormancy-associated traits, future modeling should address the transitional phase between the chilling and forcing period, as well as the negative effect of extremely high or low temperatures. Recently, Luedeling, et al. [87] proposed an integrated model, PhenoFlex, to predict spring phenology in temperate fruit by combining Dynamic Model for chill accumulation with the GDH model for heat accumulation via flexible transition. Similar to this, many other phenological models, with different levels of complexity that are based on the correlation between the plant responses to environmental cues are available [88]. As an alternative, process-based models were recently proposed as a more robust option to predict tree responses to future climate scenarios [89]. To be able to utilize these advanced models, we need a better understanding of the biology behind the HR and the transition between the endo- and eco-dormancy stages in temperate fruits. Further studies are needed to properly characterize HR, as well as improved methodologies for establishing the end of an endo-dormancy and more accurate models to quantify the effect of temperatures on phenology.

The information provided in this study contributes towards further understanding of genetic background and inheritance of HR in peach that could lead to the development of new peach cultivars with adaptive plasticity to environmental change.
Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy12051002/s1, Figure S1: BLUP and annual (2014–2021) bloom date (BD) distributions. BD are expressed in Julian days (JD; days from 1 January); Figure S2: (A) Daily average air temperature in the eight seasons from 1 November to 1 April. (B) Season evolution of chill hours (CH) accumulation from 1 November until 15 February using Weinberger (1950) model; Figure S3: BLUP and annual (2014–2021) heat requirement (HR) distributions. HR are expressed in growing degree hours (GDH); Table S1: Peach germplasm included in the study. Phenotypic data for bloom and heat requirement observed per accession averaged across eight years (2014–2021). Min—minimum; max -maximum; and BLUP—best linear unbiased prediction values for bloom date. Heat requirement was calculated as the growing degree hours using Richardson’s model [27] at three different base temperatures (2.5 °C, 4.5 °C and 6.5 °C) for each accession. Chilling requirements (CR), fruit type, origin and cultivar release date are also included; Table S2: Description of phenotypic data for bloom and heat requirement observed in the peach germplasm per year of study. Minimum (Min), maximum (Max), mean and standard deviation (SD) of bloom dates expressed in Julian days, and heat requirements using different threshold temperatures (Tb) (2.5 °C, 4.5 °C and 6.5 °C) expressed in growing degree hours in each year (2014–2021) are shown; Table S3: Correlation between bloom date (BD), heat (HR), and chilling requirement (CR) among years (2014 to 2021). Asterisks indicate Pearson correlation coefficient at significance level of $p < 0.05$ (*) and $p < 0.01$ (**); Table S4: Description of statistical significance of chilling (CR) and heat requirements (HR) on bloom date (BD) in the U.S. peach germplasm in each year of the study (2014–2021) and for BLUP values. $p$-values of analysis of variance (ANOVA) using multiple regression model and standardized model (z-scores), and t-test ($p < 0.05$) for each model are shown. Asterisks indicate significant correlation at a level of $p < 0.05$; Table S5: Chilling requirements (CR), and heat requirements (GDH) in the U.S. peach germplasm according to the classified group. HR is expressed in growing degree hours (GDH) under 4.5 °C (Tb) and CR in chill hours (CH).

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