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Climatic Requirements for Rest Completion in Dormant Peach and Apple Buds

A. Erez, G.A. Couvillon

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Title of Proposed Research

Climatic requirements for rest completion in dormant peach and apple buds

Name and Address of Investigators

Principal Investigator: Amnon Erez, ARO, The Volcani Center, Israel

Cooperating Investigator: Gary A. Couvillon, University of Georgia, U.S.A.

Name and Address of Affiliated Institutions

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Principal Investigator

A. Erez

Amnon Erez

Institution's Authorized Official

Yuval Eshdat

Dr. YUVAL ESHDAT
Head, Div. for Research Projects and Budgets
Agricultural Research Organization

1) Peach 2) Apple 3) Dormancy in plants 4) Buds

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Table of Contents

1. Abstract

Catalase and lipase activities in dormant apple and peach buds showed a complex change with exposure to winter chilling. In apple, catalase showed a reduced activity during the mid rest period, followed by regained activity with increased exposure to chilling.

With peach lateral leaf buds, the trends were not clear. With peach flower buds, a gradual decrease in activity in chilled material relative to the control was evident.

Variations in acid lipase activity were noted with peach flower buds. Increased activity was found after partial exposure to chilling followed by a drop in activity and the appearance of strong activity of basic lipase. In both peach and apple vegetative buds, lipase activity was low throughout the rest period. Activity of both lipase enzymes was lower when incubated at 6^{o} than at $28^{o}C$.

Use of a crude determination indicating a certain physiological age does not seem to be reliable enough at this point, although lipase determination for peach flower buds seems promising.

Three temperature effects on dormant peach buds were characterized and quantitatively defined, and the overlapping effects were separated. Chilling was found to have a similar effect between 0 and $8^{o}C$, with a reduced effect at higher temperatures up to $14^{o}C$. High temperatures were found to antagonize chilling already at $17^{o}C$, with increased activity at higher temperatures. An interaction of high temperature level and duration was found. The negating high temperature effect was found to be accentuated by increased light irradiance. A third - moderate - temperature effect was characterized, showing maximal activity at $13^{o}C$ and having a lower Q_{10} than the high-temperature effect. A scheme of a two-step reaction was adopted to explain the data obtained and those reported in the literature. Use of the data obtained to improve climate in the orchard by reducing excessive heat in winter by evaporative cooling, was found successful.

2. Enzymatic activity of catalase and lipase in dormant peach and apple buds

2.1 Materials and methods

2.1.1 Catalase

The enzyme preparation involved maceration of a certain number of freshly excised buds by an ultra Turax at a speed of 13000 rpm in 3 to 5 ml of phosphate buffer, pH 7.0, for 30 seconds. The maceration test tube was immersed in an ice bath to prevent heating of the system.

Two systems were used for determination of the enzymatic activity: the disc floatation method and the polarographic method. The disc floatation method of Gagnon et al. (2) was used with M&M paper discs.

An aliquot of 100 µl in four replicates was put on every disc and dropped into 5 ml solution of 3% H_2O_2, at ambient room temperature. The time for disc floatation was monitored with a stop watch. Every determination was replicated four times (true replicate of different set of buds). Catalase activity was calculated using the formula $\frac{h \cdot w}{a}$, where h=seconds of floatation; w==f.wt. of tissue examined or mg of protein in examined aliquot; and a= reading per certain equal wt of tissue or level of protein.

At every sampling, fresh weight of buds was determined. Checking pure catalase (Sigma) activity in this method produced a hyperbolic graph (Fig. 1). Between readings of 15 and 80 seconds, a response very close to the linear was obtained. Reduced sensitivity of the test was observed at high catalase activities.

Polarographic determination of catalase was checked using a Clark oxygen probe after Rorth and Jensen (4). The system included 2.8 ml phosphate buffer, pH 7.0, 100 µl enzyme and 100 µl of H_2O_2.

Reaction took place at 27°C for 90 min. Activity was expressed as µg of oxygen liberated per min and per 100 mg f.wt. of tissue.

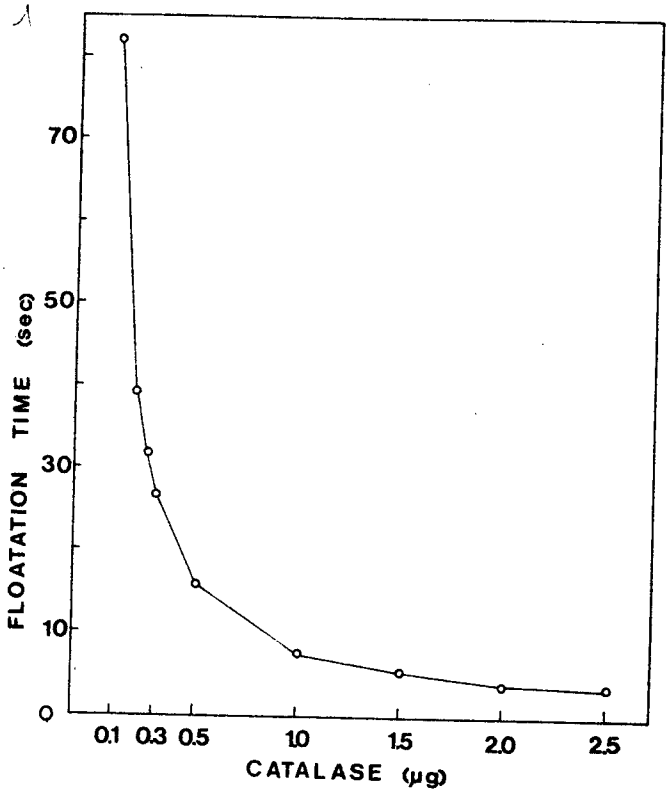

Fig. 1. Time for disc floatation at various catalase levels.

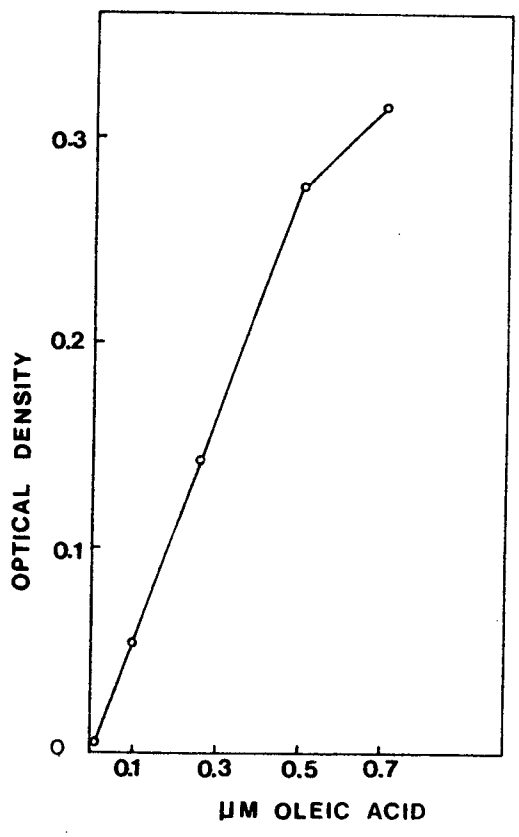

Fig. 2. Optical density with the rhodamine reagent at various concentrations of oleic acid.

2.1.2 Lipase (Acid and Basic)

Acetone powder of groups of 40 peach leaf or flower buds, and of apple leaf buds, was prepared at 2- to 4-week intervals starting from zero time in autumn before exposure of the plants to chilling and throughout the chilling period. All samples were kept in a deep freezer until examination.

The acetone powder was suspended in 1 ml of phosphate buffer at pH 5.0 for acid lipase, and at pH 8.0 for basic lipase, and was shaken with fresh olive oil (5) and gum arabicum at a ratio of 1 ml of enzyme with 5 ml of substrate, according to Chakrabathy et al. (1).

Reaction took place in a shaking bath at a temperature of either 6^{o} or $28^{o}C$.

Lipase activity was determined by following the fatty acids, hydrolized using either the Rhodamine color reaction test with acid lipase, or by using back titration to pH 8.0 with the basic lipase. Two systems were checked simultaneously, in two replicates: A 'reaction system', which contained the enzyme and the substrate, and a 'time 0 reaction', which contained the enzyme and into which the substrate was added at the end of reaction. In addition, a substrate blank was checked with every determination. The duration of the reaction was 3 to 24 h.

Readings from the Rhodamine reaction at 535 nm were determined using a calibration curve of oleic acid reacted with the same reagent (Fig. 2). Readings from the titration reaction are presented as µM oleic acid by converting micro equivalents acids into µM of oleic acid.

Data are presented as µM acid per ten buds per hour of incubation.

2.2 Results

2.2.1 Catalase

In the first season, working with material collected from the orchard, a gradual increase in activity was found with apple vegetative leaf buds on a per-bud basis (Fig. 3; Fig. 4). (Note: activity proportional to reduction in disc floatation time !). During early December the increase in activity was steep with both systems examined, a further mild increase in activity conti-

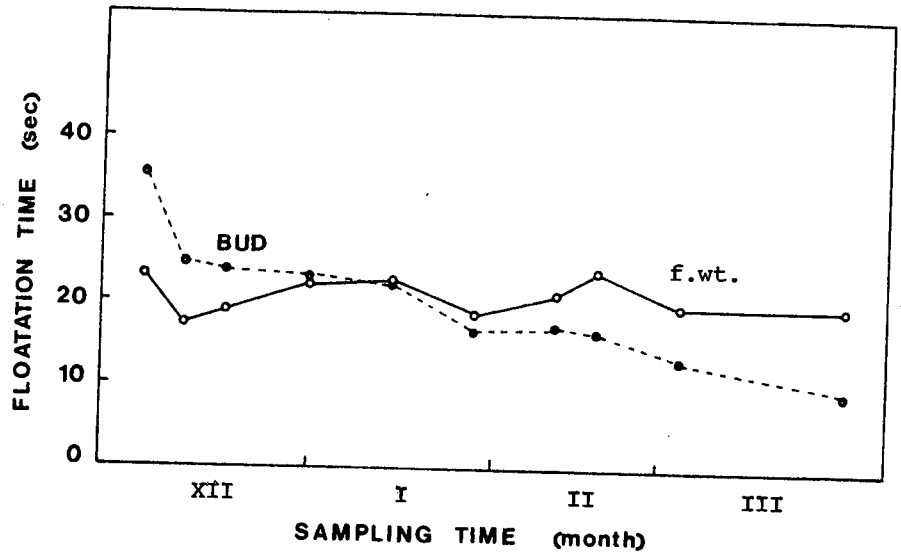

Fig. 3. Catalase activity in 'Golden Delicious' apple leaf buds collected from an orchard in the Jerusalem mountains throughout the winter. Activity expressed as time for disc floatation per 0.1 g of buds per single bud.

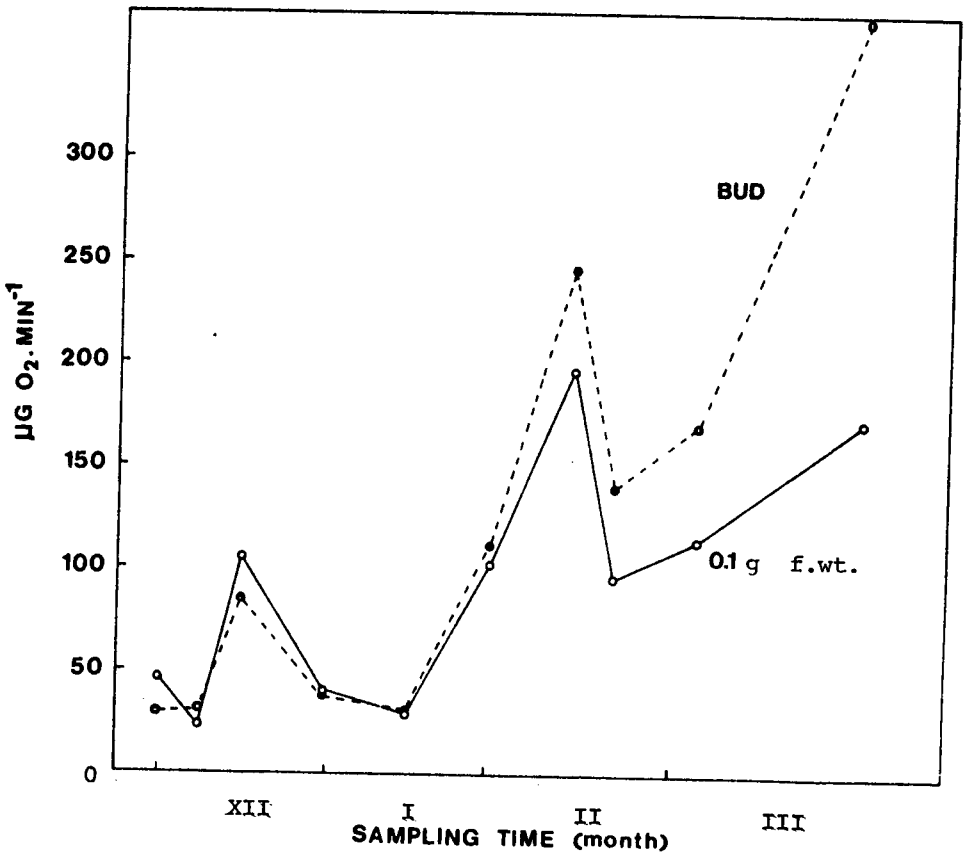

Fig. 4. Catalase activity in 'Golden Delicious' apple leaf buds. Activity expressed as μg oxygen liberated per bud or 0.1 g fresh bud weight (details as in Fig. 3).

nued until mid January with the floatation method, while with the polarographic method reduced activity was evident during this period. A steeper increase until the end of March with the disc floatation method, and a re-increase in activity with the polarographic technique, were found. Highest activity in both methods was found at the last sampling date, at the end of March. On a fresh-weight basis a gradual smaller increase during winter was noted with the polarographic method (Fig. 4), while no clear effect was found with the disc floatation method (Fig. 3).

With 'Redhaven' peaches activity of leaf buds, on a fresh-weight basis (Fig. 5), was reduced to a low at the beginning of January, with a re-increase until the end of January, followed by a gradual decrease until bud break.

Similar results were obtained with flower buds on a per-bud basis (Fig. 6): a sharp reduction in activity in early December was followed by a gradual increase until bud break. When expressed on a per-fresh-weight basis, a continuous reduction in activity was obtained until Dec. 24 (Fig. 7). Up to the beginning of February, a more or less constant activity was evident, after which there was a reduction in activity until bud break.

Examination of leaf buds of both the 'Golden Delicious' apple and the 'Redhaven' peach was carried out in the second season in parallel from continuously chilled plants and from greenhouse-held plants that were not exposed to any chilling lower than $15^{o}C$. As very few flower buds were present on the young plants, only leaf buds were analyzed. Both disc floatation and oxygen electrode techniques were used. In the peach (Fig. 8), an initial relative increase in activity with chilling was followed by decrease toward the end of rest. These trends were more pronounced with the oxygen electrode than with the disc floatation method. With the apple (Fig. 9), a sharp initial decrease in catalase activity was followed by an increase in activity at midrest.

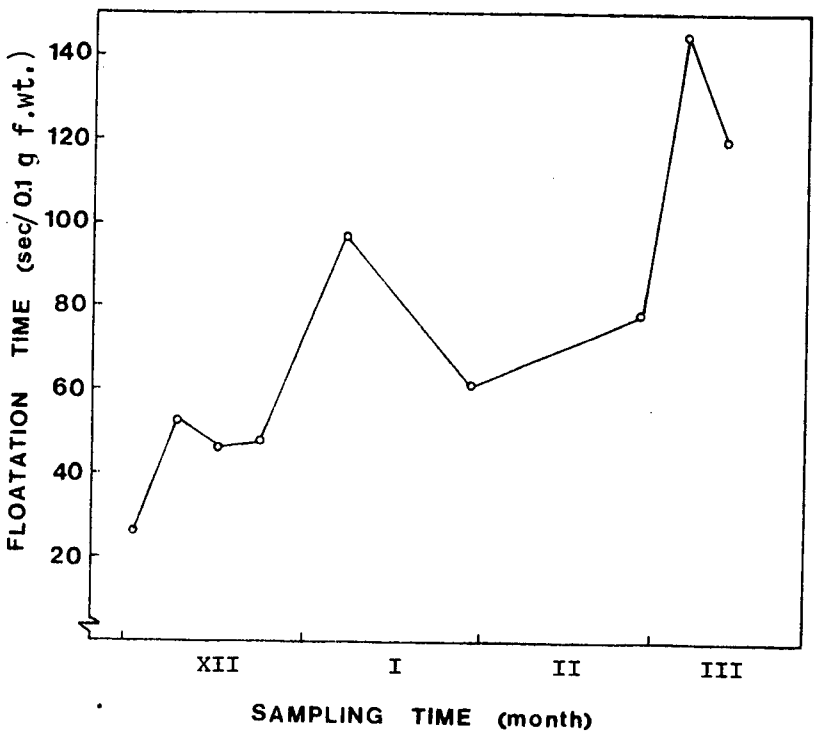

Fig. 5. Catalase activity in 'Redhaven' peach leaf buds collected from an orchard in the Jerusalem mountains throughout the winter. Activity expressed as time for disc floatation per 0.1 g of fresh buds.

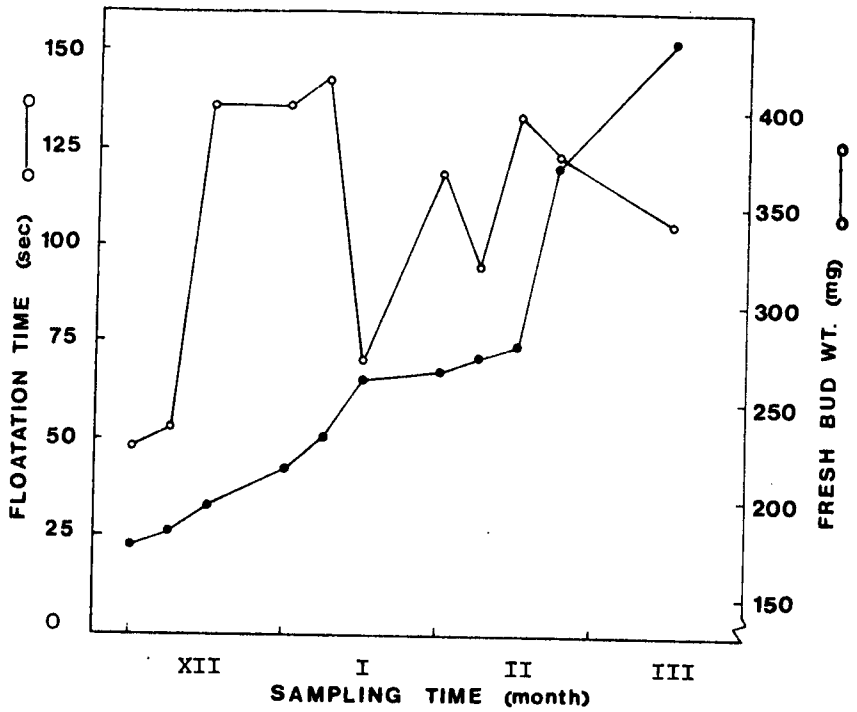

Fig. 6. Catalase activity in 'Redhaven' peach flower buds in comparison with bud weight. Activity expressed as time for disc floatation per bud (details as in Fig. 5).

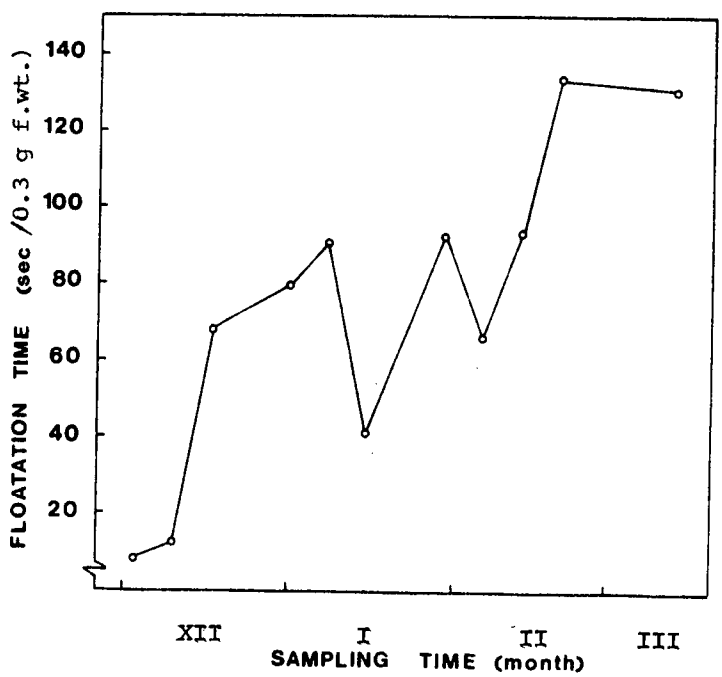

Fig. 7. Catalase activity in 'Redhaven' peach flower buds. Activity expressed as time for disc floatation per 0.3 g of fresh buds.

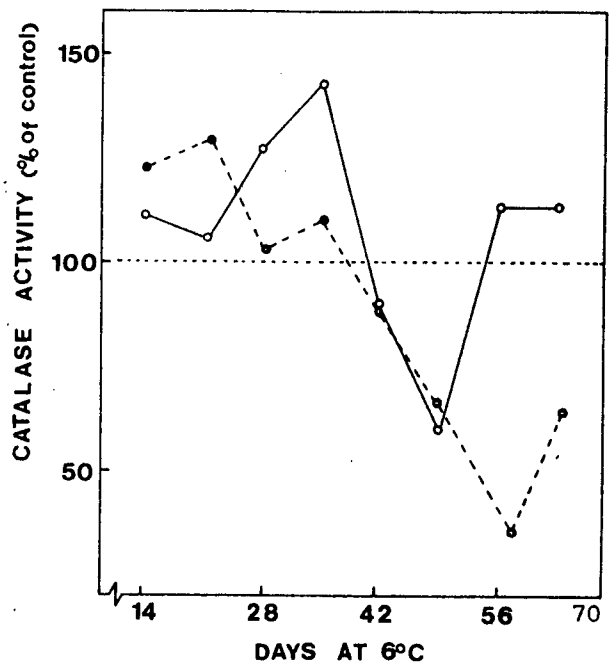

Fig. 8. Catalase activity in 'Redhaven' peach leaf buds after exposure for various periods of time to continuous 6°C, in comparison with nonchilled control. Activity expressed as percent of control in both disc floatation and oxygen electrode determination, on the basis of 0.3 g fresh bud weight.

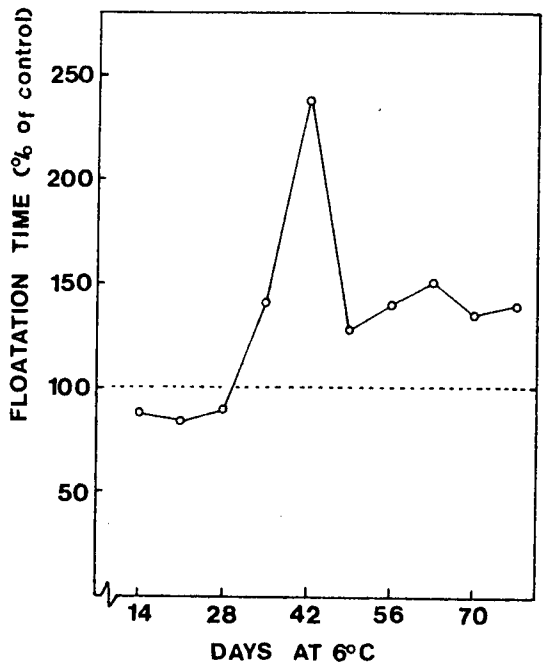

Fig. 9. Catalase activity in 'Golden Delicious' apple leaf buds after exposure for various periods of time to continuous 6°C, in comparison with nonchilled control. Activity expressed as percent of control of disc floatation on the basis of 0.1 g fresh bud weight.

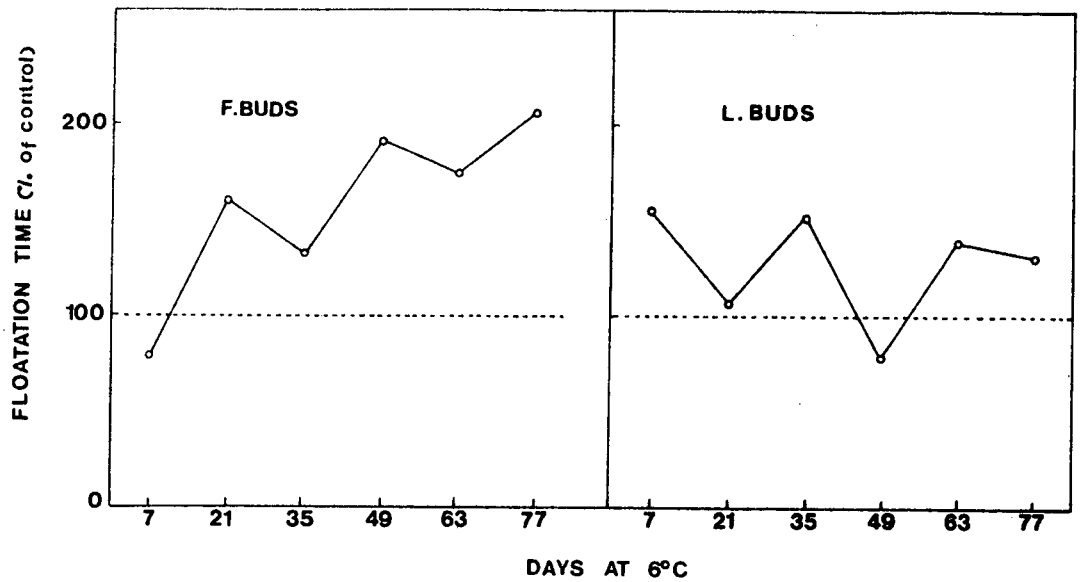

Fig. 10. Catalase activity in 'Redhaven' peach flower buds (left) and leaf buds (right) after exposure for various periods of time to continuous 6°C in comparison with nonchilled control. Activity expressed as time for disc floatation as percent of control. Determined per 0.3 g or 0.1 g fresh weight of flower and leaf buds, respectively.

A repeat examination of catalase activity in dormant peach leaf and flower buds was carried out in the third year with 'Redtop' potted plants. Both floral and lateral vegetative buds were examined. Buds chilled at 6°C continuously were compared with similar buds from trees left in the greenhouse (temp 15°C).

With flower buds, a reduction in activity was evident starting from early January (Fig. 10), but leaf buds did not show any clear change in catalase activity due to chilling.

2.2.2 Lipase

Basic lipase of peach leaf and flower buds was determined in 'Redhaven' plants held at 6°C for various periods. Activity was determined by titration of the liberated fatty acids with NaOH 0.01 N after incubation of the enzyme from acetone powder with olive oil and gum arabicum for 24 h at either 6° or 28°C. Data calculated as µM oleic acid per ten buds per 24 h, for both leaf and flower buds, are presented in Fig. 11.

Basic lipase activity in leaf buds was found to be rather low throughout the sampling period, showing a mild reduction in activity with chilling for up to 55 days, with no change in activity later. However, at 28°C incubation, flower buds showed a distinct pattern of increased basic lipase activity with chilling between the 26th and the 55th day of chilling, when peak activity was reached. Later, there was a reduction in activity. At 6°C too little activity was found for both bud types to define any trend of changing activity with chilling. At the peak activity of flower buds on the 55th day, 78% of all flower buds were able to break as well as 93% of all vegetative lateral buds. It is clear that with flower buds a correlation between readiness to break and level of basic lipase activity could exist, but this is not the case with leaf buds.

Apple vegetative buds exhibited very low basic lipase activity when incubated at 6°C (Fig. 12). Only on the last sampling date, after 96 chilling

days, was there measurable activity. At 28°C, on the other hand, a peak after 29 chilling days was followed by decreased activity and then an increase at the last sampling date.

Acid lipase with peach buds (Fig. 13) was also more active in flower than vegetative buds, with a higher peak in the 28°C incubated system. At that temperature peak activity was noted after 25 days of chilling, the first determined sample. There was a gradual decrease in activity until the 55th chilling day, when peak activity of basic lipase was noted (see Fig. 11). Lower activity of vegetative peach buds was noted, especially at 6°C incubation. In all cases, the lowest activity was found at the last date of sampling, after 82 chilling days.

In 1982, acid lipase activity in 'Babcock' peach (leaf and flower buds) and 'Golden Delicious' apple (leaf buds) was examined using the Rhodamine test. Care was taken to collect early samples. With the peach (Fig. 14), practically no activity was found in leaf buds, while in flower buds enzymic activity was found after 14 days of chilling decreasing gradually to zero at 35 days. Activity at 6°C was always lower than at 28°C except at the last determination, after 35 days of chilling. With apple leaf buds almost no activity of acid lipase was noted throughout 56 days of chilling (Fig. 15).

2.3 Discussion and Conclusions

2.3.1 Catalase

Catalase activity as measured in dormant apple and peach buds collected from the orchard during the winter is not reliable, as a dormant non-chilled control was not measured concomitantly. From examinations carried out in the second and third years of the study it became apparent that a considerable change in catalase activity took place in the non-chilled control. So that the relative activity of chilled vs. non-chilled buds will be relevant to the aim of this work namely the change in enzymic activity resulting from chilling accumulation.

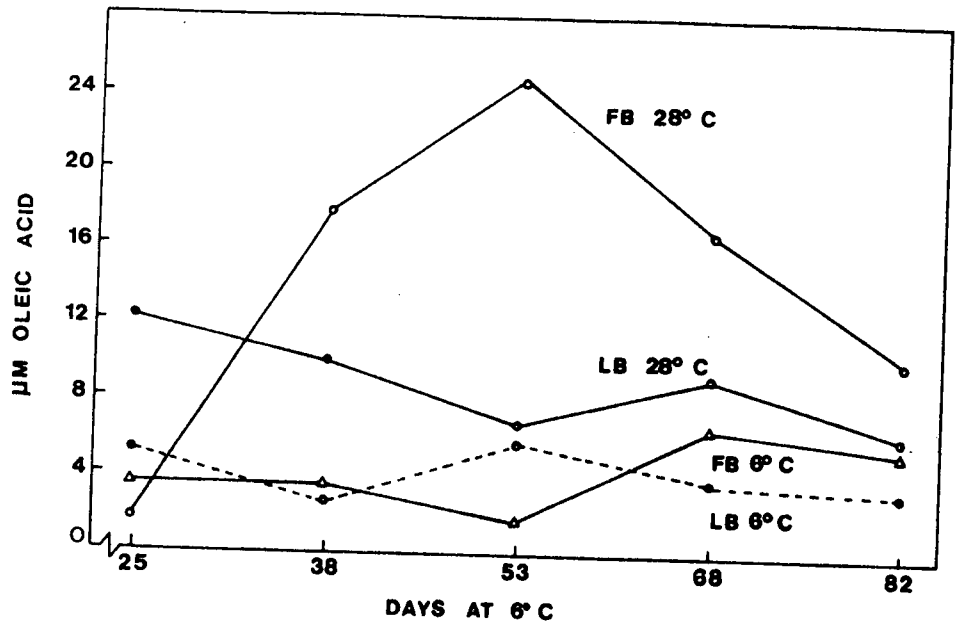

Fig. 11. Basic lipase activity in 'Redhaven' peach leaf buds (LB) and flower buds (FB), after exposure for various periods to chilling at $6^{o}C$. Activity expressed as µM of oleic acid liberated from olive oil during 24 h of incubation at 6^{o} or $28^{o}C$.

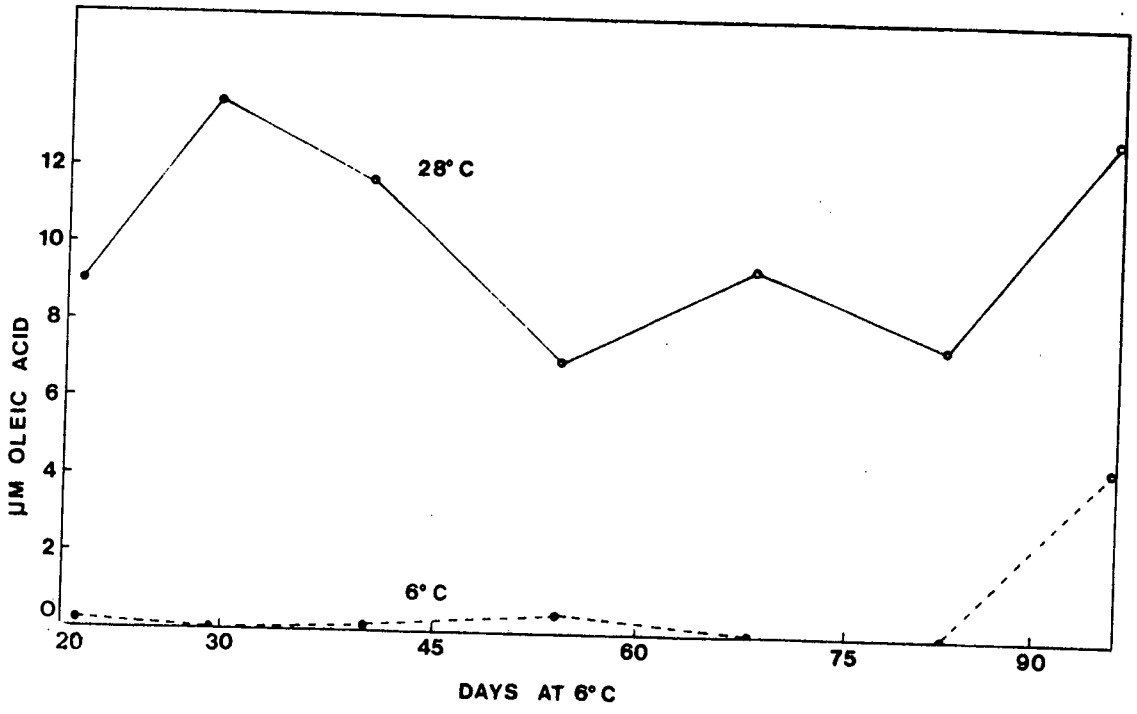

Fig. 12. Basic lipase activity in 'Golden Delicious' apple leaf buds after exposure for various periods to chilling at $6^{o}C$. (Details as in Fig. 11).

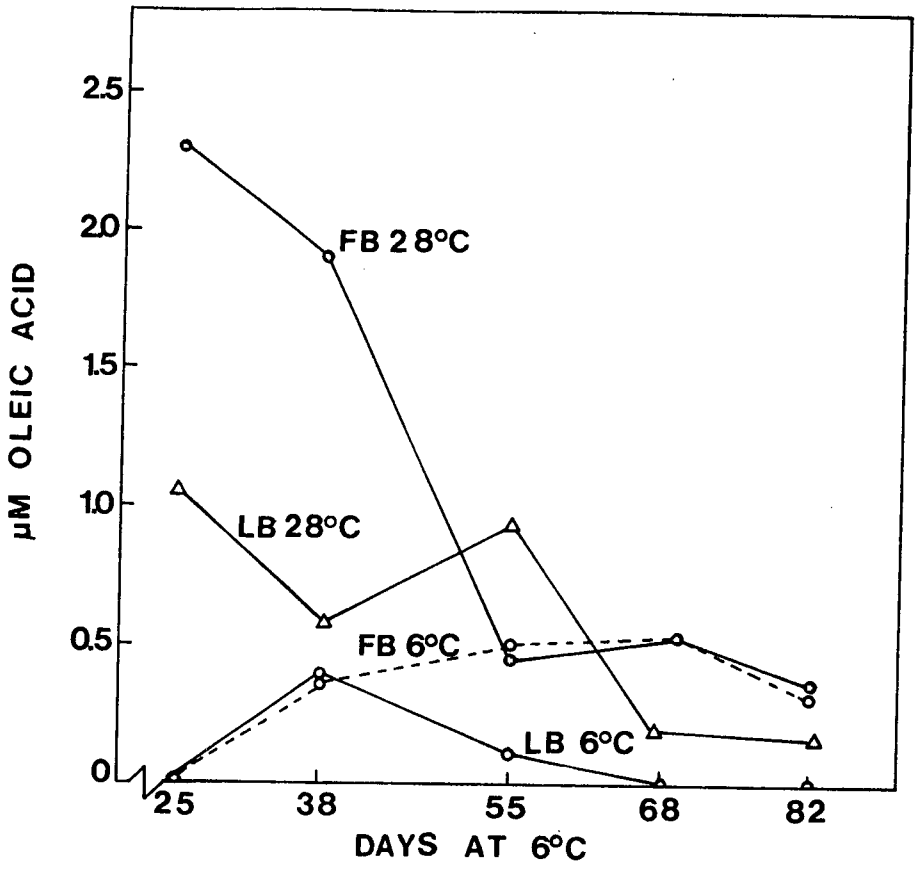

Fig. 13. Acid lipase activity in 'Redhaven' peach leaf buds (LB) and flower buds (FB) after exposure for various periods to chilling at 6°C. (Details as in Fig. 11).

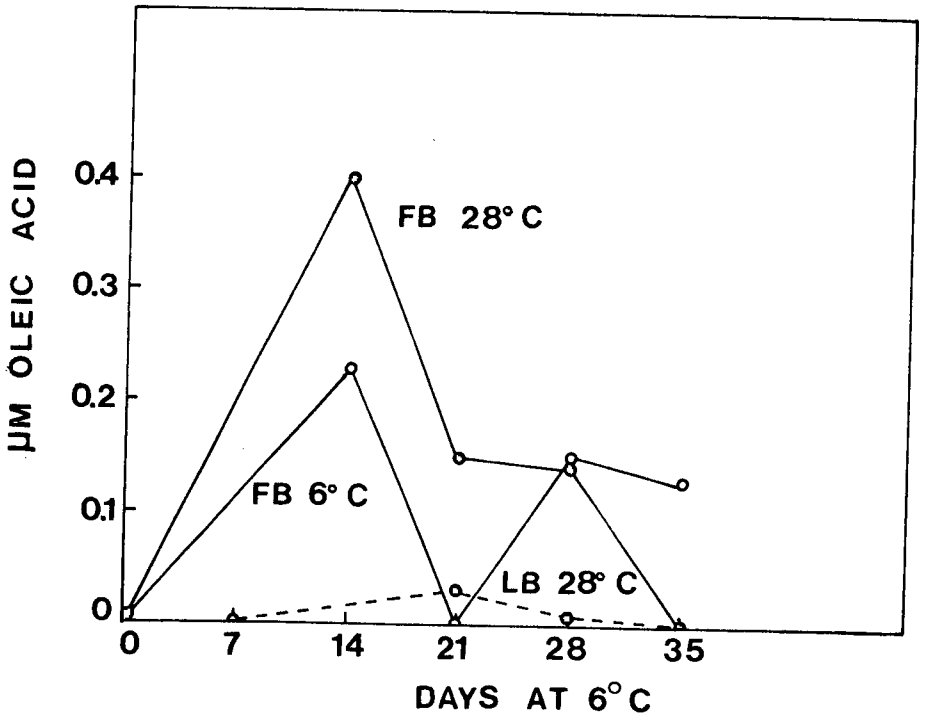

Fig. 14. Acid lipase activity in 'Babcock' peach leaf buds (LB) and flower buds (FB) after exposure for various periods to chilling at 6°C. (Details as in Fig. 11).

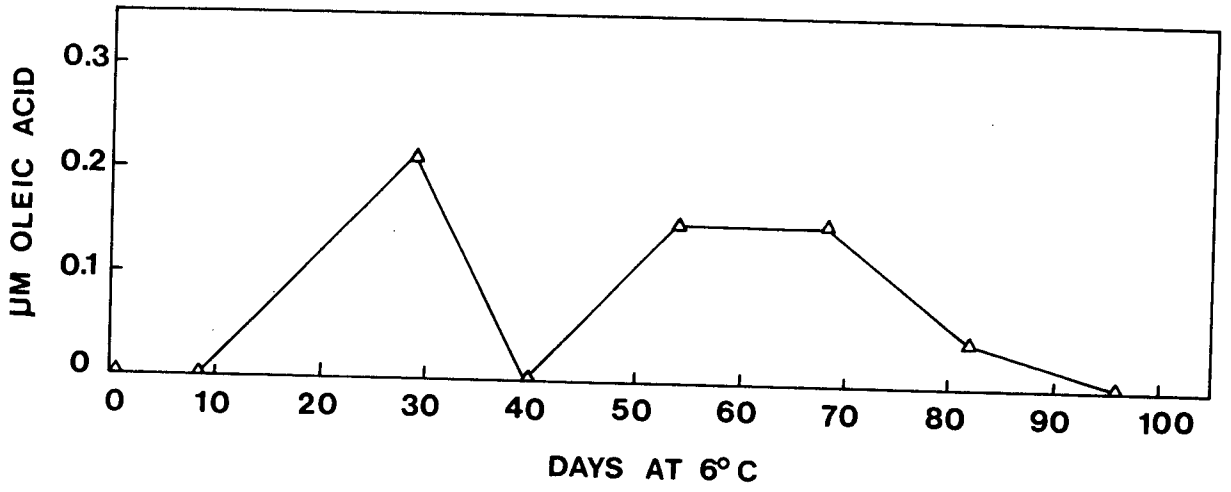

Fig. 15. Acid lipase activity in 'Redhaven' apple leaf buds after exposure for various periods to chilling at $6^{o}C$. (Details as in Fig. 11)

In doing so it became apparent that, in apple, with leaf buds (the only bud type studied) a temporary reduction in activity is followed by an increase (Fig. 9); no clear pattern was obtained with peach leaf buds, as conflicting results were obtained in the second and third years of study. With 'Redhaven' (Fig. 8), an initial increase in activity was followed by a strong reduction, whereas with 'Redtop' (Fig. 10), fluctuating activity at a level lower than unchilled control was found. Peach flower buds, exhibited a clear gradual decrease in activity with chilling exposure, as was shown previously (3). It seems that this pattern could be adapted for use as an endogenous marker. However, considering the strong variations in catalase activity in the control buds, one realizes that the activity of this enzyme is influenced also by factors other than chilling. Whether these factors have a parallel effect on bud rest is not yet known. Thus, use of catalase as a physiological indicator is not recommended at this stage, even when compared with non-chilled plants.

2.3.2 Lipase

Acid lipase activity was noted in all determinations with peach flower buds. A peak in activity was found after exposure to partial chilling; additional chilling resulted in lowered activity in the buds. Basic lipase activity appeared in peach flower buds when acid lipase activity diminished. The same sequence as reported for dormant apple seeds (5,6) was verified with peach flower buds. In all cases of incubation at $6^{o}C$, activity was lower than at $28^{o}C$. We did not obtain higher activity for acid lipase at 6^{o} than at $28^{o}C$, so that in this respect the data obtained with apple seeds (5,6) could not be repeated with dormant buds.

Total activity found for acid lipase was low compared with basic lipase.

It is interesting that total lipase activity was lower in vegetative buds. It should be noted, though, that the activity obtained is expressed per bud unit, and vegetative buds are similar than floral ones.

The sequential change in acid and basic lipase may be utilized as a physiological marker for rest development in peach flower buds. In particular, basic lipase determination, which is rapid, may be useful. Only that sequence of determinations is needed. The 14-fold change in level of activity (Fig. 11) is large enough to allow easy detection even with crude measurements.

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The Effect of Level and Duration of High Temperatures on Rest in the Peach.[1]

Gary A. Couvillon

Department of Horticulture, University of Georgia, Athens, GA 30602

A. Erez

ARO, The Volcani Center, Institute of Horticulture, Bet Dagan, Israel

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ABSTRACT. Rooted 'Redhaven' peach cuttings were exposed to diurnal temperature cycles of 6°C (±0.1°C) for 16 hrs. and either 18, 19, 20, or 21°C (±0.1°C) for 8 hrs. The cycles were continued until the plants were exposed to 1200 hrs. of 6°C. A severe reduction in lateral vegetative bud break (Lb) was found in plants exposed to cycles in which the high temperature was 19° or 20°C (±0.1°C) and complete chilling negation in plants exposed to cycles in which the high temperature was 21°C. Plants exposed to cycles which had a high temperature of 18°C (±0.1°C) showed no chilling negation. The exposure of rooted 'Redhaven' peach plants to a diurnal cycle in which the high temperature was either 20 or 24°C(±0.1°C) for 0, 2, 4, 6, or 8 hrs. and 6°C (±0.1°C) for the remainder of the cycle showed that there was an increased negation effect with increased time exposure to 24°C. In cycles in which the high temperature was 20°C there was an increase in chilling efficiency with 2 and 4 hrs exposure to 20°C and gradual increases in chilling negation with longer exposures when compound to plants chilling continuously at 6°C.

Exposure of 'Harvester' peach plants to either 2, 7, or 12 days of 23°C following the accumulation of either 1/4, 1/2, or 3/4 of the chilling requirement revealed that chilling negation occurred only with the 12 day exposure to 23°C when the high temperatures were applied following the accumulation of 1/4 and 1/2 of the chilling requirement. No chilling negation due to 12 days exposure to 23°C was found if 3/4 of the chilling requirement had accumulated before the high temperature exposure.

High temperatures are known to have a negative effect on rest development in dormant peach buds (4,6). Erez et al. (4) have shown that a diurnal cycle in which 8 hrs of 21°C are cycled with 16 hrs of 4°C, results in complete chilling negation. However, 18°C in a similar cycle with 4°C results in no chilling negation and a diurnal cycle in which the high temperature was 15°C resulted in chilling enhancement. These studies suggest that a radical change in the effect of temperature on chilling negation occurs between 18° and 21°C. A determination of the exact point at which chilling negation occurs is very important in developing an accurate climatic model for the prediction of rest termination and subsequent bud break. Also, data are not available concerning the effect of duration of high temperatures in diurnal cycles on negation of chilling in peaches.

This study was undertaken to quantify the effect of level and duration of high temperature on chilling negation in peach buds.

Materials and Methods

'Redhaven' shoots of current seasons growth were removed from trees grown on the Horticultural Farm in Athens, Georgia, and rooted as previously described (1). Leaf drop on the cuttings occurred by the end of October and they were transported to the Duke University Phytotron (2) in Durham, North Carolina. Three "C" chambers capable of maintaining a temperature variation of ±0.1°C were used for 3 cyclic temperature treatments. The cycles were diurnal in which the low temperature (4°C) was maintained for 16 hrs. The high temperatures of the diurnal cycles were either 19, 20, or 21°C and the cycles were continued until all plants received 1200 hrs at 4°C. A group of plants were placed in growth chambers of the Horticulture Department in Athens and exposed to a diurnal cycle of 15/4 and 18/4 (±1°C) or 4°C continuously

until 1200 hrs at 4°C were accumulated. A third group of plants were held continuously at 22°C (±1°C) in the laboratory.

Following 1200 hrs exposure to the 4°C portion of the diurnal cycle, all plants were placed in the laboratory at 22°C for forcing in light. Bud break counts were taken weekly for 8 weeks.

Similar plants were placed in "C" chambers of the Duke University Phytotron in which the diurnal cycles consisted of either 20° or 24°C for 0, 2, 4, 6, or 8 hours with the remainder of the diurnal cycle at 6°C. The plants remained in the chamber until they were exposed to 1200 hrs of 6°C. They were then moved to the laboratory as previously described for forcing.

A 3rd group of plants of the Harvester cultivar were placed in growth chambers of the Horticultural Department in Athens. Following the completion of either 1/4, 1/2, or 3/4 of their chilling requirement at 6°C (±2°C), they were exposed to either 2, 7, or 12 days of 23°C then returned to the chambers for completion of chilling. Following 800 hrs at 6°C, they were removed to the laboratory for forcing at 23°C.

To define the degree of promotion or inhibition induced by each temperature treatment, a modulation factor was calculated using the equation:

$$\text{Modulation factor per hour of high temperature} = \frac{xy - cy}{24c - cy}$$

where: c = level of bud break at continuous temperature

x = level of bud break induced by temperature cycle

y = number of hours of chilling per day

The chamber used for all studies were held at 50 $\mu E\ m^{-2}S^{-1}$ of fluorescent light. Previous data (unpublished) had shown that light intensities of 50 $\mu E\ m^{-2}S^{-1}$ of fluorescent light did not result in increases in bud temperature over that of the ambient air.

The experimental design for all studies was a randomized complete block design with 4 replications of 16 plants each. The data were analyzed by analysis of variance and the means separated by Duncan's Multiple Range Test.

Results

Peach plants exposed to a diurnal cycle in which 15°C (8 hrs) was alternated with 4°C (16 hrs) had higher bud break levels than plants exposed to 4°C continuously (Fig. 1). Percent bud break did not differ on plants exposed to the 4° continuous and the 18°C/4°C treatments. These data agree with that already published (3). On the other hand, plants exposed to diurnal temperature cycles in which the high temperature was 19°, 20°, or 21°C had drastic reductions in bud break when compared to the 4°C continuous or the 18°/4°C and 15°/4°C temperature treatments (Fig. 1). Plants exposed to diurnal cycles in which the high temperature was 20° or 21°C for 8 hrs had poorer bud break levels than plants exposed to a diurnal cycle in which 19°C was the high temperature (Fig. 1). Bud break on plants exposed to temperature cycles in which the high temperature portion was 20° or 21°C did not differ in bud break level (Fig. 1).

These data are supported by data collected relating to the duration of various high temperature levels on chilling negation (Fig. 2). In diurnal cycles in which 8 hrs of either 20°C or 24°C were applied with 16 hrs of 4°C, the higher temperature had the greater adverse effect on bud break (Fig. 2). The duration of exposure to the high temperature in a diurnal cycle had an effect on chilling enhancement or negation. Bud break on plants exposed to either 2 or 4 hrs of 20°C cycled with 22 or 24 hrs of 6°C indicated chilling enhancement by these cycles when compared to buds chilled at 6°C continuous temperatures (Fig. 2). Increases in the high temperature exposure period to 6 or 8 hours resulted in chilling negation. When 24°C was the high temperature

in diurnal cycles with various lengths of high temperature exposure, various degrees of chilling negation were induced by all lengths of exposure to 24°C (Fig. 2). As the duration of exposure to the high temperature increased, so did the negative effect on bud break.

Exposer of 'Harvester' peach plants to either 2, 7 or 12 days of 23°C following the accumulation of either 1/4, 1/2, or 3/4 of their chilling resulted in chilling negation at only the 12 day exposure following the accumulation of of 1/4 or 1/2 of the chilling requirement (Fig. 4). Exposure of the plants to 23°C for 2 or 7 days had no influence on chilling regardless of when it was applied in the chilling period (Fig. 4).

Discussion

These data show that in teperature cycles consisting of high and chilling temperatures chilling negation can change with the level and duration of the high temperature. High temperatures of 18 to 15°C in a cycle with chilling temperatures will result in no chilling negation or chilling enhancement depending upon the level of the high temperature (3). The chilling enhancement effect of moderate temperatures in a diurnial cycle with chilling temperature can be complicated by light intensity (5). On the other hand, high temperatures of 19°C or greater in a similar diurnal cycle with chilling temperatures will result in chilling negation(3). To characterize the degree of chilling negation for each high temperature level, a modulation factor was calculated for each treatment (Fig. 4). Plants chilled at 4°C had a 0 modulation factor. The 15°/4° cyclic treatment had a modulation factor of +1.8 which means that peach buds exposed for 1 hr to this cycle responded as though they had 1.8 times the chilling of buds exposed for 1 hr to the 4°C

continuous temperature (Fig. 4). Buds on plants exposed to temperature cycles in which the high temperature was 19°, 20°, or 21°C for 8 hrs had modulation factors of-0.8,-1.6, and-1.9 respectively. These data point out the rather drastic effect of temperatures of 19°C or greater received in diurnal cycles on chilling negation in peaches on the other hand 2 or 4 hrs exposure to 20°C in a diurnal cycle with 6°C resulted in modulation factors of +1.8 and +0.9 respectively (Fig. 4). Six or 8 hrs exposure to 20°C gave modulation factors of -1.1 and -1.3 respectively. When 24°C was the high temperature in similar cycles, modulation factors of -1.5, -2.5 and -2.5 were obtained for 2, 4, or 6 hrs of exposure to 24°C respectively. A modulation factor for 8 hrs exposure to 24°C could not be accurately calculated since data are not available for 7 hrs exposure to 24°C. Since the % bud break for plants exposed to diurnal cycles in which there was 6 hrs of 24°C was near 0, it could be assumed with some certainty that 0% bud break could occur in the cycle with 7 hrs exposure to 24°C. Thus, from the data available, an accurate modulation factor calculation cannot be made for the cycle with 8 hrs at 24°C. The promotion effect on chilling of high temperatures (20°C) in a diurnal chilling cycle has been reported previously. It was shown (2) that 12 days of exposure of peach buds to 20°C following the accumulation of approximately 75% of the chilling requirement resulted in a promotive effect on bud break. An effect of this type where both chilling enhancment and negation can be obtained by exposure of buds to the same high temperatures in a diurnal cycle can only be explained when 2 antogonizing reactions are promoted by the same temperature at the same time. This point is discussed in detail elsewhere (5).

Long periods (7 or 12 days) of exposure to 23°C will have a chilling negation effect only if applied during the early stages (¼ or ½) of chilling accumulation. These long periods of high temperature exposure must be at least

12 days in length. The degree of chilling negation induced by these exposure periods does not seem to be as severe as similar temperatures given in shorter cycles (3,4).

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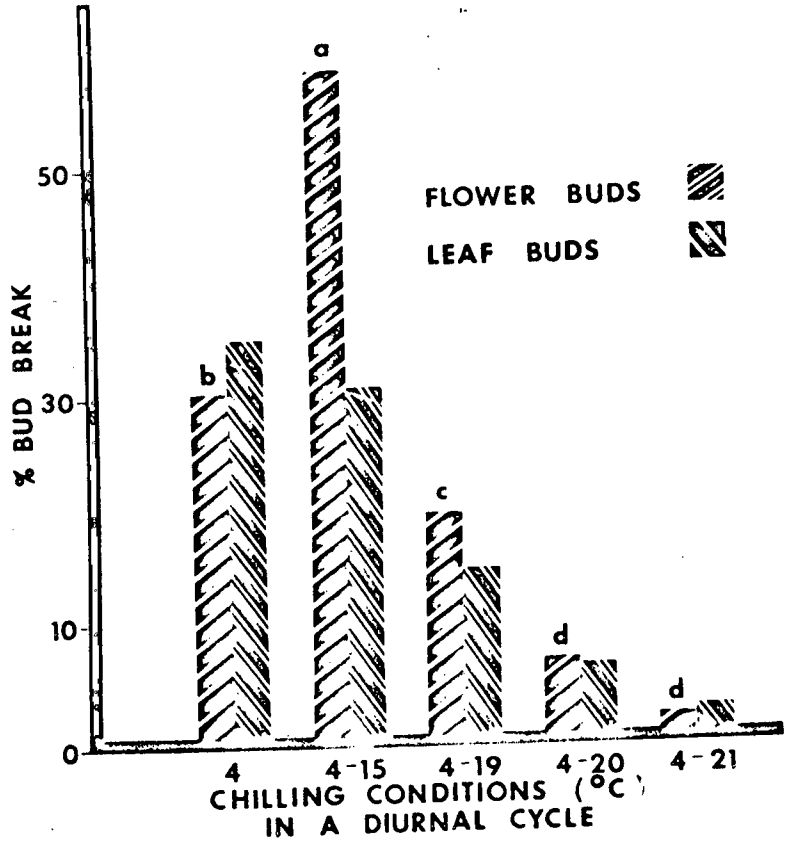

Figure 1. The influence of diurnial temperature cycles on bud break in 'Redhaven' Peach.

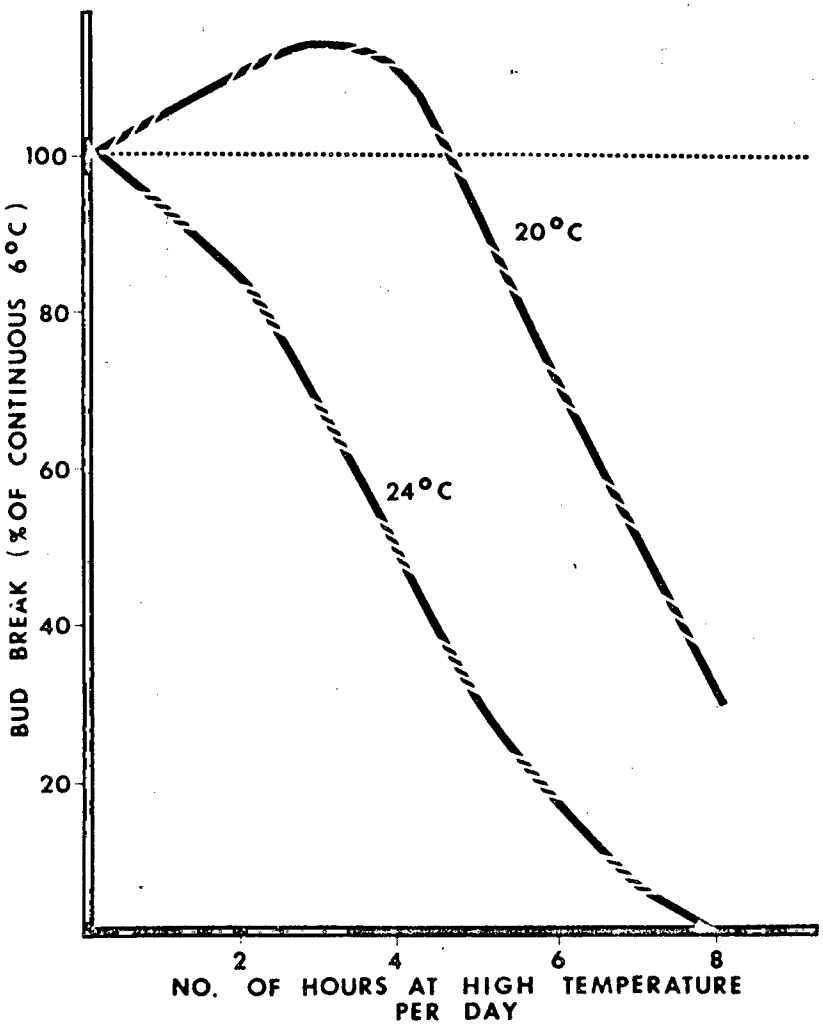

Figure 2. The influence of the duration of high temperatures in a diurnal cycle on chilling negation in 'Redhaven' peach.

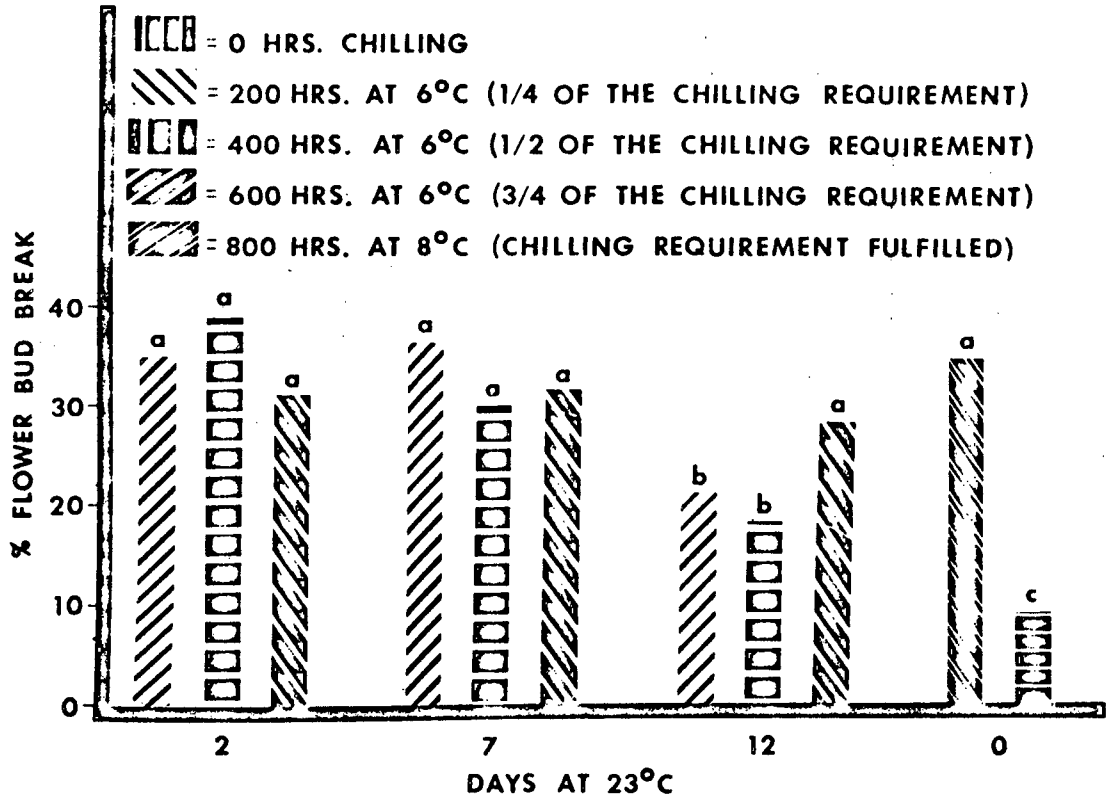

Figure 3. The influence of long periods of high temperature exposure following the completion of ¼, ½, or 3/4 of the chilling requirement on chilling negation in 'Coronet' peach.

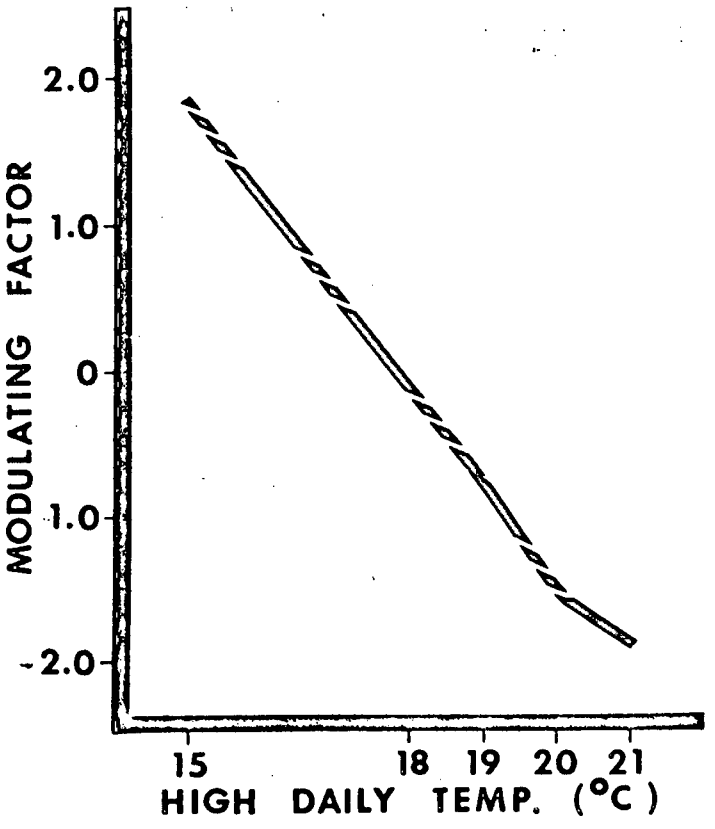

Figure 4. Calculated modulation factor for high temperature influences in a diurnal cycle.

Characterization of the Moderate Temperature Effect on Peach Bud Rest.[1]

A. Erez

Institute of Horticulture, Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel

G.A. Couvillon

Department of Horticulture, University of Georgia, Athens, GA 30602, U.S.A.

Additional Index Words. Dormancy, chilling requirement, Prunus persica

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Appreciation is expressed to the staff of the Duke University Phytotron for their assistance.

ABSTRACT

A specific effect of moderate temperatures on completion of rest in peach buds was verified. This effect was observed only when moderate temperatures were applied following prior exposure to chilling. It seems that moderate temperatures acted in a second stage following the initial chilling effect.

It was shown that the reduced chilling efficiency of temperatures between 8 and 0°C is due mostly to lack of moderate temperatures that affect the reaction of the second step.

Maximum efficiency of the moderate reaction seems to be at 13°C and its activity more prominent in the latter stages of bud rest. Leaf and flower buds react similarly, although the reaction of the former is more prominent.

A two-step scheme is proposed for the temperature effects on rest completion in peach buds. The first reaction is advanced by low temperatures and can be negated by high temperatures. The second one fixes the chilling effect and has maximal activity at moderate temperatures.

INTRODUCTION

Rest in dormant peach buds has long been known to be affected both by low temperatures - which will advance rest completion, and by high temperatures - which will negate chilling, especially when alternated with chilling in a daily cycle (3,4). A third reaction of $15^{o}C$ was noted lately. Erez et al. (3) reported a marked beneficial effect of $15^{o}C$ when cycled daily with $4^{o}C$ on lateral vegetative peach buds. As $15^{o}C$ is not supposed to have a chilling-breaking effect, this temperature effect could not agree with any rest completion model developed (e.g. 11).

In this paper a study of the third temperature effect, designated as the moderate temperature effect (MTE), is reported and a unified temperature-dependent rest-completion scheme is proposed.

MATERIALS AND METHODS

Peach semihardwood cuttings rooted according to Couvillon et al. (2) were used in the experiments. In one case hardwood cuttings rooted in the preceding winter (7) were used. Forty single-plant replicates were used for every treatment. Temperature-controlled chambers ($\pm 0.1^{o}C$) were utilized in the Duke University Phytotron facilities. In addition, Conviron E7H chambers (with an accuracy of $\pm 0.5^{o}C$) or walk-in Sherer chambers (with an accuracy of $\pm 0.4^{o}C$) were used. Light was maintained during the high temperature period and darkness when chilling was applied. Light quantum flux density was kept at 50 $\mu E\ m^{-2}sec^{-1}$ unless otherwise mentioned. Forcing conditions following the chilling treatments were $22^{o}\pm 1^{o}C$ under continuous fluorescent light of quantum flux density of 10 $\mu E\ m^{-2}sec^{-1}$.

Data were collected after 30 to 40 days of forcing and are expressed in % of buds that opened out of those that were present.

Statistical analysis according to Duncan's Multiple Range Test was carried out after arcsin $\sqrt{\%}$, transformation.

RESULTS

The effect of exposure of peach plants to continuous temperatures in the range of 0 to $20^{o}C$ was examined under controlled temperature and light con-

ditions. The response curve obtained (Fig. 1) shows a maximal effect at 8°C for both leaf and flower buds, with reduced activity towards lower and higher temperatures. No activity was found for 14°C and only low activity for 0°C. The reduction of the effect of the lower temperatures was smaller with flower buds.

The effect of moderate temperatures - 15°C - cycled daily with 0°C, 4°C and 6°C, in comparison with a continuous low temperature, was examined with small 'Redhaven' plants (Fig. 2). With constant temperatures the level of bud break was superior at 6°C than when exposed to continuous 4°C and the latter was superior to constant 0°C; when cycled with 15°C, these differences practically disappeared after 28 days of forcing, i.e., the lower the chilling temperature - the more pronounced was the effect of cycling it with 15°C.

The relative efficiency of the moderate temperature effect was checked by comparing bud break levels of plants produced from hardwood cuttings exposed to the same low temperature for 16 h daily but to various moderate temperatures for 8 h a day. Light intensity was set at 150 $\mu E\ m^{-2}sec^{-1}$. When 13°, 15° or 17°C was cycled with 6°C and compared with continuous 6°C, an enhanced effect by moderate temperatures was observed only with 13°C, while 6-15°C acted similarly to continuous 6°C and 6-17°C had a negative effect. These data were obtained under high light intensity, which may have an effect on the temperature response curve.

A wider series of cyclic temperatures was tested with 'Redhaven' plants exposed to 1200 chilling hours at 6°C for 16 h/day, and 9,11,13,15,18 and 21°C for 8 h/day. Light intensity in the high temperature in the cycle was kept at 50 $\mu E\ m^{-2}sec^{-1}$. Bud break of leaf and flower buds showed (Fig. 3) a beneficial effect for cycling with 9,11,13 and 15°C. Level of bud break was calculated on an equal basis of weighted chilling hours, taking into consideration the effect of 9,11 and 13°C exposure periods on added chilling effect according to Fig. 1.

The calculated equivalents of 6°C (Table 2) assumed a linear response of bud break to added chilling. On this basis a different pattern of response was

obtained, with a maximal effect at 13°C (Fig. 3).

The relative importance of exposure to moderate temperatures in the course of the rest period was tested by comparing continuous exposure to 4°C with diurnal cycling with 15°C during the first, second and third parts of the rest period. It was found that the significance of cycling with moderate temepratures is felt mostly during the last third of the rest period (Fig. 4).

DISCUSSION

The present data complement previous data (1) and enable us to describe the complex effects of temperature on resting peach buds. Chilling effect, as measured by response to exposure to various continuous temperatures, shows an optimum curve with a peak at 8°C. The previous data showed an optimum at 6°C (5), and 6°C was used in the Utah model, too, as a basis for the model developed (11). On the other hand, Gilreath and Buchanan (9) reported an optimum effect at 8°C. The present data were obtained under much more strictly controlled temperature conditions ($\pm$ 0.1°C), as compared with previously reported data, and the tests were replicated with a much greater number of plants. It should be noted, though, that only small differences in efficiency are found around the peak of activity.

We have demonstrated the temperature action curve for rest breaking in the range of 0 to 14°C. While a zero effect was achieved around 14°C, a little activity was found at 0°C, thereby attributing rest-breaking activity also to temperatures lower than 0°C. Flower buds especially, showed a rather mild reduction in response to this low temperature.

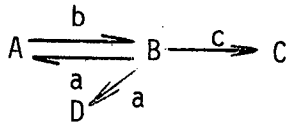
The striking similarity with Gilreath and Buchanan's data rules out the suggested qualitative difference in response of various peach cultivars to low temperature (9).

Diurnally cycled low temperatures with 15°C, revealed a striking similarity in the effect of all three cycling treatments, while continuous low temperatures showed a weaker effect the lower the temperature between 6 and 0°C verifying former data. This finding leads us to conclude that the poor efficiency of continuous low temperatures is not due to a lower efficiency of the chilling reac-

tion per se, but to a low activation of another reaction - the moderate temperature effect. This conclusion is based on the effect of 15°C, which has no "chilling" power by itself but nevertheless enhanced bud break in the cyclic treatments to a higher degree, the lower the chilling temperature. Thus, the actual low temperature effect between 0°C and probably 8°C seems to be almost the same.

The poorer response to 15°C after chilling under relatively high light intensity (150 $\mu Em^{-2}sec^{-1}$) in comparison with lower temperatures stresses again the negative effect of light during rest on its development in peach buds, as was shown before (6,8). The MTE was maximal at 13°C, as proved by its greatest enhancement of former chilling. The relatively poor MTE when applied in the first third of the chilling period, points again to the MTE being important in a later stage of the temperature effect on rest. It may give some indications as to the capacity of the pool of the direct product of chilling.

In order to understand the multiple temperature effects on dormant peach buds, we propose a two-step scheme with the first step being reversible, as follows:



where A represents the dormant primary stage; B represents the product of the chilling effect sensitive to reversion to A or to decay to D.
C is the product of fixation of B. Likewise, "b" represents the chilling reaction proper; "a" represents the chilling negation reaction by high temperatures and "c" is the moderate temperature reaction that fixes the chilling effect.

This scheme is similar to that proposed long ago by Gregory and Purvis for vernalization of rye plants (10). It incorporates three basic phases and describes the three temperature reactions found with dormant peach buds. These reactions have different temperature response curves that are described graphically in Fig. 5.

The chilling effect (reaction "b") has a broad maximal effect between 8^{o} and $0^{o}C$ (activity below $0^{o}C$ not known). As higher temperatures are neared, its activity decreases sharply, reaching zero close to $14^{o}C$. The high temperature reaction ("a") increases in activity sharply from 16-$17^{o}C$ and up to $24^{o}C$, the highest temperature tested (1,3). The moderate temperature reaction ("c") is most difficult to describe, due to its overlapping with reactions "a" and "b". Nevertheless, it is still effective at $0^{o}C$ (as can be deducted from the fact that bud break occurs after continuous exposure to this temperature), but its maximal observed effect is at $13^{o}C$. Both the "a" and "c" reactions compete on the same substrate but it is obvious that reaction "c" has a much lower Q_{10} than reaction "a", and that at temperatures higher than $13^{o}C$, reaction "c" is partly or fully masked by reaction "a". Reaction "a" seems to be affected both by the level of the high temperature and its duration. Short periods of exposure to $20^{o}C$ could split B between "a" and "c" and end up in a no-negative effect (1).

The scheme can explain the effect of cycle length of high-low temperature. Under short cycles B was not fixed to C in the course of the low temperature, and hence its sensitivity to reversion, while under long cycles at least part of B could be fixed in the course of the long period of chilling (4). The scheme may also explain the beneficial effect of exposure to long cycles of low-high temperatures in the course of the rest period (5). After a long period of chilling, $20^{o}C$ could have an intermediate effect producing more "c" than under continuous low temperature. Continuous low temperature, on the other hand, is limiting in its effect by limiting the "c" reaction.

From this scheme it is obvious that a phenoclimatological model aiming at simulating the overall effects of the climatic conditions to which the dormant plant was exposed to, will fail unless all three reactions proposed are considered.

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Table 1: The effect of continuous and alternate chilling on bud break of 'Redhaven' lateral leaf buds[z].

Chilling treatment (°C)	Bud break (% ± S.E.)
No chilling	0
6	27.6 ± 6.2
6 - 13[y]	42.7 ± 5.2
6 - 15[y]	25.3 ± 6.1
6 - 17[y]	0

[z]- 1200 chilling hours, followed by 40 days of forcing at 22°C.

[y]- 16 h at 6°C in the dark, 8 h at high temp. and 150 $\mu Em^{-2}sec^{-1}$. High temperature set according to bud temperature.

Table 2 : Corrected readings by equalizing exposure to chilling

Temperature regime ^{o}C	Duration of exposure (hrs)	Total chilling hrs applied, in equivalents of $6^{o}C$ (from Fig. 1)	Corrected reading (%)
4	1200	1080	+11
6 (16h) - 9 (8h)	1800	1740	-31
6 (16h) - 11 (8h)	1800	1620	-26
6 (16h) - 13 (8h)	1800	1320	- 9
6 (16h) - 15 (8h)	1800	1200	-
6 (16h) - 18 (8h)	1800	1200	-
6 (16h) - 21 (8h)	1800	1200	-

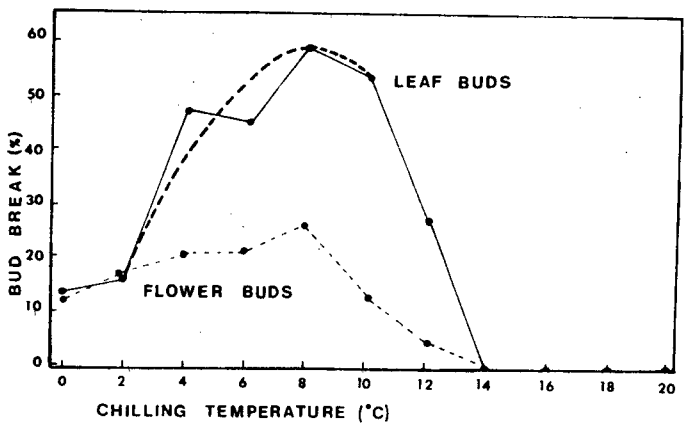

Fig. 1: The effect of exposure of 'Redhaven' peach plants to 1200 h at various continuous temperatures on leaf and flower bud break. Bud break was recorded after 40 days of forcing at 22°C.

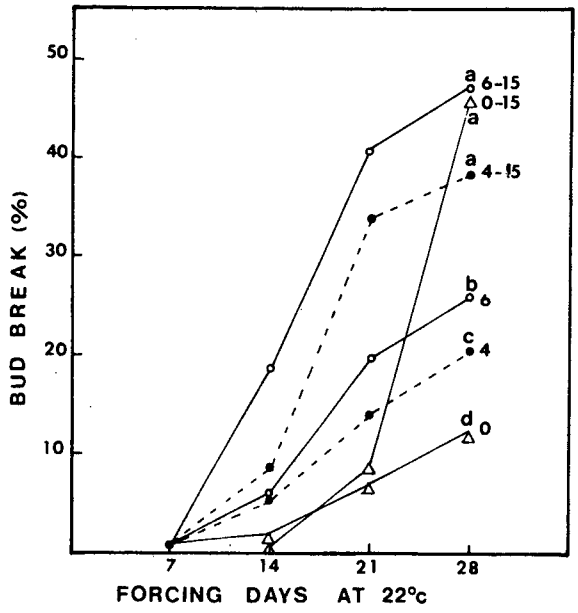

Fig. 2: The effect of exposure of 'Coronet' peach plants to 900 h at 0, 4 or 6°C applied either continuously or in a diurnal cycle with 15°C for 8 h a day, on lateral vegetative bud break after up to 28 forcing days at 22°C. Significant difference on the 28th forcing day by Duncan's MRT.

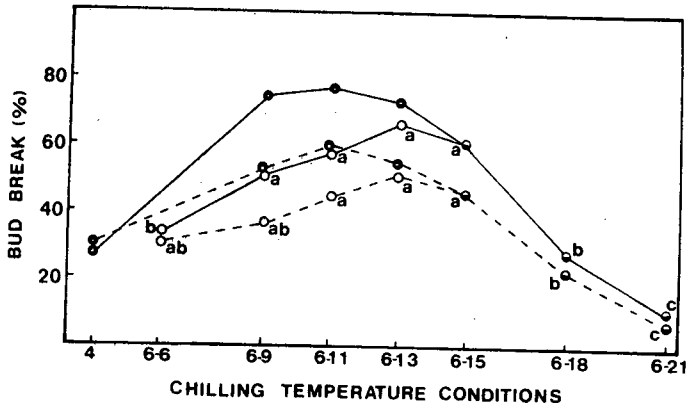

Fig. 3: The effect of exposure of 'Redhaven' peach plants to 50 days continuously at 4°C and to 75 days of alternating 6°C with various higher temperatures, on flower (dashed line, black dots) and vegetative (solid line, black dots) lateral bud break. High temperature duration in the alternating temperature treatments - 8 h a day. Corrected reading to equalize exposure to 1200 h of chilling at 6°C according to Table 2 - (circles). Statistical significance marked with different letters on each of the corrected curves according to Duncan Multiple Range Test, 5% level.

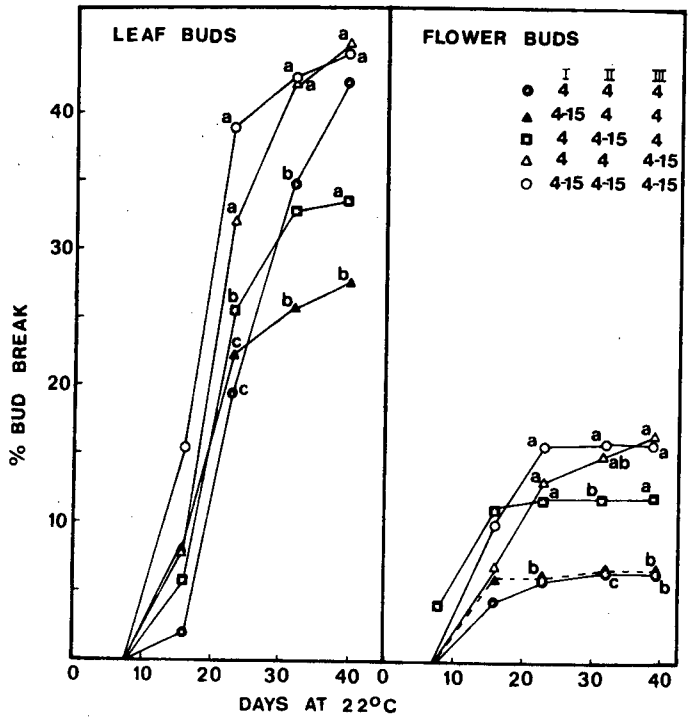

Fig. 4: The significance of the time of cycling chilling with moderate temperature in the course of the rest period, on breaking the rest of 'Redhaven' peach buds. ('4' - continuous $4^{o}C$; '4-15' - 16 h $4^{o}C$ and 8 h $15^{o}C$.) The differential chilling treatment was given in each third of the chilling period. A total of 1200 h at $4^{o}C$ was given to all treatments. Significance at each date according to Duncan's Multiple Range Test, 5% level.

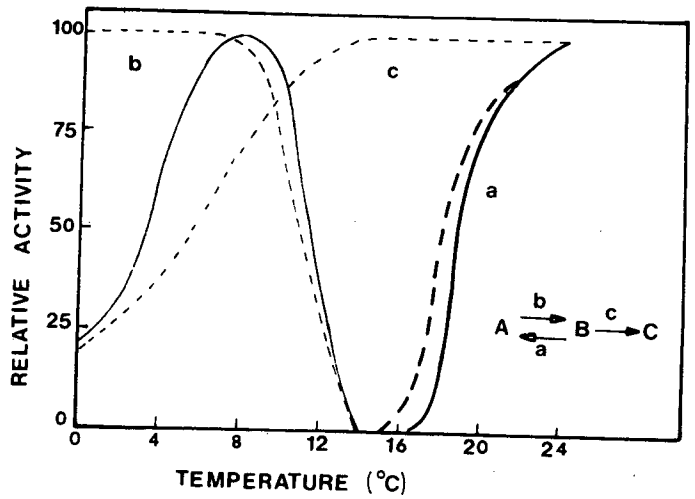

Fig. 5 : Temperature response curves of the three reactions involved in resting peach buds. (The 'a' curve was obtained at designated temperatures for 8 h daily, with 16 h at $6^{o}C$. Solid lines represent the apparent temperature effects and the dashed lines represent the actual temperature effect of the three temperature reactions.)

3.3 The effect of light intensity on the response of dormant peach buds to chilling

Light was found to have a direct effect on dormant peach buds. With increased light intensity of 150 μE to 300 μE $m^{-2}sec^{-1}$ during the chilling period, negative effects were obtained (Table 1). Lateral leaf buds and terminal buds as well as flower buds of 'Desertgold' peach showed a tendency for retarded bud break. Terminal buds of 'Redhaven' were inhibited under these conditions, in comparison with darkness.

In most of our former work light irradiance was kept low, at 50 μE $m^{-2}sec^{-1}$, and it seems that under these conditions no negative effect is obtained.

4. Evaluation of the research achievements

Specifying and quantifying the three temperature reactions can explain the complex effect of temperature on dormancy in deciduous orchards. Low temperature effect was quantified and shown to have a similar effect between 0 and $8^{o}C$. High temperature was shown to have a negative effect already at $17^{o}C$; this effect was both temperature level- and duration-dependent. The moderate temperature effect was shown to have a maximal activity around $13^{o}C$.

The scheme proposed may lay the basis for a climatic model describing the authentic response of the dormant bud to all temperature conditions, as well as setting a basis for physiological work into the mechanism of rest development in the buds. The definition of the moderate temperature effect, especially, adds a novel aspect not presented previously in any detail. Additional information regarding the involvement of light in moderating temperature effects is of importance as well.

Lipase and catalase activities were determined throughout the dormant period of vegetative apple buds and of flower and vegetative peach buds. The pattern of change of activity during rest is important information for understanding the mechanism of bud rest.

Table 1: EFFECT OF LIGHT IRRADIANCE ON PERCENT BUD BREAK OF PEACH PLANTS

Treatment[z]	Cv. Desertgold			Cv. Redhaven[x]
	Laterals	Terminals	Flower Buds	Terminals
No chilling	1.5 ± 1.5	42.4 ± 14.7	27.0 ± 11.4	23.0
6°C	24.6 ± 8.6	77.7 ± 10.3	51.9 ± 13.4	-
6°- 15°C[y], darkness	44.1 ± 7.0	100.0	37.7 ± 10.9	62.3
6°- 15°C[y] 150 μE $m^{-2}sec^{-1}$	20.4 ± 8.4	76.9 ± 10.0	17.3 ± 10.3	32.2
6°- 15°C[y] 300 μE $m^{-2}sec^{-1}$	21.3 ± 8.6	78.6 ± 11.4	23.2 ± 10.6	6.2

[z] 480 chilling hours; bud break examined after 40 days of forcing.

[y] 16 h at 6°C in the dark, 8 h at light irradiance stated. High temperature set according to measured bud temperature.

[x] Only one replicate of eight plants per treatment.

5. Cooperation

Very close cooperation in the course of this project was maintained between the Israeli and the American investigators. Planning of experiments, summarizing of data and discussion were conducted by correspondence and during the visits of the Israeli investigator to the U.S.A. in 1981, and the American investigator to Israel in 1982.

6. Benefit to Agriculture

A practical conclusion of this work was that the main cause of poor bud break in a subtropical climate is not the lack of chilling but rather the excess of high temperatures. Considering the major reversion in effect of high and moderate temperatures, use of evaporative cooling to turn excessive heat into promotive moderate temperature was tried with success with nectarines (see enclosed reprint and see also under research achievements).

7. Reprints originated from this BARD project

7.1 Evaporative cooling to improve rest breaking of nectarine buds by counteracting high daytime temperatures.

EVAPORATIVE COOLING TO IMPROVE REST BREAKING OF NECTARINE BUDS BY COUNTERACTING HIGH DAYTIME TEMPERATURES [1,2]

A. EREZ, Institute of Horticulture, Agricultural Research Organization, The Volcani Center, Bet Dagan, Israel

G.A. COUVILLON, Department of Horticulture, University of Georgia, Athens, Ga 30602, U.S.A.

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Abstract. Evaporative cooling (EC) of nectarine buds during rest by overhead sprinkling when day temeprature exceeded 16°C lowered bud temperature in bright days by 3 to 5°C. EC resulted in an enhanced break of vegetative and floral buds.

Under climatic conditions prevailing in countries having mild winters, it is very common to have a daily fluctuation of temperature between relatively low night temperatures and high (20°C or higher) day temperatures. This situation is typical of locations with a lack of precipitation and cloudiness during winter. Under such conditions total chilling accumulation could amount to a considerable sum of chilling hours if the night chilling was not counteracted by the excessive day time temperature.

Small differences in maximal bud temperatures can result in completely different response to chilling. Eight hrs of 21°C in a diurnal cycle with 4°C negated chilling completely while 18°C in an identical cycle had no negating effect (3,5). On the other hand 15°C in a diurnal cycle with 4°C enhanced bud break (3). These data led us to examine the possibility and effect of reducing bud maximum temperature during winter.

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The only practical way to reduce plant top temperature is by evaporative cooling. This system is in use for delaying bloom when applied after rest completion (1,2), and for reducing excessive foliage and fruit temperature (8).

Recently it was tried also as a means to improve bud break by operating the system when temperature rose above 10°C (6,7). This paper reports preliminary data obtained with evaporating cooling during warm winter days in Israel.

Five-year-old 'Sunred' nectarine trees on their own roots, grown in a meadow orchard system at Bet Dagan, Israel (31°N), were used in this study. One row of 20 trees was treated while another row of 20 trees served as an untreated control. Data were collected from 12 preselected trees in each row. The evaporative cooling system was operated automatically by a "cloud 9"[3] unit, time operated hydraulic valve controlled by a thermostat located in the shade. The unit was operational only when the air temperature exceeded 16°C, then the trees were sprinkled for 1 min every 11.2 minutes. Under very warm days the cycle was shortened to 5.6 minutes. Irritech[4] minisprinklers with an output of 50 l/h were installed at 3 m intervals along the row above the top of the trees. These minisprinklers excel in producing an even droplet size with an average diameter of 0.5 mm and with 1% or less of the droplets having a diameter of 0.1 mm. These characteristics reduce drop evaporation and the effect of wind. The system was operated for 31 days from Dec. 6, 1981 to Jan. 5, 1982; bud temperature was measured using a Grant Instruments[5] miniature recorder equipped with 0.75 mm needle thermistor probes. The percent of bud break out of the total buds present on one-year-old twigs was counted.

The mean daily maximum temperature during the experimental period was 20.7°, and the minimum was 8.7°C. In 26 out of 31 days maximum temperatures reached 20°C or higher. It is obvious that very little chilling accumulation could occur with the high day temperatures (3). This period was also rather bright: there was an average of 6.2 hours of sunshine per day, or 62% of the total possible, and only 13 mm of rain fell during this period.

3- Obtained from Amnad, Tel-Aviv, Israel; 4- Irritech, Israel; 5- Cambridge, England.

The sprinkling system was in operation for an average of 5 h a day. The EC treatment reduced, bud temperature considerably averaging 3°C (Fig. 1). As can be expected under bright conditions, bud temperature increased over air shade temperature, while with EC it dropped below air shade values. As long as the buds did not dry completely, chilling effect was maintained; once the buds became completely dry, temperature increased rapidly. The total amount of water applied during the 31 days of the experiment amounted to about 100 mm.

Bud break was considerably enhanced, leading to an early and more uniform bloom and leafing than in the adjacent control plants (Table 1, Fig. 2).

Gilreath and Buchanan (5,7) reported that sprinkled peach and nectarine trees bloomed 9 to 13 days earlier than the non-sprinkled control. They operated the overhead sprinkling system when temperatures exceeded 10°C. From their data it is clear that sprinkling considerably reduced maximum bud temperature as compared with the dry buds. Gilreath and Buchanan showed greater accumulation of chilling below 10°C with the wet treatment, but not enough to explain the whole effect obtained. It seems that also under their conditions counteracting of high day temperature was an important cause for the favorable effect obtained. Since they failed to predict the date of the rest termination for the sprinkled treatment using various models (7) they suggest that other factors are also involved in breaking bud rest when using overhead sprinkling. It still could be that the models used are not accurate enough or that the cause for the response observed could have been other than reduced daytime temperature, as proposed by Westwood and Bjornstand (9). They claim that leaching of growth retardants would be responsible for better bud break under rainy conditions. In the present work we could not differentiate between the two effects. It should be mentioned that the favorable effect of rainfall in Westwood and Bjornstand's work could well have been due to bud temperature reduction rather than leaching of inhibiting substances. Also,

the question has been raised (4) that the efficiency in bud break in Westwood and Bjornstand immersion studies was due to a reduction in bud oxygen level rather than a result of leaching of growth retardants. Night sprinkling when dew point will be reached and no further cooling will be obtained by sprinkling, could serve as a test for the role of leaching in overhead sprinkling.

Poor water quality is a major hindrance to the use of this system on foliated trees; with dormant trees no such problem exists. As overhead sprinkling improves bloom and leafing in nectarines and possibly other deciduous species under bright and warm winter conditions, it could become an important technique in locations with such conditions.

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Table 1: The effect of overhead sprinkling during the period Dec. 6, 1981 to Jan. 5, 1982 on rest completion of 'Sunred' nectarine dormant buds. The system operated when temperatures rose above 16°C, at cycles of 1 min. every 5.6 or 11.2 min.

Bud type	Date checked	% Bud break[z]			
		Control		Sprinkled	
Terminal	Feb. 5	16.6	a[y]	75.0	b
	Feb. 17	25.0	a	100.0	b
Flower	Feb. 5	5.6	a	49.0	b
	Feb. 17	32.5	a	80.5	b
Leaf	Feb. 5	4.2	a	48.0	b
	Feb. 17	41.0	a	76.1	b

[z] 12 randomly selected one-year-old twigs, 40 cm long, were checked.

[y] Mean separation in lines by Duncan's Multiple Range Test (5% probability).

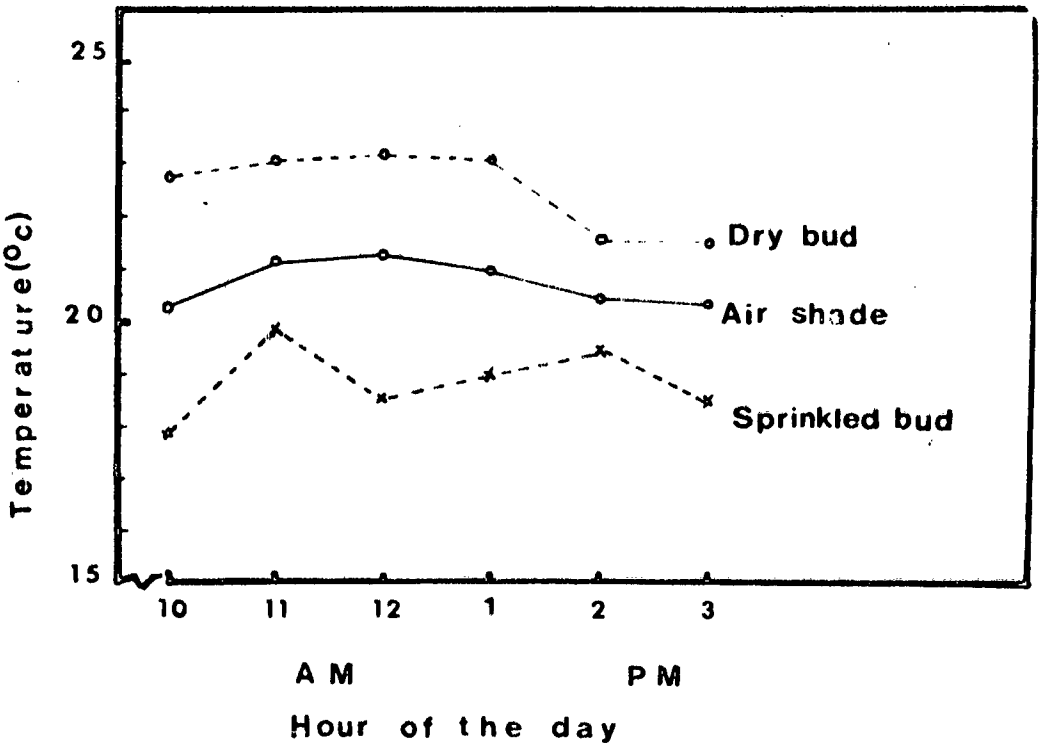

Fig. 1: Typical daily temperatures of dry and sprinkled dormant buds of 'Sunred' nectarine in comparison with air temperature. Measurements were taken on Dec. 15, 1981, a bright day, using Grant Instruments thermistor miniature probes.

Fig. 2: The effect of overhead sprinkling for 31 days during the warmest period of the day on bud break in the 'Sunred' nectarine (left) as compared to unsprinkled control (right).