Spring temperatures have a major effect on early stages of peach fruit growth

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(Accepted 10 February 2007)

SUMMARY

Previous research has shown that Spring temperatures within 30 d after bloom (expressed as accumulated growing degree hours, GDH) are useful for predicting the harvest date of specific peach cultivars. The goal of the present research was to explore the relationship between GDH and additional environmental parameters on peach fruit development and growth during the period from the full bloom date (FBD) to the reference date (RD). Since heat accumulation during the first 30 d after bloom is a primary driver of fruit phenology, we hypothesised that years with high early Spring temperatures would result in smaller RD fruit size (RDFS) because trees cannot supply resources rapidly enough to support the potential growth associated with high rates of phenological development. Data on FBD, RD, and RDFS were collected at different locations in California between 1988 - 2004 and were analysed in conjunction with seasonal environmental data including accumulated GDH, rainfall, soil temperature, and solar radiation, from FBD to RD. Early Spring air temperatures appeared to be a primary environmental factor influencing RDFS. GDH accumulation during the first 30 d after bloom (GDH30) caused a decrease in the number of days between FBD and RD. RDFS increased with increases in the number of days between FBD and RD, and was negatively affected during years with high Spring temperatures. High GDH30 accumulations increased the rates of fruit growth d⁻¹ but not enough to compensate for the shorter growth period from FBD to RD that occurred when GDH30 accumulation was high. The data supported the hypothesis that, with excessively high Spring temperatures, trees could not supply resources rapidly enough to support their maximum potential fruit growth rates.

DeJong and Goudriaan (1989) showed that relative growth rate (RGR) analysis could explain the double-sigmoid pattern of peach fruit growth, and that the carbohydrate requirements for any interval of fruit growth could be estimated by knowing the size of the fruit at the beginning of the interval and the RGR during that interval. Subsequently, it was shown that fruit RGR analysis can be used to estimate fruit growth potential, and to study how the availability of carbohydrate, nitrogen and water resources influence fruit growth potential, as well as actual fruit growth under normal crop load conditions (Pavel and DeJong, 1993; Grossman and DeJong, 1995a,b; Berman and DeJong, 1996; Rufat and DeJong, 2001). In conducting this research it became apparent that, while fruit growth and development are often considered to be synonymous, they are in fact distinct, but inter-related processes. Growth over a specific time-interval cannot occur without phenological development of the fruit. However phenological development can proceed without the growth potential of fruit being fully realised during that same interval. Given the importance of phenological development in determining fruit growth potential, we recognised that understanding the factors that drive fruit development may also provide a better understanding of factors that control fruit growth.

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The length of the fruit development period has been suggested to be related to early Spring temperatures in peach (Weinberg, 1948), in apple (Austin *et al.*, 1999), and in apricot (Brown, 1952). The use of quantitative methods to estimate heat accumulation (Anderson *et al.*, 1986; Caruso *et al.*, 1992) has confirmed that growing degree hours (GDH) accumulation during the 30 d after full bloom (DAFB) affects the length of the fruit development period in different stone-fruit cultivars (Ben Mimoun and DeJong, 1999; Marra *et al.*, 2002). This may explain the early harvests of California peaches in 2004, when record high temperatures were registered during full bloom (DeJong, 2005). During the same harvest season, fruit growers experienced problems attaining the fruit sizes desired by the market (DeJong, 2005).

Fruit growth is a function of fruit growth potential, the quantity of resources available to support growth, and a competition among plant organs for resources (Grossman and DeJong, 1994). Thus, it is unrealistic to expect that final fruit size can be explained only by temperature patterns during early Spring. Nevertheless, we were interested in studying the effect of Spring temperature on fruit size during the period of initial peach fruit development from the full bloom date (FBD; the date on which 50% of the flowers on a tree, or in an orchard are estimated to be fully open) until the reference date (RD; the date used by growers to determine the status of fruit sizing and subsequent

thinning requirements). RD is defined as the date on which 80% of sliced fruits have hardened pits near their distal end, plus 10 d (Rizzi, 1967).

Carbon supply from FBD to RD is dependent on the mobilisation of reserves (Priestley, 1970; Loescher, 1990) and on photosynthesis in newly-formed leaves (Grossman and DeJong, 1994). As soil temperatures lag behind air temperatures in the Spring, it is unlikely that mobilisation of root reserve carbohydrates are increased to meet the increased carbohydrate demand of fruit during warm Springs. Similarly, as photosynthetic carbon assimilation is largely driven by day-length and diurnal light conditions (Goudriaan, 1986; Kropff et al., 1987), and as day-time temperatures do not influence the amount of light on a daily basis, it is highly unlikely that there is a corresponding increase in photosynthesis to match the increased carbohydrate demands of fruit growth during warm Springs. On the other hand, the carbohydrate demand of peach fruit is closely-related to fruit sink activity, which can be modified by environmental conditions (Grossman and DeJong, 1994). In fact, high temperatures also increase maintenance respiration rates, and thus decrease the amount of carbon available for growth (DeJong and Walton, 1994).

Since high heat unit accumulation during early Spring increases the rate of fruit phenological development, which translates into increased fruit growth potential without the corresponding expectation of increased carbohydrate supply to support fruit growth, we hypothesised that RD fruit size (RDFS) would be negatively affected during years of high Spring temperatures. To test this hypothesis, we analysed 10 years of historical data on RDFS (1994 – 2004; archived by the California Canning Peach Association) and early Spring temperature conditions at three different locations in California.

MATERIALS AND METHODS

Pooled data on FBD, RD, and RDFS, from all California clingstone peach cultivars, were obtained from the California Canning Peach Association (data previously collected by University of California Cooperative Extension and CCPA field staff) for three different locations in California; Fresno/Kings Counties (Kingsburg), Stanislaus County (Modesto) and Yuba/Sutter Counties (Yuba City). FBD and RD data were collected from 1984-2004. RDFS data were collected from 1994-2004.

Cumulative data on GDH, rainfall, solar radiation and soil temperatures, from FBD to RD, were calculated from the daily sums for specific intervals during peach fruit growth (10, 20 and 30 DAFB, and at the RD). Daily sums of GDH were calculated using hourly temperature data based on the GDH equation presented by

Anderson *et al.* (1986). Daily sums of solar radiation and soil temperature were calculated using hourly solar radiation and hourly soil temperature data, respectively. Hourly climatic data were obtained from the California Irrigation Management Information System (CIMIS) weather stations closest to the locations where the fruit data were collected: Parlier Station in Fresno County, Modesto Station in Stanislaus County, and Nicolaus Station in Yuba County. Climatic data were available from 1984-2004 at Parlier and Nicolaus, and from 1988-2004 at Modesto.

Since temperature affects the regulation of all biological processes, relationships between the different GDH parameters, time intervals, and the number of days between FBD and RD were evaluated for each location.

Absolute fruit growth rates (FGR) were calculated as mm of fruit diameter growth d⁻¹ between FBD and RD. RDFS and FGR were analysed in conjunction with seasonal environmental data, including accumulated GDH, rainfall, soil temperature and solar radiation from FBD to RD.

The effects of location and year on environmental factors were analysed by analysis of variance (ANOVA). The effects of the different GDH accumulation intervals on the number of days between FBD and RD, RDFS and FGR were evaluated by regression analysis, independent of location, since their slopes were identical, as determined by analysis of covariance (ANCOVA). The effects of the other environmental data, and the number of days between FBD and RD, on RDFS and FGR were evaluated by regression analysis, as described previously. The procedure, PROC GLM (SAS Institute, Cary, NC, USA), was used for all analyses. Statistical significance was established for P < 0.05, and Tukey's test was applied to separate least square means (LSM) that differed significantly.

RESULTS

There were substantial differences in FBDs and RDs among locations and years over the 20 years for which data were analysed, and the number of days between FBD and RD was not clearly related to FBD (Table I). FBD and RD were always earlier at Kingsburg than at Modesto or Yuba City; but there was very little difference between the latter two locations (Table I).

There were also significant differences in GDH30 between the three locations (Table II). Kingsburg consistently had higher GDH30 values than Modesto and Yuba City. There was also significant variation in GDH30 values among the different years. However, there were no significant differences in accumulated GDH from FBD to RD (GDH FBDtoRD) among years, although Yuba City generally had lower GDH FBDtoRD values than Kingsburg and Modesto (Table II).

Table I Recorded full bloom date (FBD), reference date (RD), and time from the period FBD to RD in relation to the different peach orchard locations, from 1984-2004

Location	Full bloom date (FBD)			Reference date (RD)			Average
	Earliest	Average	Latest	Earliest	Average	Latest	FBD to RD (d)
Kingsburg	19 February	5 March	11 March	3 May	13 May	27 May	69 ± 6
Modesto	27 February	9 March	17 March	12 May	21 May	3 June	73 ± 6
Yuba City	26 February	9 March	19 March	9 May	21 May	4 June	72 ± 8

Table II

Accumulated growing degree hours (GDH) and solar radiation 30 d after the full bloom date (FBD) and from the FBD to the reference date (RD) in relation to the different peach orchard locations, from 1984 – 2004

Effects tested on	Sum of	GDH	Sum of solar radi	iation (J s ⁻¹ m ⁻²)	Solar radiation/heat accumulation (J s ⁻¹ m ⁻² GDH ⁻¹)
environmental factors	30 d after FBD	FBD to RD	30 d after FBD	FBD to RD	FBD to RD
Location Year LSM for the locations	0.0001 ^Y 0.0001	0.0001 0.3703	0.7404 0.0001	0.0314 0.1260	0.0001 0.0267
Kingsburg Modesto Yuba City	$6.7 \times 10^{3} \text{ a}^{Z}$ $5.8 \times 10^{3} \text{ b}$ $5.9 \times 10^{3} \text{ b}$	1.75×10^4 a 1.72×10^4 a 1.69×10^4 b	1.46×10^{5} 1.49×10^{5} 1.48×10^{5}	$3.96 \times 10^{5} \text{ b}$ $4.34 \times 10^{5} \text{ a}$ $4.19 \times 10^{5} \text{ a}$	22.8 c 25.2 a 24.7 b

^YProbability according to ANOVA analysis.

Table II also contains a ratio of sunlight to temperature for each location that we termed the "solar radiation:heat accumulation ratio". These values were obtained by dividing the accumulated solar radiation from FBD to RD, by GDH FBDtoRD. Although this ratio was not correlated with any of the variation observed among years for a specific location (data not shown), Kingsburg had the lowest mean solar radiation:heat accumulation ratio of the three locations, and Modesto had the highest.

There was a clear negative correlation between GDH30 and the number of days from FBD to RD (Figure 1A). But the number of days between FBD and RD was not correlated with the accumulated GDH for the same period (Figure 1B).

There was a clear positive correlation between the number of days from FBD to RD and the RDFS (Figure 2A). However, RDFS was not correlated with GDH FBDtoRD (Figure 2B).

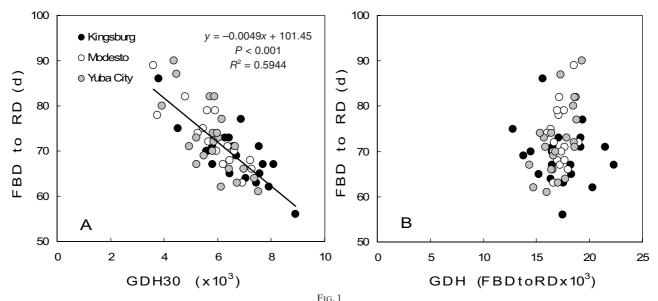
RDFS was not correlated with accumulated rainfall, solar radiation, or soil temperature for any time interval during early peach fruit growth (results not shown). Nevertheless, RDFS was negatively correlated with GDH30 (Figure 3).

There was a linear relationship between absolute FGRs (mm fruit diameter growth d⁻¹ between FBD and RD) and GDH30 (Figure 4). However, comparing these

FGR values with the daily growth rates required to achieve the same RDFS as in the coolest Springs (Figure 4; dashed line), clearly indicated that FGRs did not keep up with fruit development rates in warm years, particularly when GDH30 was substantially above 6,000.

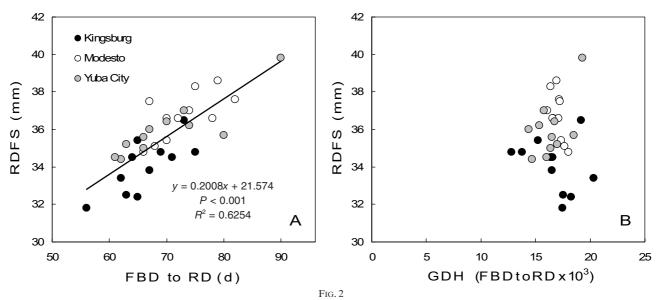
DISCUSSION

This study used fruit growth analysis from FBD to RD as an indicator of the influence of early Spring weather conditions on RDFS, and tested the hypothesis that RDFS is generally lower in years when early Spring temperatures are high. FBD, RD and RDFS data were collected on an area-wide basis by CCPA field staff. Therefore, the samples that were analysed came from different peach orchards with different characteristics (i.e., cultivars, training systems, etc) and different commercial practices (i.e., irrigation systems, pruning practices, crop loads, etc). The inherent variability in the source of the fruit samples, and in the environmental conditions within any given year (Table II), provided an excellent opportunity to test variations in fruit size among years, in relation to environmental factors. Thus, if a relationship between fruit size and a climatic factor was found, one could assume that the factor played a significant role in fruit growth. We found that the



Relationships between the sum of GDH 30 d after the full bloom date (GDH30) and the number of days between the full bloom date (FBD) and the reference date (FBDtoRD; Panel A), and between the sum of GDH from FBD to RD (GDH FBDtoRD) and the number of days for the same period of time (Panel B) at three different peach orchard locations in California. Regression statistics for the line are provided in Panel A.

^ZMean values followed by different lower-case letters in the same column are significantly different at P = 0.05.



Relationships between days from the full bloom date (FBD) to the reference date (FBD to RD) on peach fruit size at the reference date (RDFS; Panel A), and between the sum of GDH from FBD to reference date (GDH FBDtoRD) on peach fruit size (in mm) at the reference date (RDFS; Panel B) at three different peach orchard locations in California. Regression statistics for the line are provided in Panel A.

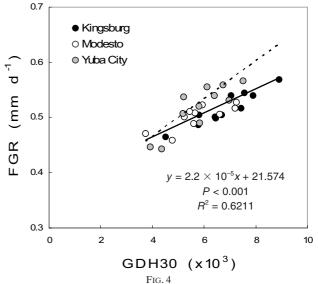
number of days between FBD and RD was negatively correlated to heat accumulation for the first 30 d after FBD (GDH30; Figure 1A), and that RDFS was a function of the number of days between FBD and RD (Figure 2A). On the other hand, there were no clear relationships between GDH accumulated between FBD and RD and the number of days between FBD and RD (Figure 2B), or RDFS (Figure 2B). This clearly indicates that heat accumulation during the first 30 days after FBD was a driver for both fruit development and growth. The first result (Figure 1A) was not surprising, as temperature is a well-known driver of plant phenology, and the period from FBD to fruit maturity has already been shown to be negatively correlated with GDH30 (Ben Mimoun and DeJong, 1999). However, the positive relationship between RDFS and the number of days between FBD and RD (Figure 2A) was not as predictable, because phenology and growth are often

y = -0.001x + 41.55 Kingsburg P < 0.001 40 Modesto $R^2 = 0.4117$ Yuba City RDFS (mm) 38 0 36 34 32 30 0 2 4 6 8 10 GDH30 $(x10^3)$

FIG. 3
Relationship between the sum of GDH 30 d after the full bloom date (GDH30) and fruit size (in mm) at the reference date (RDFS) at three peach orchard locations in California. Regression statistics for the line are provided.

linked and thus might be related to temperature in a similar manner.

Our results indicated that accumulated temperature 1 month after FBD (GDH30) was a major environmental factor influencing peach fruit growth during the Spring (Figure 3; Figure 4). A comparison of the actual data points in Figure 4, with the dashed line, indicates what the relationship would look like if FGR kept pace with increased temperature exposure (GDH30). While low temperatures apparently limited FGR when early Spring temperatures were cool (low GDH30), final fruit size at the RD was good (Figure 2A) because fruit development rates were also slow, and resource supply was less limiting (Figure 1A). Ben Mimoun and DeJong (1999)



Relationship between the sum of GDH 30 d after the full bloom date (GDH30) and the calculated fruit diameter growth rate (FGR; in mm d⁻¹) at three peach orchard locations in California. The solid line is the regression fit to the real data. The dashed line indicates an estimate of the fruit growth rate that would have been required for fruit exposed to higher Spring temperatures (higher GDH30) to reach the same RDFS as in the year with the lowest GDH30. Regression statistics for the line are provided.

showed that fruit harvests were probably also relatively late in these years. It is noteworthy that, as GDH30 values increased substantially beyond 6,000, there was a clear departure of the data points from the dashed line (Figure 4). The dashed line indicates what the growth rate d⁻¹ should have been in order to reach a final RDFS comparable to that of fruit exposed to the coolest Spring temperatures. This shows that high temperatures after FBD became a major factor affecting actual fruit growth rates and, ultimately, RDFS. Under high temperature conditions, fruit development rates were high (Figure 1A), but the trees may not have been capable of supplying resources rapidly enough to support the potential fruit growth rates that apparently accompanied the higher temperatures (Grossman and DeJong, 1994; DeJong and Grossman, 1995). Thus, because actual fruit growth rates apparently could not keep up with the potential growth rate, RDFS was less than in years when the accumulated GDH30 was below 6,000 (Figure 3).

It is likely that some of the apparent inability of trees to support the full potential fruit growth demand in very warm Springs could be related to transport limitations rather than to a lack of resource supply. DeJong and Grossman (1995) estimated that transport limitations could be substantial, particularly during the Spring. It could be that, during exceptionally warm Springs, development of nutrient transport pathways may also not be sufficiently rapid to keep up with demand.

It is possible that fruit set, and thus initial crop load, may have been a factor influencing the RDFS and GDH30 relationship, as fruit set is known to vary with weather conditions at FBD and can also have substantial effects on fruit growth rates and final fruit size (RDFS; Grossman and DeJong, 1995b; Berman *et al.*, 1998). However, from our data-set, it was not possible to evaluate this variable independently.

Initially, we anticipated that solar radiation, or the ratio of solar radiation:heat accumulation from FBD to RD (Table II), could explain some of the annual variation in RDFS, but this was not the case. Kingsburg tended to be the warmest location and received the lowest amount of solar radiation between FBD and RD (Table II), but the decreased solar radiation was due mainly to the shorter period between FBD and RD, and the shorter days associated with an earlier FBD (Table I).

We also anticipated that root temperature may have influenced RDFS, since it affects root activity and the rate of mobilisation of root reserves (Nightingale, 1935; Cockroff and Olsson, 1972). However, the soil temperature data was not correlated with the fruit size

data. This may have been because the CIMIS soil temperature sensors were not installed deeply enough, or in the actual orchards, so were probably not truly representative of the orchard root temperatures.

It is well-documented that there is a strong relationship between early fruit size and final fruit growth, when trees are thinned appropriately (Davis and Davis, 1948; Proebsting, 1962; Grossman and DeJong, 1995a; Wu et al., 2005). This is apparently because peach fruit growth, for any time interval, is a function of fruit size at the beginning of that interval, the potential growth rate, and the resources available to support growth (Grossman and DeJong, 1995a). Therefore, this research may provide practical information that can help growers to anticipate difficulties in obtaining marketable fruit sizes from the weather experienced during the first 30 DAFB, and to make general recommendations to optimise the timing and extent of fruit-thinning operations.

It is well known, with normal peach fruit set, that fruitthinning at any time before harvest reduces fruit-to-fruit competition for water and carbohydrates, but fruitthinning early in the season results in the greatest increase in size (DeJong et al., 1990; Grossman and DeJong, 1995b; Costa and Vizzoto, 2000). In apple, Jones et al. (1992) documented that every 7 DAFB a tree carries too many fruit, costs 3-6 % in final fruit size. However, growers often delay fruit-thinning until late Spring because thinning costs are greater when the fruit are small (DeJong et al., 1990). This study indicates that early fruit growth is likely to be more resource-limited in warm Springs and, therefore, growers may substantially improve production by early thinning in years with higher Spring temperatures and heavy fruit sets. In these years, it is recommended that growers should thin as early as is economically feasible, and plan to thin the earliest harvested cultivars first (DeJong, 2005). Thus, we recommend that growers monitor bloom dates (FBD) and use local weather information (e.g., in California, visit http://fruitsandnuts.ucdavis.edu/weather/index.shtml) to determine GDH accumulation 30 DAFB, and use these GDH30 values to predict the RD and fruit-sizing potential for the coming season.

Gerardo Lopez received an FPI grant from the Spanish Ministry of Research and Technology to conduct this research at the University of California, Davis, USA. The authors wish to thank Rich Hudgins and staff of the California Canning Cling Peach Association for providing the FBD, RD and RDFS data that made this study possible.

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