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Clinal variation of dormancy progression in apricot

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Abstract

The aim of this study was to determine the bud dormancy progression in apricot at different latitudes and altitudes. Six locations in regions with a Mediterranean climate in South Africa (SA) and Spain were chosen. The study was carried out during two consecutive years, 2007 and 2008, in SA and results were compared to those obtained in Spain in 2008. Locations ranged from low-chill areas, such as Ladismith and Villiersdorp in SA and Campotéjar in Spain, to high-chill areas, such as Ceres in SA and Barranda in Spain. A number of apricot cultivars comprising the range of chilling requirements in both countries were selected. In addition, a second, parallel study was performed to evaluate the paradormancy progression in ‘Palsteyn’ (SA) and ‘Rojo Pasi3n’ (Spain). Deeper dormancy was not observed in high-chill cultivars located in cold areas than in low-chill cultivars in warm areas. However, low-chill cultivars located in warm areas entered and released from dormancy earlier than high chill cultivars in warm areas. Thus, a clinal variation in dormancy progression under warm temperatures in apricot cultivars is suggested. The role of photoperiod and minimum temperatures is proposed to have a key role in dormancy onset. Paradoxically, an earlier maximum depth of dormancy was found in those areas with higher minimum temperatures at the end of summer. Before the beginning of winter, all cultivars showed an important increase of budburst rate, which indicated the end of endodormancy. Afterwards an ecodormancy period followed during winter, while chilling continued to accumulate. These results contrast with the assumed concept of the breaking of dormancy through chilling accumulation during winter and suggest a possible mediation by photoperiod in overcoming of dormancy. On the other hand, paradormancy exerted a reduction in budburst rate during dormancy entry, whereas decapitation increased the budburst rate throughout the dormant season, indicating interaction between different plant parts during this period.

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1. Introduction

Bud dormancy is a phase in the annual developmental cycle of temperate-zone fruit trees that is essential to their survival of freezing temperatures in winter. Dormancy is not achieved instantly by plants, but progressively develops during autumn, increasing in depth until reaching so-called deep rest (Amling and Amling, 1980; Fuchigami et al., 1977; Lang et al., 1987). The variation in climatic conditions may affect the dormancy cycle and consequently the overall plant phenology. The study of plant material under different climatic conditions may supply

interesting cues about the effect of the changes due to global warming. A dominant characteristic of winter dormancy is that it is released by a quantitative accumulation of adequate chilling (chilling requirement), which can be substituted only partially by rest-breaking manipulations (Faust et al., 1997). Incomplete dormancy release affects tree behaviour in three main ways: delayed budburst; reduced budburst; and uneven budburst and flowering (Erez, 2000). Knowledge of the dormancy depth of a cultivar has practical and economic implications for the production of deciduous fruit trees (Fennell, 1999). An understanding of the depth of dormancy and date of dormancy breaking is required to optimize the geographical distribution of species based on their adaption and application date of rest-breaking chemicals.

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Chilling requirement studies in different locations on both apricots (Andres and Duran, 1999; Bailey et al., 1978, 1982; Guerriero et al., 2002; Ruiz et al., 2007; Tabuenca, 1964; Viti et al., 2010) and peaches (Balandier et al., 1993a,b), led to the conclusion that the chilling requirement of a species is not a constant factor (Tromp et al., 2005). Though the chilling requirement is determined genetically, other factors such as latitude, elevation or climatic conditions during endodormancy inception, can affect its value (Lang, 1989). However, to date, no work on dormancy progression in different climatic conditions has been done in *Prunus*.

In spite of the identification of new mechanisms and genes involved in dormancy control (Horvath, 2009; Olsen, 2010), a high throughput method to assess dormancy is still lacking, and the technique of forcing of detached shoots to measure dormancy depth is still considered appropriate (Mathiason et al., 2009; Mazzitelli et al., 2007; Sreekantan et al., 2010). In addition, in detached shoots of other *Prunus* species a similar response than that of whole plants has been observed (Arias and Crabbé, 1975). Budburst rate has been considered the better criterion when compared with the percentage budburst within a fixed time interval (Dennis, 2003; Saure, 1985). The rate of budburst under forcing conditions is determined by the sum of the endodormant and paradormant components. The paradormant component largely consists of inhibition by distal shoot tissues (Champagnat, 1983; Cook et al., 1998; Faust et al., 1995). The intensity of the inhibition is quantified by the period of time until budburst occurs under forcing conditions.

The aim of this study was to determine the influence of latitude and altitude on the seasonal progression of bud

dormancy in apricot. An evaluation of the budburst rate in detached shoots from a number of apricot cultivars, which spanned the full range of different times of bloom, was conducted in different locations in Mediterranean climates in Spain and South Africa (SA). In addition, one cultivar in each country was selected to determine the progression of paradormancy.

2. Materials and methods

2.1. Plant material

Due to the unavailability of germplasm collections to carry out the experiments in every location, plant material was sampled from commercial orchards, except for the shoots collected in the experimental orchard of the CEBAS-CSIC in Cieza. Commercial orchard cultivar choice is determined by the suitability of the cultivar to the prevailing geographical conditions in the region. Therefore, the possibility of sampling the same cultivar in commercial orchards in different geographical regions was mostly impossible. Apricot cultivars evaluated in each location and country (Spain and SA) are summarized in Table 1. No rest-breaking agent was applied during the periods studied.

Spain: The plant material comprised apricot cultivars spanning the range of chilling requirements and flowering times in the apricot species grown commercially in Spain. The cultivars were ‘Currot’, ‘Rojo Pasión’, ‘Dorada’, ‘Murciana’, ‘Búlida’, ‘Búlida de Arques’ and ‘Orange Red’. Cultivars were grafted onto the traditional apricot seedling rootstocks.

Table 1
Classification of the cultivars studied by country, location, year and chill requirements (CR).

CR	South Africa					
	Villiersdorp		Ladismith		Ceres	
	2007	2008	2007	2008	2007	2008
Very low ^a			Super Gold	Super Gold		
Low ^a	Charisma	Charisma	Charisma	Charisma		
Low ^a	Palsteyn	Palsteyn	Palsteyn	Palsteyn		
Low ^d				Suapriseven		
Low, Medium ^a			Canino	Canino		
High ^c					Orange Red	Orange Red
CR	Spain					
	Campotéjar		Cieza		Barranda	
	Low ^a		Palsteyn			
	Low ^{b,c}		Currot			
	Low-Medium ^b	Rójo Pasión	Rojo Pasión			
	Medium ^b	Búlida de Arques ^e	Búlida		Búlida	
	Medium ^b		Dorada			
	Medium ^b		Murciana			
High ^{b,c}		Orange Red				

^a Infruitec-ARC South Africa.

^b Ruiz et al., 2007.

^c Viti et al., 2010.

^d United States Patent PP10165.

^e ‘Búlida de Arques’ is a cultivar slightly earlier than ‘Búlida’.

SA: The plant material comprised five apricot cultivars spanning the range of chilling requirements and flowering times in the apricot species in SA. The cultivars were ‘Super Gold’, ‘Suapriseven’, ‘Palsteyn’, ‘Charisma’, ‘Canino’ and ‘Orange Red’. Cultivars were grafted onto the traditional apricot seedling rootstocks.

2.2. Experimental design

2.2.1. Endodormancy progression

In Spain, the experiments were conducted during one season, namely 2007–2008. The cultivars studied were distributed in three different areas of the Murcia region: Campotéjar (mild area, altitude 142 m, lat. 1°13'W, long. 38°8'N); Cieza (moderately cold area, altitude 241 m, lat. 38°16'N, long. 1°16'W); and Barranda (cold area, altitude 866 m, lat. 38°2'N, long. 1°58'W) (Table 1). Apricot cultivars sampled in each location are shown in Table 1. Shoots were cut and put in forcing conditions at CEBAS-CSIC in the same day.

In SA, the experiments were conducted during two seasons, in 2007 and 2008. The cultivars studied (Table 1) were collected in three locations in the Western Cape: Villiersdorp (mild area, altitude 466 m, lat. 33°58'S, long. 19°16'E); Ceres (cold area, altitude 980 m, 33°22'S, 19°0'E); and Ladismith (very mild area, altitude 550 m, lat. 33°28'S, long. 21°15'E). Shoots were delivered to the laboratories at Stellenbosch University by overnight courier. Ten shoots per cultivar, location and date were collected at each of the locations in SA and Spain. Every shoot was evaluated.

2.2.2. Paradormancy progression

In order to assess paradormancy progression one cultivar was chosen in SA, ‘Palsteyn’, and Spain, ‘Rojo Pasión’. Sampling of these cultivars took place during the same physiological periods in both experiments. Three treatments were done: Treatment 1 — intact shoots; Treatment 2 — a distal 10 cm shoot piece removed (decapitation); Treatment 3 — a distal 10 cm shoot piece disbudded. Each treatment consisted of three replications of 10 shoots each. Shoots were forced and evaluated as in endodormancy progression. Standard error for each date and treatment was calculated.

2.2.3. Temperature, chill accumulation and budburst rate (TB^{-1}) assessment

Hourly temperatures were recorded in each location with automatic data-loggers: Escort Junior (Escort Data Logging Systems) in Spain and Tiny tag (Gemini Data Loggers UK) in SA.

The start date for chilling accumulation was considered to be the first day of consistent chilling accumulation and infrequent occurrence of temperatures producing a negative effect (chilling negation) (Erez et al., 1979; Guerriero et al., 2002; Richardson et al., 1974). Chilling accumulation was assessed by chill hours (Hours below 7.2 °C) (Weinberger, 1950); Chill Units of the Utah Model (Richardson et al., 1974); and Portions of the Dynamic Model (Fishman et al., 1987a,b).

Unbranched one-year-old apricot shoots with a length of 30 cm were sampled ca. every 15 days from mid-May to August

in SA in 2007, and from mid-September 2007 to February 2008 in Spain. Given the results obtained in the first year, the shoot collection period was extended in 2008, and the shoots were collected from the end of January to August in SA.

The shoots were bundled in groups of 10 shoots per cultivar, location and date, and placed in 5 L plastic buckets containing 1 L of water. To determine the depth of dormancy, the shoots were forced in a growth chamber with constant illumination (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation) and a constant temperature of 25 °C (Jacobs et al., 2002). The water was changed every two to three days, and the distal shoot end was dipped in 0.25% (v/v) sodium hypochlorite solution (3.5%) for ca. ten minutes. Approximately 1 cm of the distal shoot section was cut off weekly to ensure that the vascular system remained functional. Vegetative and reproductive budburst was recorded every two to three days. Time to budburst (TB) was calculated as the time in days needed for budburst to occur on three shoots per bundle, i.e. days to budburst in 30% of the shoots (3 out of 10 shoots). Budburst in one shoot was considered when at least one bud had opened. The inverse value of the time to budburst (TB^{-1}) was calculated.

3. Results

3.1. Maximum and minimum daily temperatures

Daily maximum and minimum temperatures recorded during the periods studied are indicated in Fig. 1 (Spain) and Fig. 2 (SA). Temperatures recorded during 2007–2008 in Spain were comparable to the long-term average. Barranda was the coldest area studied in Spain; on numerous days the minimum temperatures were below 0 °C from November to the first fortnight of February, and maximum temperatures were lower than those registered either in Campotéjar or Cieza. In Campotéjar, the minimum temperatures were higher than in Barranda, which is consistent with the lower altitude of this location. In Cieza, the temperatures were intermediate between Barranda and Campotéjar (Fig. 1).

In SA, the winter of 2007 started earlier and was colder than in the winter of 2008. Ceres was the coldest area studied in SA (Fig. 2), even though the minimum temperatures were higher than those registered in Barranda (Spain). In Ladismith, high daily thermal amplitude was observed, which is characteristic of a semi-desert inland area. In Villiersdorp, the area closest to the ocean, daily minimum temperatures were higher than in the other areas (Fig. 2).

3.2. Chilling accumulation in the different locations studied

Fig. 3 indicates the chilling accumulation in Spain between 1 November and 28 February in Barranda, Campotéjar and Cieza, measured by ‘Chill Units’ (CU) (Utah Model), ‘Portions’ (Dynamic Model) and ‘Hours below 7.2 °C’. In Barranda, the chilling period began earlier and the chilling accumulation was higher than in Cieza and Campotéjar. The chilling accumulation in Barranda (ca. 1800 CU) was considerably higher than in Cieza (ca. 1200 CU) and Campotéjar (ca. 900 CU) (Fig. 3).

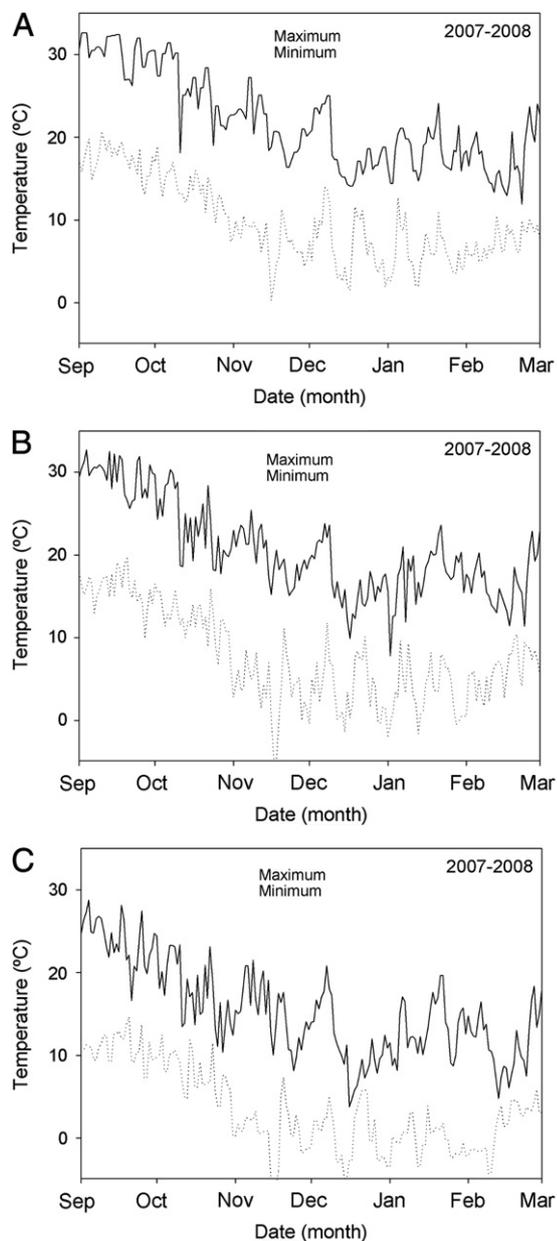


Fig. 1. Maximum and minimum daily temperatures registered in 2007–2008 in different locations studied in Spain: Campotéjar (A), Cieza (B) and Barranda (C).

In both countries, the chilling accumulation in the late autumn (November in Spain and May in South Africa) was generally low compared to accumulation during the winter months (December and January in Spain and June and July in SA). No chilling accumulation was registered in October, except in Barranda.

In South Africa, the onset of chilling accumulation varied considerably between the areas studied (Fig. 4). In Ceres, the coldest area, the chilling accumulation began earlier (second fortnight of April) than in the intermediate area, Villiersdorp, and the warm area, Ladismith, (second fortnight of May). The total chilling accumulation in Ceres was considerably higher than in Villiersdorp and Ladismith (Fig. 4), and was even higher than in Cieza, Spain. However, in Villiersdorp and Ladismith,

the chilling accumulation was very low (ca. 650 and 550 CU, respectively) compared to the values registered in the areas studied in Spain.

3.3. Dormancy progression in Spain

Fig. 5 shows the time to budbreak in the different locations and cultivars in Spain. In Campotéjar, the location with the lowest altitude and mildest winter, the first budburst rate data (expressed as TB^{-1}) in vegetative buds was recorded in mid-September. By that date, ‘Rojo Pasión’ and ‘Búlida de Arques’ were in a state of shallow dormancy, which rapidly increased, as indicated by reduction in budburst rate observed on the subsequent sampling dates. The deepest dormancy was achieved in the beginning of October in ‘Rojo Pasión’ and at the end of October in ‘Búlida de Arques’. From that date, a continuous increase in budburst rate was observed, except for a minor decrease in the first days of January. Dormancy had been released completely by the end of January (Fig. 5). In the instance of reproductive buds, no budburst was recorded until November in a high percentage of cases. However, the trend in dormancy release in reproductive buds observed from November onwards was similar to that in vegetative buds. This suggests that this period coincides with the fulfilment of the chilling requirement for dormancy release. In ‘Rojo Pasión’, endodormancy of reproductive buds at the beginning of November was clearly deeper than that of vegetative buds.

In Cieza, a similar dormancy pattern was found in vegetative and reproductive buds (Fig. 5). On the first sampling date (14 September), the shallowest level of dormancy in vegetative buds was observed in ‘Búlida’, whereas ‘Murciana’ and ‘Orange Red’ already showed an intermediate value. On the next sampling date, a generalized decrease in budburst rate was found in all cultivars. By the end of October all cultivars had entered a state of deep dormancy, even though the recorded values were slightly lower than on the previous sampling date (Fig. 5). During the second fortnight of November, a sharp increase in budburst rate was observed in all cultivars. By that time, less than 200 CU had been accumulated under field conditions (Fig. 3). During December, depth of dormancy was maintained or even increased in all cultivars, except in the low-chill cultivar ‘Currot’, in which the budburst rate increased. By the first week of January dormancy release had occurred in ‘Currot’. From December onwards, the lowest levels of endodormancy were observed in ‘Currot’, and the highest in ‘Orange Red’, which is concomitant with the chilling requirements calculated for those cultivars under the same climatic conditions (Ruiz et al., 2007). From January until the last sampling date in mid-February, a generalized decrease in the depth of dormancy was observed. In reproductive buds, the pattern of dormancy progression in ‘Dorada’, ‘Murciana’ and ‘Búlida’ differed from that observed in low-chill cultivars. A gradual, but constant, increase in budburst rate occurred in ‘Currot’ and ‘Rojo Pasión’ from November to February, without a dormancy release pause in December.

In Barranda, the pattern of dormancy progression in ‘Búlida’ differed from that observed in Cieza (Fig. 5). The state of

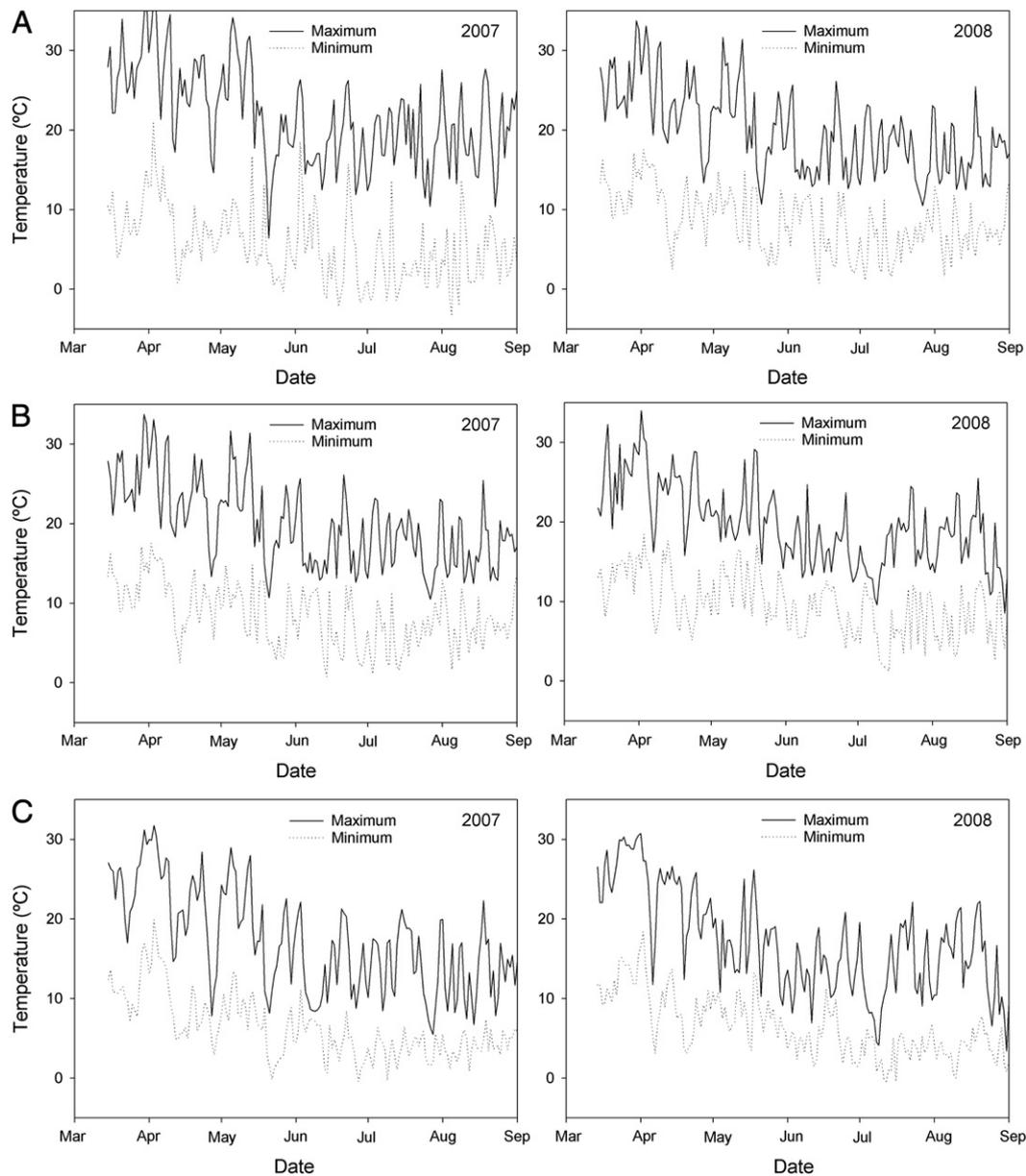


Fig. 2. Maximum and minimum daily temperatures registered in 2007 and 2008 in different locations studied in South Africa: Ladismith (A), Villiersdorp (B) and Ceres (C).

dormancy continued to deepen during October and November, reaching the minimum budburst rate in the second fortnight of November (when ca. 400 CU had accumulated), two months later than in Cieza. By that time, the budburst rate in all cultivars in Cieza and Campotéjar had increased considerably. Thereafter, a continuous increase was observed until mid-February, which coincided with dormancy release (Fig. 5).

3.4. Dormancy progression in South Africa

The dormancy progression curves of the different cultivars studied in three areas of the Western Cape, SA, in 2007 and 2008 are shown in Fig. 6.

In Villiersdorp, dormancy decreased from late May until August 2007, and a pause in the release of dormancy occurred

during the second fortnight of June. A similar trend was observed in reproductive buds (though only a few values indicating the budburst rate in reproductive buds were obtained) but with a pause in the release of dormancy occurring during the second fortnight of July. In 2008, buds reached dormancy in early March, and the level of dormancy was maintained until late May, when a further, but slight increase in dormancy was observed. This was followed by a decrease in dormancy coinciding with dormancy release. In reproductive buds, budburst values showed a continuous increase in dormancy intensity from the first of May (Fig. 5).

In Ladismith, a general increase in budburst rate was observed from late May (November in Spain) to late July 2007 (January in Spain), although a pause in the dormancy release phase occurred in vegetative and reproductive buds of

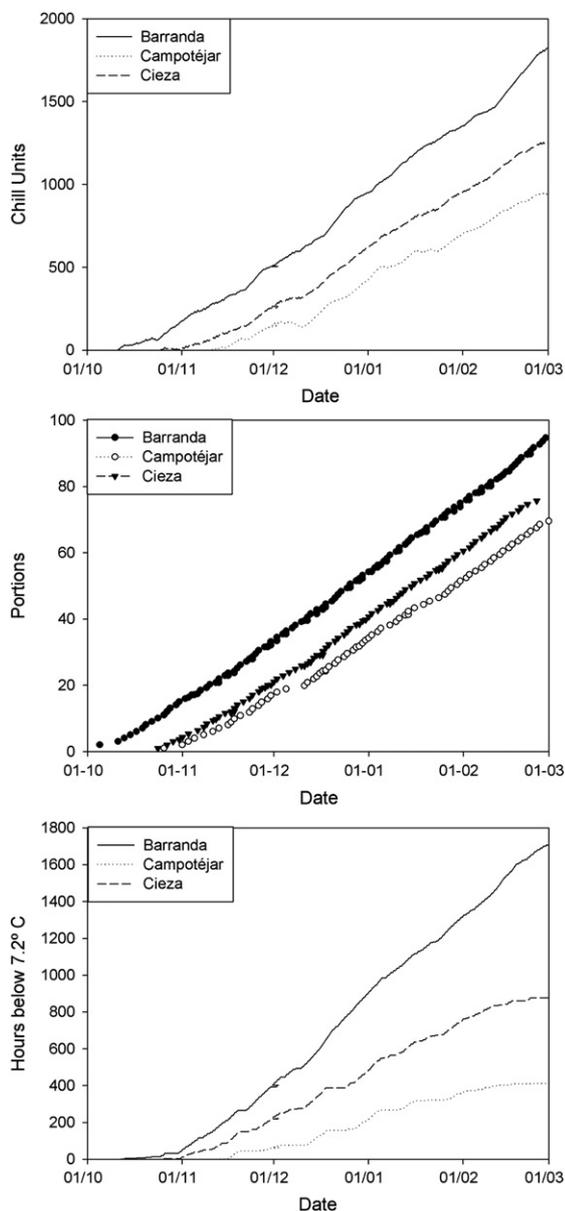


Fig. 3. Chill accumulated in 2007–2008 in the different areas studied: Barranda, Campotéjar and Cieza. Results are expressed in Chill Units, Portions and Hours below 7 °C.

‘Palsteyn’ and ‘Super Gold’. ‘Canino’ had reached maximum dormancy by the second sampling date (beginning of June to December in Spain) in reproductive and vegetative buds. In 2008, when budburst rate data were available from the end of January (July in Spain), the results showed that dormancy had already developed in all cultivars. A general decrease in dormancy was observed during the first days of February in all cultivars. ‘Suapriseven’ was the first cultivar to enter into maximum dormancy (March 1). This was followed by a sharp decrease in dormancy, a pause in dormancy breaking and a subsequent dormancy release. ‘Palsteyn’ followed the same pattern as ‘Suapriseven’, but the different phases occurred two months later than in ‘Suapriseven’, and maximum dormancy was reached at the beginning of May. ‘Charisma’, ‘Canino’ and

‘Super Gold’ reached maximum dormancy at the end of May, and released dormancy thereafter without pause. In reproductive buds, results were similar to 2007, although a deeper level of dormancy was observed (Fig. 5).

In Ceres, the coldest area studied in South Africa, an increase in budburst rate in ‘Orange Red’ was observed from mid-May to July of 2007. This was followed by a slight increase in dormancy intensity during July and a sharp decrease in early August. In 2008, maximum depth of dormancy was achieved in the beginning of April, and dormancy intensity was maintained until 1 July. Thereafter, TB^{-1} values decreased, coinciding with dormancy release by the end of July. With regard to reproductive buds, no budburst was registered until May. Nonetheless, the data observed suggested a decrease in TB^{-1} from May to August (Fig. 6).

In South Africa in 2007, no significantly different trends in paradormancy progression were found in during dormancy overcoming (Fig. 7). Thus, the sampling period was extended in 2008 in Spain and South Africa. In these locations and years, significant differences were found among treatments. Disbudded shoots (T3) showed a higher dormancy level than control (T1) or decapitated (T2) shoots during the onset and maintenance of dormancy, until these differences were reduced and paradormancy was no longer observed. However, in South Africa, significant differences between control and disbudded shoots were observed from 5 May. In 2008 entry into dormancy started in February (August in the Northern Hemisphere). In this case, the decapitated shoots showed a later and shallower level of entry into dormancy, whereas control shoots rapidly entered into dormancy from mid-February.

4. Discussion

4.1. Maximum and minimum daily temperatures

The variation in temperature registered in the three locations evaluated in Spain is consistent with the differences in altitude. Considering the proximity of the areas and the similarity in climatic conditions, altitude is the most important factor accounting for the variability in temperatures between these areas. In general, the locations studied in South Africa were warmer than in Spain. The greater variation in maximum and minimum temperatures between consecutive days observed in South Africa should be noted. This is consistent with the changeable winters of the Western Cape area. Besides, the differences in temperature registered in South Africa were associated with both altitude and geographical location. Thus, high thermal amplitude was found in Ladismith, which is situated more inland in a semi-desert area.

4.2. Chilling accumulation in the different locations studied

Based on the chilling accumulation in each area, the locations in Spain could be classified as cold (Barranda), moderately cold (Cieza) and warm (Campotéjar). Similarly, in South Africa, Ceres could be classified as a cold area, whereas Villiersdorp and Ladismith could be classified as very warm

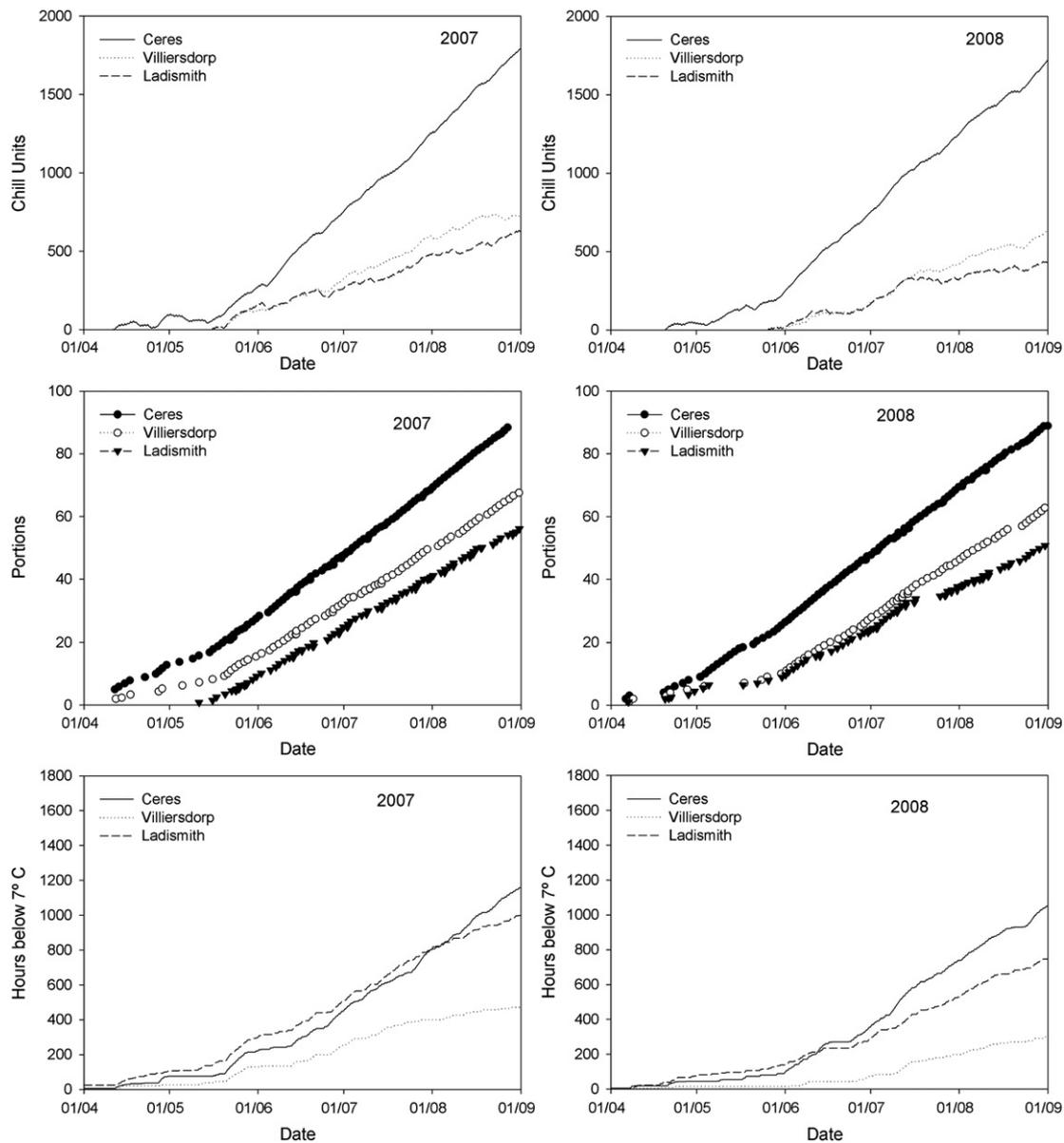


Fig. 4. Chill accumulation in 2007 and 2008 in the different areas studied in South Africa: Ceres, Villiersdorp and Ladismith. Results are expressed in Chill Units, Portions and Hours below 7 °C.

areas. However, this classification depends largely on the model used for assessing chilling accumulation. In Ladismith, which is characterized by a semi-arid climate and high daily thermal amplitude, Hours below 7 °C were similar to those registered in Ceres in 2007 and in Cieza, Spain, although the CU accumulation was considerably lower. In Ladismith and Villiersdorp a similar CU value was recorded, but Hours below 7 °C in Ladismith were more than double the values registered in Villiersdorp. According to the Hours-below-7 °C Model, Ladismith would be a moderately cold area, whereas Villiersdorp would be a warm area.

In Spain, the differences in chilling accumulation among locations were considerably higher when the Hours-below-7 °C and Utah Models were used. The Dynamic Model minimized the differences among the locations. In South Africa, the

Dynamic Model also minimized the differences between locations, as well as between years. This can be explained by the fact that this model considers the synergistic effect of moderate temperatures coupled with low temperatures on dormancy breaking (Fishman et al., 1987a,b). This is the factor responsible for equalising the total chilling accumulation between years. However, the Dynamic Model also considerably reduced the variability between locations in Spain and South Africa. In South Africa, the Dynamic Model calculated the lowest variability between years (Fig. 4). A high variability was found using the Hours-below-7 °C Model. These results agreed with those previously found by Ruiz et al. (2007) in Spain. In both cases, the Dynamic Model and Utah Model calculated a lower variation between years, but the Hours-below-7 °C Model registered a high variability. It should be noted that the

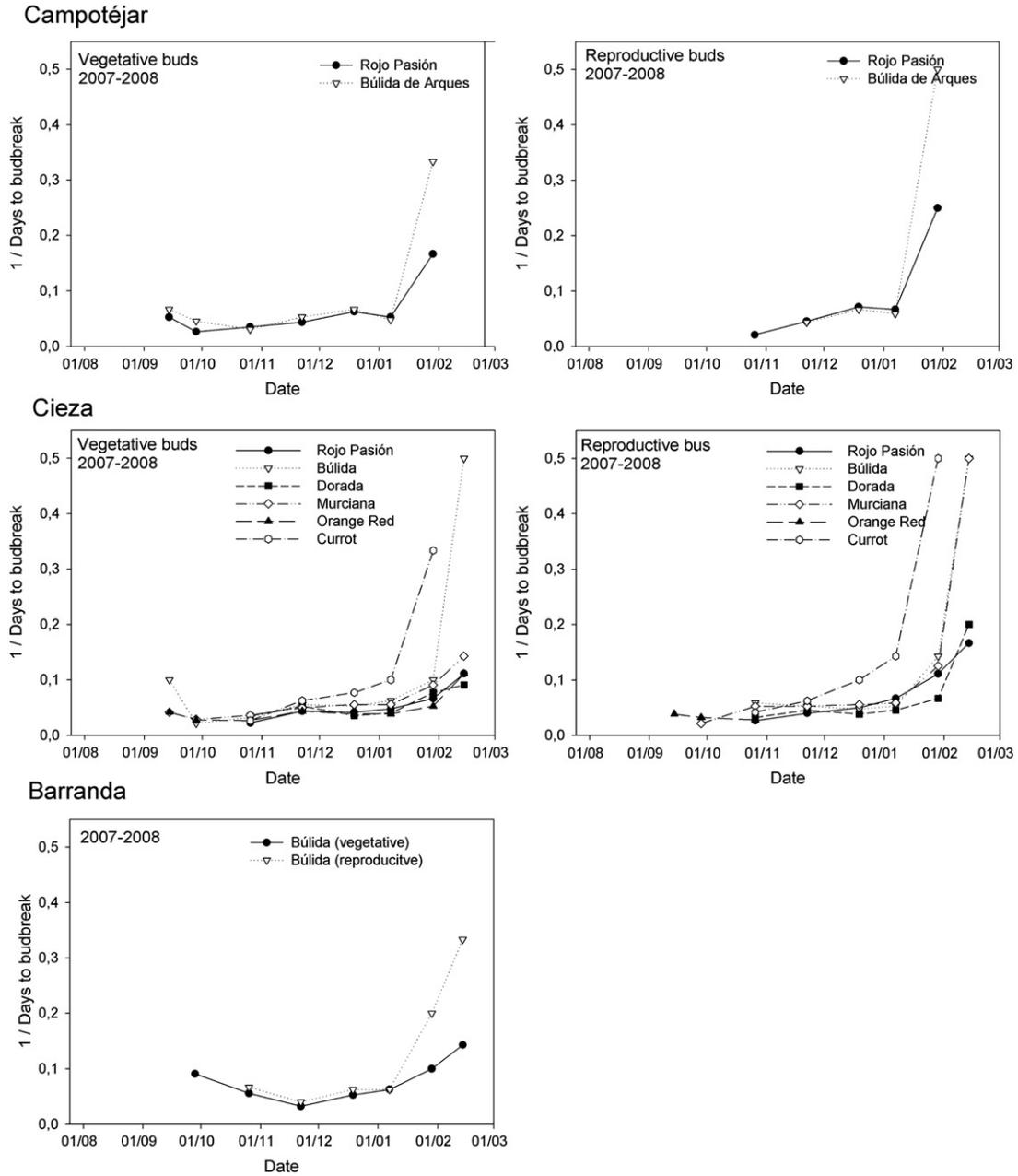


Fig. 5. Growth inability progression (expressed as 1/Days to budbreak) in vegetative (right) and reproductive (left) buds in the different areas studied in the period 2007–2008 in Spain.

Dynamic Model indicated a very low variability in spite of the markedly different temperatures registered in the different locations and years (Figs. 1 and 2). This indicates that the Dynamic Model is conservative with regard to showing differences between patently different years and locations. The use of chilling accumulation values calculated by the Dynamic Model under these climatic conditions could mask the negative effect of an insufficient chilling accumulation in a mild winter area.

It is worthwhile to mention that a standard meteorological station was used to record the temperature values. Temperature values in apricot buds during daylight hours are usually higher than the values registered in the meteorological station, except

in wet or windy conditions. Therefore, the chilling accumulation calculated using a meteorological station is higher than values calculated using the bud temperatures.

4.3. Dormancy progression in Spain

The pattern of dormancy progression in Cieza was very similar to that observed in Campotéjar. However, the chilling accumulation in Cieza was higher than in Campotéjar (200 CU or 400 Hours below 7 °C more in Cieza). In both areas, all cultivars reached the deepest level of dormancy before any chilling accumulation. This contrasts with the common belief that buds reach dormancy with the onset of chilling, closer to

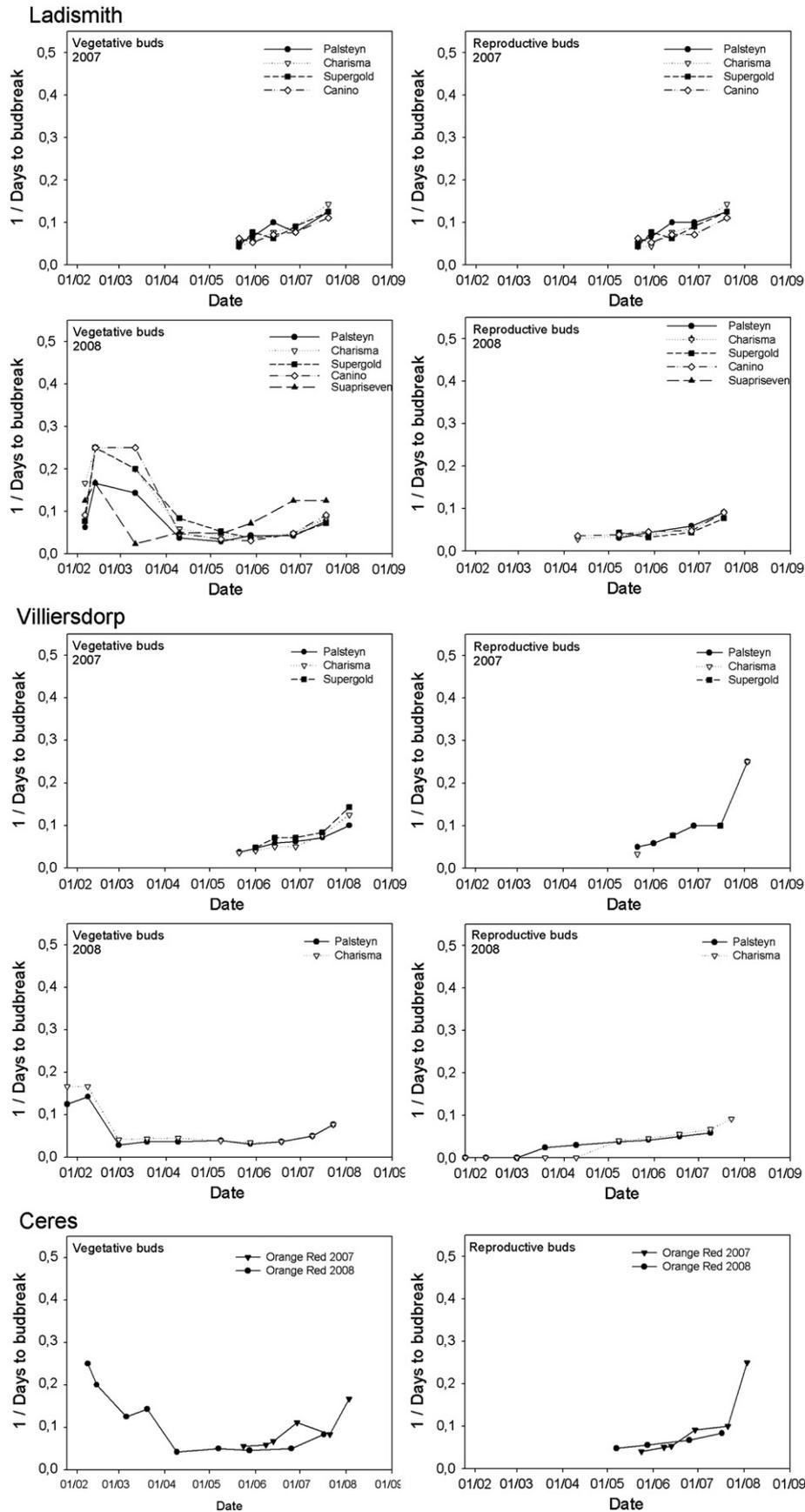


Fig. 6. Growth inability progression (expressed as 1/Days to budbreak) in vegetative (right) and reproductive (left) buds in the different areas studied in South Africa.

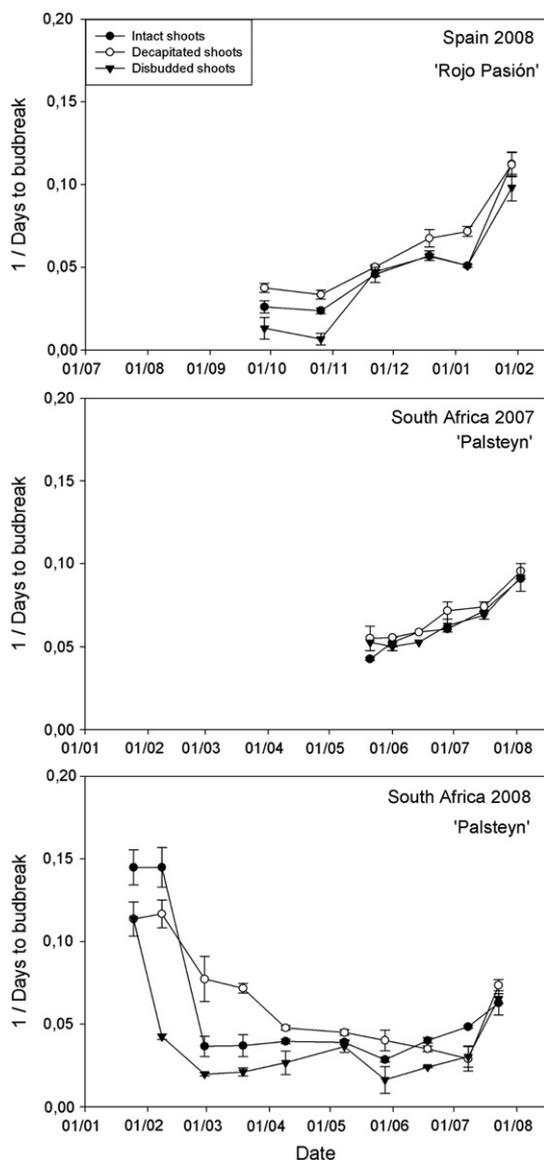


Fig. 7. Growth inability (expressed as 1/Days to budbreak) in vegetative buds of the treatments: Treatment 1: Intact shoots; Treatment 2: A distal 10 cm shoot piece removed; Treatment 3: A distal 10 cm shoot piece disbudded. Bars show standard error.

winter (Crabbé, 1994). In apples, Hauage and Cummins (1991b) found that significant increases in dormancy started to occur only after the first frost and the beginning of chilling accumulation. However, Cook and Jacobs (2000) found that the lower-chill apple cultivar 'Granny Smith' and higher-chill cultivar 'Golden Delicious' reached maximum dormancy before any considerable amount of chill had been accumulated in a moderately cold area (1350 CU of mean chilling accumulation). Amling and Amling (1980), working on pecan, found that the onset of rest occurred prior to the advent of chilling accumulation. Cook et al. (1998) found apple rootstocks in Belgium to be dormant already in the beginning of October. Besides, Tromp et al. (2005) stated that winter dormancy is usually started in summer and could have been terminated by mid-winter. Heide (2008) indicated that the photoperiodic

response of the *Prunus* species is highly temperature dependent. The onset of lower minimum temperatures in September (compared to summer) and the rapidly shortening photoperiod around the autumn equinox could trigger the induction of dormancy. This could explain the early arrival of dormancy. However, the reason for variation among locations remains unclear. In Barranda, the coldest location studied in Spain, the maximum level of endodormancy is not reached until the end of November, although dormancy begins in late summer (Fig. 5).

On the other hand, the data obtained in Cieza are, in general, in accordance with the dormancy release dates of reproductive buds from other locations and cultivars in the same year. However, some differences should be noted. For example, similar budburst rates were recorded by mid-February in cultivars with different chilling requirements, namely 'Rojo Pasión' (low medium), 'Dorada' (medium) and 'Orange Red' (high). Thus, this methodology did not allow for accurate differentiation of dormancy release among cultivars with manifestly different chilling requirements. Besides, the low-chill cultivar 'Currot' and the high-chill cultivar 'Orange Red' had the same minimum budburst rate value, although no budburst had been recorded in 'Currot' previously. Regarding the cultivar differences in dormancy patterns in reproductive buds, a more continuous decrease in dormancy intensity was observed in 'Currot' and 'Rojo Pasión', cultivars with lower chilling requirements, compared to the other cultivars in Cieza (Fig. 5).

In Barranda, the level of dormancy of 'Búlida' began to deepen in late September with the advent of low temperatures and a decreasing photoperiod, which agreed with the findings of Heide (2008). However, 'Búlida' reached its deepest level of dormancy only when ca. 400 Chill Units had been accumulated, which coincided with leaf fall. Hauage and Cummins (1991b) stated that apple bud dormancy started to intensify soon after bud formation and reached maximum intensity by the time of leaf fall/senescence. In Cieza and Campotéjar, with higher minimum temperatures in late summer, the deepest dormancy was achieved nearly two months earlier, when no Chill Units had been accumulated. This contradicted the findings of Cook and Jacobs (2000) in the apple cultivars 'Granny Smith' and 'Golden Delicious'. These cultivars reached maximum dormancy before any considerable amount of chill had been accumulated in a moderately cold area (1350 CU of mean chill accumulation), whereas ca. 600 CU was required to reach maximum dormancy in a warm area.

To summarize, dormancy increased more rapidly in warm areas than in cold areas, and maximum depth of dormancy was achieved earlier. As the photoperiods were quite similar in these areas, the climatic conditions imposed by different altitudes might explain these differences. Thus, the warmer the area, the earlier deep dormancy is achieved. The depth of dormancy (minimum budburst rate value) was not related to the chilling requirements of the cultivars. However, during dormancy release, higher budburst rate values were generally recorded in vegetative and reproductive buds of cultivars with low chilling requirements, whereas the cultivars with high chilling requirements also showed higher endodormancy values during this period.

4.4. Dormancy progression in South Africa

The time of the onset of dormancy was dissimilar in the different locations studied in South Africa. In Ladismith and Ceres, all cultivars except ‘Suapriseven’ entered into dormancy at the beginning of April, which was in accordance with the low minimum temperatures registered at the end of summer. In Ladismith, the location with the lowest chill unit accumulation (Fig. 4), an already established dormancy was found in the middle of summer in 2008. This agreed with the findings of Crabbé and Barnola (1996), who stated that the very act of bud formation was evidence of the establishment of dormancy. In Villiersdorp, where Chill Units and hours below 7 °C were very low, a high level of dormancy had already been achieved by March. In Ceres, maximum dormancy had already been achieved in April. This result was in agreement with the dormancy progression found by Cook et al. (1998) in apple in a nearby area. Thus, dormancy was reached earlier in the areas with higher minimum temperatures (warmer areas). This result disagreed with those found by Cook and Jacobs (2000) in apple, where maximum dormancy was achieved earlier in the colder area. As for the dormancy pattern, most of the cultivars had reached maximum depth of dormancy by late autumn (during May in South Africa). This was followed by an increase in budburst rate, a pause period (when dormancy depth remained constant or even increased), and subsequent overcoming of dormancy. The exceptions were the cultivars ‘Canino’, ‘Charisma’ and ‘Super Gold’, studied in Ladismith in 2008, which reached maximum dormancy at the beginning of June, followed by dormancy release without a pause period. The difference in maximum depth of dormancy found in these cultivars with different chilling requirements agreed with previous findings in several species such as apple (Cook and Jacobs, 2000; Hauagge and Cummins, 1991a); Pecan (Amling and Amling, 1980); cherry (Kapp and Cook, personal communication); and peach (Balandier et al., 1993b). Maximum depth of dormancy was also similar in the different locations studied in both countries, which could contrast with the different mean times to bud break found by Balandier et al. (1993a) on Reunion Island (21°5′ S, 55° E) and in Clermont-Ferrand, France (46°N, 3°E). The greater similarity between climatic conditions in our experiment than observed in the study of Balandier et al. (1993a) could explain the differences in results.

The generally earlier dormancy release of reproductive buds compared to vegetative buds is in agreement with the established concept of the lower chilling requirement of reproductive buds (Erez, 2000).

Within each country, the cultivars in the locations with higher minimum temperatures in late summer reached dormancy earlier than those in colder locations. In areas with similar minimal temperatures, dormancy onset was generally earlier in SA than in Spain. The dormancy patterns in SA were similar to those found in Spain. However, some differences should be noted. ‘Suapriseven’, for example, showed the same pattern as ‘Búlida’ in Cieza (Spain), but maximum dormancy and dormancy release occurred ca. one month earlier in ‘Suapriseven’ in Ladismith, considering the sixth month lag.

Dormancy release in ‘Búlida’ occurred on similar dates in the different areas, but the amount of chill accumulated was significantly different. In addition, the chilling requirement of ‘Canino’ was considerably lower in Ladismith (ca. 304 CU) than when grown in Cieza (ca. 806 CU). These results agreed with those found by Balandier et al. (1993a) under markedly different climatic conditions. This lack of consistency in the chilling requirement to overcome dormancy raises serious doubts about the reliability of the models used. Consequently, several hypotheses and questions may arise. For example, can we use these linear models during the endodormant period to characterize dormancy progression, using the effect of temperature as the only variable? Could there be an unequal effect of temperature and other variables during the endodormant period? Is the chilling requirement of a cultivar a constant, or is it variable and dependent on environment? (Variables such as photoperiod (Heide, 2008), time of temperature application and combination of cold and warmth should be included in the models (Campoy et al., 2010)). Furthermore, do these models really describe the physiology of the tree? Could the previous success of the models used in the areas where they were developed be a result of the fact that the models corresponded with the real physiological processes that guided dormancy behaviour? Yet, once the models are used in different areas, the link between the model and the physiology of the tree seems to disappear, raising the question whether the models are really measuring the signals that control dormancy behaviour in the plant.

Moreover, the dormancy curves described in the six locations studied reflect a shift towards precocity compared to previous results in colder areas. What is more, within all the areas studied, dormancy onset and release was earlier in warmer than colder areas in countries with no significant latitude variation, endodormancy was achieved earlier in the warmer locations. Similarly, the critical photoperiod for growth cessation (first stage before dormancy) clinally decreased in northern tree ecotypes according to variation in latitude or altitude (Olsen, 2003; Olsen et al., 2004). A clinal variation in light quality requirements to maintain growth has also been demonstrated in woody species, at least for northern populations (Olsen, 2006).

Consequently, and taking into account our results, a clinal variation in dormancy progression under warm temperatures could be hypothesized for apricot cultivars in warm-winter areas. Thus, the earlier resumption of growth due to the earlier, favorable temperatures from late winter to spring could be related to the subsequent precocity to reach endodormancy. This would be in accordance with the clinal variation between cold and warm areas regarding flowering, growth capacity after grafting, and even ripening observed in apricot in the climatic conditions studied.

This hypothesis would be in accordance with the questioning of the accuracy of the models, generally developed in colder areas, under warmer climatic conditions (Balandier et al., 1993a; Linsley-Noakes and Allan, 1994; Ruiz et al., 2007). Some adaptations of the models to accommodate warm conditions could also be interpreted as a way to reduce the effect of warm temperatures, negating the effect of very warm

days (Positive Chill Units Method, Linsley-Noakes et al., 1995), or considering the properly documented, positive effect of moderate temperatures (Dynamic Model, Fishman et al., 1987a), or minimizing the variability through the selection of the most suitable temperature threshold (Cesaraccio et al., 2004).

As for paradormancy progression, decapitated shoots always showed the highest budburst rate, except on a few sampling dates at the onset and release of dormancy in South Africa in 2008. This is in accordance with the stimulating effect of the cut on overcoming of dormancy and with the fact that the lateral buds have a lower endodormancy than terminal buds during the dormant period (Champagnat, 1983, 1992; Crabbé and Barnola, 1996; Mauget and Rageau, 1988; Williams et al., 1978). On the other hand, disbudded shoots showed the highest level of dormancy, except on the sampling dates close to dormancy release. From November onwards, control and disbudded shoots showed similar dormancy levels, except in South Africa in 2008, which reflected the low level of paradormancy during this stage. On the other hand, the difference between intact shoots and disbudded shoots at the end of summer in that year, indicated the high level of paradormancy, confirming previous results (Champagnat, 1989).

5. Conclusions

In spite of the different chill accumulations, the dormancy patterns and maximum depth of dormancy found in South Africa were similar to those found in Spain, with the exception of certain phase differences, depending on the area. An earlier maximum depth of dormancy was found in those areas with higher minimum temperatures at the end of summer. Similar results were obtained in cultivars with different chilling requirements, even though dormancy release tended to be earlier in cultivars with low chilling requirements. The dormancy patterns and maximum depth of dormancy were similar in vegetative and reproductive buds, but dormancy release was earlier in reproductive buds.

Dormancy induction took place in late summer, prior to the advent of chilling temperatures. The decrease in minimum temperatures in late summer, coinciding with the decreasing photoperiod, could trigger the onset of dormancy. Nonetheless, an interaction with other factors, such as altitude, might be implied, as maximum dormancy occurred earlier in warmer areas.

The assumption that dormancy induction is a result of chilling accumulation seems erroneous in the warm areas studied in both countries. Considerable decrease in dormancy depth was observed before the advent of chilling accumulation in warm areas, suggesting that dormancy release could be influenced by other factors. These factors appear to be related more to the previous growing season than to the winter itself. The amount of chill accumulated by the time of dormancy release in the same cultivars in different locations differed considerably.

Improvement of the physiological knowledge of the basis of dormancy, especially regarding the external signalling related to dormancy, would facilitate the development of more multifaceted and reliable models.

Finally, a clinal variation in dormancy progression under warm temperatures for apricot cultivars in warm-winter areas is suggested. The wide range of plant material, with quite diverse climatic origins, and consequently, different adaptations, could have contributed to the complexity of the responses.

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