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Effect of Warm Temperature Interruption on the Accumulation of Winter Chilling in Kiwifruit (*Actinidia chinensis* Planch. and *A. deliciosa* A. Chev.)

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Abstract. **Warm temperature exposure during winter has reportedly resulted in the apparent negation of chilling in several fruit species. This study was conducted to investigate the floral and vegetative response of two pistillate kiwifruit cultivars to intermittent warm temperature interruption during chilling accumulation. Dormant 1-year-old canes of *Actinidia chinensis* 'AU Golden Dragon' and *Actinidia deliciosa* 'AU Fitzgerald' were collected in December 2018 and 2019 (334 and 360 chilling units, respectively), shortly after leaf abscission. Canes were cut to 10 nodes after removing the first six basal nodes, placed in jars filled with distilled water, and transferred to respective chilling treatments. Treatments included continuous chilling (CC) (in addition to base chilling) at 1-week (168 chilling units) increments (0–5 weeks) and chilling exposure at the same increments with intermittent warm temperature (WT). For the WT treatments, each week of chilling was followed by 3 days of exposure to warm conditions. Chilling and warm temperature exposure were simulated by 7/4 °C and 25/17.2 °C (day/night) air temperatures, respectively, using separate climate-controlled growth chambers. After treatments, canes were forced in a third chamber at 21.1 to 25.0 °C with light-emitting diode lighting. Vegetative budbreak, floral bud number (from here on defined as floral response), and floral development stage were recorded for each cane at 2-day intervals. For 'AU Golden Dragon', WT did not result in any reduced floral response at any of the observed chilling levels. However, lower mean floral response was observed with WT, as compared with CC for 'AU Fitzgerald' at 5 weeks of chilling over the 2 years ($P = 0.05$). WT also lessened the effect of apical dominance with respect to vegetative/floral response to node position for both cultivars. Chilling type had no significant effect on vegetative response in either cultivar. Estimated chilling requirements (CC) in this experiment were similar to those reported previously for these cultivars. Results suggest that *A. chinensis* cultivars may respond more favorably than *A. deliciosa* to the erratic winter temperature patterns experienced in the southeastern United States.**

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Kiwifruit (*Actinidia chinensis* Planch. and *Actinidia deliciosa* A. Chev.; Actinidiae) are woody vining species native to the southern portion of China, where winters are cool, but relatively mild (Ferguson 1991). Plants are dioecious and produce mixed buds that give rise to floral buds borne on leaf axils of the emerging shoot. Flower buds are produced on new shoots arising from dormant ("winter") buds that are found in the leaf axils of the previous season's canes (Brundell 1975). Nodes 5 through 12, beginning from the basal end, on fruiting canes are observed to have the greatest floral potential (Hopping 1990), whereas the basal buds are typically not fruitful (Snowball and Considine 1986). Many woody plants in temperate zones require exposure to cold temperatures to satisfy rest requirements and resume normal growth in the spring. After exposure to a certain amount of cold, buds on these plants enter endodormancy, which is imposed internally and physiologically (Melke 2015). In this deep state of rest, resumption of growth and flowering is very difficult unless the chilling requirement is satisfied (Couvillon 1995). In the case of kiwifruit, chilling is required before the final phase of floral development can take place (Snelgar et al. 1997; Snowball and Considine 1986). Consequently, sufficient accumulation of winter chilling is one of the most limiting climatic factors for selection of temperate fruit cultivars. Such chilling requirements vary by species and individual cultivar, but also may be affected by other factors, including rootstock (Couvillon 1995). Estimates for winter chilling requirements in kiwifruit range from 700 chilling units for 'Bruno' to as much as 1150 chilling units for 'Hayward' (Caldwell 1989). In addition, many species require a specific duration of warm temperature after the chilling requirement has been satisfied. Cane cuttings, excised after natural defoliation, have been used for studying budbreak in kiwifruit (McPherson et al. 1995; Snelgar et al. 1997; Snowball 1997; Wall et al. 2008) in addition to many other temperate fruit crops.

Studies on the exposure of kiwifruit to warm temperatures during dormancy have been limited, at best. Air temperatures as high as 10 °C are reportedly effective for chilling in kiwifruit (Lionakis and Schwabe 1984), whereas those of 13 °C or greater are too warm (McPherson et al. 1995). Specifically, the potential for negation of chilling by warm temperature interruption (WT) during accumulation in this crop has not been explored. Represented by reduced or delayed budbreak, this phenomenon has been reported in apple (Young 1992), Asian pear (Tamura et al. 1995), and peach (Couvillon and Erez 1985; Erez et al. 1979), with the degree of negation depending on the level, duration, and timing of WT. Exposure to 20 °C for 200 h toward the end of the accumulated chilling cycle in Asian pear delayed budbreak (Tamura et al. 1995), whereas exposure to that same temperature for a duration of 500 h reduced budbreak during the earlier stages of chilling accumulation in apple (Young 1992). However, in the case of peach, negation by warm temperature may be limited only to the 20 to 40 h (4–6 °C) accumulated immediately before warm temperature exposure (Erez et al. 1979). Originally intended for peach, the Richardson model (Utah model) is still widely used for estimating chilling in kiwifruit. The model proposed by Richardson et al. (1974) included a negative accumulation effect in which each hour of temperatures between 16 and 18 °C, and > 18 °C, resulted in –0.5 and –1.0 chilling units, respectively.

The potential for chilling negation is a major concern in regions with highly dynamic winter temperatures such as the southeastern

United States, particularly for a crop with marginal cold hardiness and comparatively high chilling requirement such as kiwifruit. The objective of our study was to assess the potential for negation of winter chilling accumulation, as determined by vegetative and floral response in green and golden kiwifruit, as reflected by the dynamic winter temperatures observed in southeastern Texas, USA.

Materials and Methods

Plant material. One-year-old fruiting canes were collected from own-rooted plants of the pistillate cultivars AU Fitzgerald (*A. deliciosa*) and AU Golden Dragon (*A. chinensis*) that were established at the Auburn University Chilton Research and Extension Center near Thorsby, AL, USA (lat. 32.92011°N, long. 86.67463°W). Collection commenced shortly after leaf abscission on 15 Dec 2017 and 30 Nov 2018. Selection of canes was based on size, uniformity, light exposure, and apparent fruiting potential. Approximately 300 canes were collected per cultivar, bulked together by cultivar, bundled, tied, and transported immediately to the Horticulture and Forestry Sciences Building at Texas A&M University, College Station, TX, USA (lat. 30.60927°N, long. 96.35034°W), with basal ends immersed in tap water to prevent desiccation. Immediately upon arrival, canes were placed in a walk-in cooler and held at ~8.9 °C for 3 to 5 d until processing. Base chilling included a combination of field-supplied chilling (estimated based on data from a weather station located ~8.0 km away) and storage in the cooler after collection. These values were estimated as 334 chilling units in 2017 and 360 Richardson units in 2018. Canes were then cut at a 45°angle to a length of 10 nodes, following removal of the proximal five nodes. The material was graded systematically into three groups based on relative cane diameter (measured in millimeters), with those outside of an 8- to 15-mm range being discarded. A single cane was selected randomly from each of the three groups and placed in a 946-mL Ball® "regular mouth" fruit jar (Ball Corp., Westminster, CO, USA), such that each jar contained one cane from each of the three groups to minimize the effect of cane diameter. Jars were filled with reverse-osmosis water (no mineral nutrients), such that the basal two to three nodes were immersed completely at all times. Water was replaced completely every 3 to 4 d to minimize microbial growth and xylem occlusion throughout the duration of the experiment. The distal ends were also sealed with Buddy Tape (Aglis Corp., Yame City, Japan) to prevent desiccation (Fig. 1A).

Experimental design. Experimental design consisted of a 2 × 6 factorial with two chilling types and six levels of chilling exposure (duration). A randomized complete block with four blocks was used, with a single jar as the experimental unit, with three canes as subsamples. Data for cultivars AU Golden Dragon and AU Fitzgerald were analyzed separately for the 2-year study. Treatments consisted of simulated winter chilling, applied at weekly (168-h) intervals (1 h exposure 1 chilling units), with either continuous chilling (CC), which served as the control, or with alternating treatments of WT, such that each week of chilling was followed by exposure to warm temperature (Table 1). Contribution of chilling by temperature regime was based on Richardson et al. (1974). At the end of each treatment, the material was exposed to mild forcing temperatures to simulate spring conditions for resumption of growth (Fig. 1B). WT treatment conditions reflected the dynamic winter temperatures observed in the southeastern United States, and account for temperatures that result in chilling negation in other crops such as peach and pear (Couvillon 1995; Erez et al. 1979; Tamura et al. 1995).

After preparation, jars were placed in one of three respective growth chambers, depending on the treatment. The simulated chilling environment was maintained at 7.2/4 °C day/night temperatures with 70% to 85% relative humidity and an 8-/16-h day/night photoperiod using overhead fluorescent lights producing 400 to 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at cane height. These conditions were expected to provide 1 chilling unit/h of exposure (Richardson et al. 1974), resulting in an accumulation of 168 chilling units/week.

Fig. 1. Excised fruiting cane cuttings used to compare the effects of continuous chilling and intermittent warm temperature interrupted chilling exposure on floral and vegetative response in 'AU Golden Dragon' and 'AU Fitzgerald kiwifruit. (**A**) Canes were trimmed, sealed, and immersed in water during artificial chilling. (**B**) Unrooted canes exhibit vegetative and floral growth in response to forcing conditions. (**C**) 'AU Golden Dragon' flowers. (**D**) One-week continuous chilling and 1 week chilling (right) and 6 d warm temperature interruption (left) after forcing.

Table 1. List of treatments for continuous chilling exposure and warm temperature interruption during chilling exposure used in the assessment of two kiwifruit cultivar responses to chilling type and duration.

Continuous chilling	Anticipated chilling accumulation[i]	Warm temperature interruption[ii]	Anticipated chilling accumulation[i,ii]
Base[iii]	347	Base with 3 d intermittent WT	307
1 week	515	1 week chilling with 6 d intermittent WT	475
2 weeks	683	2 weeks chilling with 9 d intermittent WT	563
3 weeks	851	3 weeks chilling with 12 d intermittent WT	691
4 weeks	1019	4 weeks chilling with 15 d intermittent WT	819
5 weeks	1187	5 weeks chilling with 18 d intermittent WT	947

[i] Estimated chilling values based on 0 to 7.2 °C and Richardson models.
[ii] Warm temperature interruption (WT) defined as exposure to 72 h of warm temperature conditions. Extent of chilling negation estimated at 40 Richardson chill units based on reported limitations in peach (*Prunus persica*) (Couvillon 1995; Erez et al. 1979). Negative chilling values based on Richardson's model (Richardson et al. 1974).
[iii] Base chilling estimate of 347 units includes field-supplied and accumulation-during-storage values as the mean for both years.

WT conditions consisted of 25/17.2 °C day/night temperatures with 65% to 75% relative humidity, and the same photoperiod and light intensity. This temperature range, which reflects periods of intermittent warmer winter temperatures in southeastern Texas, USA, resulted in the theoretical accumulation of –16 chilling units (Richardson et al. 1974) per 24-h period. Simulated spring conditions for forcing consisted of a 13-/11-h day/night photoperiod with overhead light-emitting diode lighting at a range of ~185 to 340 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at cane height and 80% to 90% relative humidity for both years. Air temperatures were ~26.0/22.8 °C day/night and 23.9/19.4 °C day/night during 2018 and 2019, respectively. WatchDog® Micro Station 1000 Series (Spectrum Technologies, Inc., Aurora, IL, USA) loggers were placed in each chamber to record temperature at 15-min intervals. An additional environment was added for the second (2018–19) year for observational purposes only. This environment consisted of an additional growth chamber used to simulate WT conditions at a higher air temperature (HT) of 30.6/23.9 °C day/night (all other conditions the same as WT). Although these temperatures were higher than normal regional winter temperature patterns, this additional set of treatments was included to confirm that chilling negation was achievable at an HT regime. Warm temperature treatments at these warmer conditions followed the same sequence as the original WT treatments. CC treatments consisted of exposure to simulated chilling conditions at weekly (168 units), increments beginning at a base-level chilling to a maximum of 934 or 960 units during the first and second years, respectively, at the 5-week (highest) CC treatment. WT treatments received the same amount of simulated chilling at each level of chilling. However, each 1-week period of chilling was followed by exposure to 72 h of warm temperature conditions by moving the material physically between growth chambers. This provided a hypothetical accumulation of –40 units, based on the limitation of negation suggested by Erez et al. (1979).

Data collection. Observations of budbreak and flowering were made at 2- to 3-d intervals during the forcing stage and on a per-cane basis. Vegetative budbreak was recorded as the number of dormant buds exhibiting budburst, as defined by the opening of bud scales in conjunction with the first emergence of the shoot dome (Brundell 1975). The number of visible floral buds or flowers, along with relative stage of development (bud, bloom/anthesis, petal fall, senescence) as described by Wall et al. (2008), was recorded concurrently with vegetative observations (Fig. 1C). During the first year only, the relative nodal position along the cane was also noted for these observations (apical node = position 10, basal node = position 1). For all observations, the average of each three-cane experimental unit was reported and used in the analysis. Observations were ended for each cane independently at the onset of senescence, at which point these canes were discarded. Before removal, the total number of nodes exhibiting vegetative shoot growth was recorded, as determined by the presence of one or more leaves during the second year, along with cane diameter (measured in millimeters) using a digital caliper (Fig. 1D). Floral response per cane represented the maximum total number of floral buds, open flowers, and senescing flowers observed and was used, ultimately, to express maximum reproductive potential. Percent vegetative budbreak was calculated as the percent of total nodes exhibiting budbreak, relative to the number of nodes (n = 10) present on the cane. Percent shoot development was calculated as the percentage of nodes that produced shoots.

Data analysis. All statistical analyses were performed using JMP software v. 14.0 (SAS Institute, Cary, NC, USA). Floral response and percent shoot development were transformed using the square root method, following the Shapiro-Wilcox test ($\alpha = 0.05$) for normality. Effect of year was determined using Student's *t* test ($\alpha = 0.05$) for percent vegetative budbreak and floral response. Analysis of variance (ANOVA) ($\alpha = 0.05$) was used to test for presence of a year × treatment interaction (model construct included year, treatment, year × treatment, and block as fixed effects). When a year × treatment interaction was present ($P \leq 0.05$), data for each year were analyzed separately. In the absence of a significant interaction, the combined data from both years were used for the analysis. Comparisons between CC and WT were made separately at each level (week) of chilling for percent vegetative budbreak, floral response, and percent shoot development using Student's *t* test ($\alpha = 0.05$). Effect of chilling level on floral response and percent vegetative budbreak was estimated using ANOVA ($\alpha = 0.05$), separately by year and type of chilling (CC and WT). Estimation of chilling requirements was accomplished by identifying the lowest chilling level within the highest statistical group of the limited number of treatments (n = 6). Tukey's honestly significant difference (HSD) ($\alpha = 0.05$). Data for mean percent vegetative budbreak and mean floral response on a per-node basis was assessed exclusively during the first year for estimation of nodal position effect for these variables. Comparison of per-node mean percent vegetative budbreak and mean floral response for WT and CC was made at each level of chilling using Student's *t* test ($\alpha = 0.05$). In addition, mean percent vegetative budbreak and mean floral response across all chilling levels was calculated for each cultivar and chilling type (WT/CC) combination for general comparison of nodal position effect on vegetative and floral response. Student's *t* test ($\alpha = 0.05$) was used to compare differences in mean cane diameter 1) by year (both cultivars and all treatments); 2) by cultivar and year (all treatments); 3) by cultivar, year, and chilling type (across all chilling levels); and 4) by cultivar, year, chilling type, and at each level of chilling. The effect of cane diameter on all other dependent variables was estimated through linear regression. Existence of a significant cane diameter effect ($P < 0.05$ for $\beta 1$) was analyzed systematically 1) by cultivar (all treatments); 2) by cultivar and year (all treatments); and 3) by cultivar, year, and chilling type (all levels).

Results and Discussion

Floral and vegetative response to chilling type. Floral response to chilling type was analyzed separately by year for 'AU Golden Dragon' because of a year × treatment interaction ($P = 0.00014$) and significant year effect ($P = 0.0034$) at the 4-week level of chilling. There was also a strong year × treatment interaction ($P = 0.0019$), but no significant year effect at the 5-week chilling level (Table 2). During the first year, only the 4 and 5 weeks of chilling yielded significant ($P = 0.0181$ and $P = 0.0084$, respectively) differences between chilling type, with WT resulting in a 534% and 349% greater mean floral response compared with CC, respectively (Fig. 2). It is difficult to posit the specific physiological mechanism responsible for these surprising results. Couvillon and Erez (1985) reported that simulated chilling with air temperatures as high as 20 °C for 2 to 4 h in conjunction with 4 °C of chilling enhanced the effectiveness of chilling exposure, whereas longer exposure (> 6 h) or warmer air temperatures (24 °C) resulted in negation of chilling in peach. Porlingis and Therios (1997) discovered that an HT (30 °C) was nearly as effective as chilling in promoting budbreak, albeit vegetative, in *A. deliciosa* plants. It is also important to point out that floral response to CC conditions during the first year of the study was much lower than expected, suggesting potential problems with the plant material collected that year. Whether this unusual difference in behavior observed between WT and CC is a result of a lack of response to chilling under CC conditions or a promotive effect of WT chilling remains unknown. Crude climatological assessments of the natural geographic range of *A. chinensis* would suggest that this species is exposed to fluctuating winter temperatures. Also worth noting is that there was no significant difference in the incidence of floral bud abortion between chilling type in this cultivar during either year of this study. Comparison of the effect of chilling type on floral response during the second year (2019) yielded different, but not conflicting, results. There were no significant differences between CC and WT at any level of chilling during that year. The positive response to chilling (level) observed under CC treatments suggests that data from this second year were more reliable. Nevertheless, there was no indication of chilling negation present for this cultivar by intermittent warm temperature exposure, as simulated in our experiment.

For 'AU Fitzgerald', WT resulted in an ~18% lower ($P = 0.0476$) floral response compared with WT at 4 weeks of chilling over the 2 years of our study. Year ×

Table 2. Comparison of mean floral response to continuous chilling exposure and warm temperature interruption during chilling exposure in 'AU Golden Dragon' kiwifruit across six chilling levels over 2 years.

	Continuous chilling		Warm temperature interruption			
Chilling level[i]	Warm temperature (d)	Mean floral response[iii]	Warm temperature (d)	Mean floral response[iii]	Standard error	Significance[ii]
Base[iv]	0	0.79	3	0.88	0.226	ns
1 week	0	1.71	6	1.63	0.423	ns
2 weeks	0	2.25	9	2.54	0.798	ns
3 weeks	0	2.96	12	3.37	0.573	ns
4 weeks	0	3.60	15	6.62	1.102	ns[v]
5 weeks	0	3.29	18	6.92	1.007	ns[vi]

[i] Pairwise comparison at each level of chilling ($\alpha = 0.05$, n = 3).
[ii] ns = nonsignificant.
[iii] Mean floral response based on the number of floral buds and flowers per 10-node cane sample.
[iv] Base chilling estimate of 347 units includes field-supplied and accumulation-during-storage values as the mean for both years based on 0 to 7.2 °C and Richardson models.
[v] Significant year × treatment interaction ($P = 0.00014$) and significant year effect ($P = 0.0034$).
[vi] Significant year × treatment interaction ($P = 0.0019$).

treatment interaction ($P = 0.0089$) at the 5-week chilling level required comparisons by individual years (Table 3). Surprisingly, mean floral response was 132% higher ($P = 0.0172$) for WT compared with CC, but only at the base chilling level during the first year. However, at an estimated 334 units of accumulation supplied field and storage chilling, the plant material had likely failed to enter endodormancy (data not shown). During the second year, WT resulted in a 71% lower floral response compared with CC ($P = 0.0016$) at the highest chilling level of 5 weeks (Fig. 3). These results suggest that, unlike *A. chinensis*, the floral response of *A. deliciosa* appears to be susceptible to negation of chilling by warm temperatures. It should be noted that if the extent of negation is limited to 20 to 40 units during each previous cycle, as described by Erez et al. (1979), it is not surprising that negation would have only become evident at the culmination of several cycles of chilling with intermittent warm temperature. Based on these assumptions, effective accumulation would have differed by as few as 80 and 100 units between treatments at the two highest levels. The same climate data from the native distribution of the two species studied suggests that *A. chinensis* would not necessarily experience more intermittent warm weather. However, even when the two species overlap, *A. deliciosa* is typically found at higher elevations (Huang 2016), where short-term incursions of warm weather might not be as pronounced. It should also be noted that winter conditions where these species are native are generally not as dynamic as those in the southeastern United States. Nevertheless, WT conditions in our study proved capable of resulting in reduced budbreak and flowering in other temperate fruit species. Type of chilling had no effect on percent vegetative budbreak or percent shoot development at any level of chilling in either cultivar, although budbreak tended to trend slightly higher for WT treatments over the 2 years of the study.

Floral and vegetative response to HT interruption. Assessment of floral and vegetative response to chilling under HT conditions, relative to WT and CC, was only conducted the second year (2019) and on an observational basis. Compared with CC, HT resulted in a 46.3% and a 41.9% reduction in mean floral response compared with WT in 'AU Golden Dragon' (across all chilling levels). This was particularly evident at 3 to 5 weeks of chilling, suggesting that these temperatures were detrimental to floral development in this cultivar. In the case of 'AU Fitzgerald', mean floral response under HT conditions was 63% less than that of CC across all chilling levels. This strengthens the assertion that flowering in this fuzzy kiwifruit cultivar is affected negatively by exposure to heat during chilling accumulation. Although these conditions (30.6/23.9 °C day/night) were not reflective of normal conditions along the Gulf of Mexico, they demonstrate successfully that floral response in 'AU Golden Dragon' can be hindered by warm temperatures during chilling accumulation (data not shown).

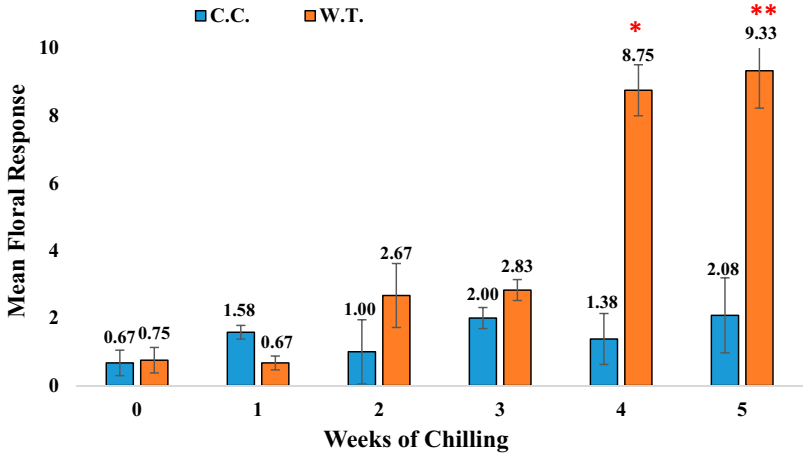

Fig. 2. 'AU Golden Dragon' kiwifruit mean floral response to warm temperature interruption (WT) during chilling exposure and continuous chilling (CC) exposure across six chilling levels for 1 year (2017–18). The mean floral response was based on the number of floral buds and flowers per 10-node cane sample (± standard error for error bars). The base chilling estimate of 334 units includes field-supplied and accumulation-during-storage values, based on 0 to 7.2 °C and Richardson models. Pairwise comparison was completed for CC and WT for each level of chilling. * $P \leq 0.05$, ** $P \leq 0.01$ (n = 3).

Effect of cane diameter. Cane diameter (all treatments) was 12.2 ± 0.13 mm and 12.6 ± 0.14 mm larger on average for both 'AU Golden Dragon' and 'AU Fitzgerald' ($P < 0.0001$), respectively, during the first year of our study. Canes were smaller during the second year, during which the fruit crop was heavier than in 2019, likely resulting in reduced vegetative growth. In general, percent vegetative budbreak tended to decrease with cane diameter in 'AU Golden Dragon' and increase with cane diameter in 'AU Fitzgerald' across all levels (data not shown). Mean cane diameter and floral response in 'AU Fitzgerald' showed a strong ($P < 0.0001$; $R^2 = 0.29$) negative ($\beta 1 = -0.60$) interaction (across all treatments) during the second year (data not shown). This was corroborated by observations that excessively vigorous canes proved less fruitful, reevaluating the assertion by Snowball et al. (1996) that smaller canes lacked sufficient carbohydrate reserves for normal flowering. Nevertheless, the diameter (8–15 mm) and weight range used were of acceptable range for both cultivars, based on the same author's suggestions. More importantly, mean cane diameter was not significantly different between the WT and CC treatments.

Effect of chilling duration and chilling estimation. Estimation of chilling requirement was carried out separately for chilling type (WT and CC) and for each year as a result of

Table 3. Comparison of mean floral response to continuous chilling exposure and warm temperature interruption during chilling exposure in 'AU Fitzgerald' kiwifruit across six chilling levels over 2 years.

	Continuous chilling		Warm temperature interruption			
Chilling level[i]	Warm temperature (d)	Mean floral response[iii]	Warm temperature (d)	Mean floral response[iii]	Standard error	Significance[ii]
Base[iv]	0	1.29	3	3.26	0.307	ns
1 week	0	2.59	6	2.42	0.468	ns
2 weeks	0	3.79	9	4.92	0.67	ns
3 weeks	0	6.87	12	7.50	1.192	ns
4 weeks	0	9.08	15	7.37	0.567	$P < 0.05$
5 weeks	0	12.88	18	7.00	1.302	$P < 0.01$[v]

[i] Pairwise comparison at each level of chilling ($\alpha = 0.05$, n = 3).
[ii] ns = nonsignificant.
[iii] Mean floral response based on the number of floral buds and flowers per 10-node cane sample.
[iv] Base chilling estimate of 347 units includes field-supplied and accumulation-during-storage values as the mean for both years based on 0 to 7.2 °C and Richardson models.
[v] Significant year × treatment interaction ($P = 0.0089$).

previously discussed year × treatment interactions. ANOVA and Tukey's HSD was used for separation of treatment means resulting from the ordinal nature of the data and limited number of treatments. Results (as estimated by identification of the lowest chilling level having the highest statistical mean) were similar to regression analyses using the Gompertz function, as described by Wall et al. (2008) for the cultivars studied here (data not shown). Chilling had a significant effect on mean per-cane floral response (across all levels) for 'AU Golden Dragon' for WT treatments in 2018 ($P < 0.0001$) and 2019 ($P = 0.0052$), and for CC in 2019 ($P = 0.0106$). Estimation under WT conditions identified maximum floral chilling requirements of ~1006 Richardson units in 2018 and 864 Richardson units in 2019. The lack of floral response to chilling level under CC conditions in 2018 might suggest that intermittent exposure to warmer temperatures, either in a diurnal cycle or period of several days, is important in the completion of rest for this cultivar. Floral development responded more predictably for CC in 2019, identifying a maximum floral chilling requirement of 1032 chilling units. The mean maximum floral chilling requirement of ~970 chilling units (both years) estimated in this experiment was comparable to the estimate of 900 chilling units by Wall et al. (2008) for 'AU Golden Dragon' (Figs. 4–6).

'AU Fitzgerald' floral response to chilling was significant in 2018 for CC ($P = 0.0015$), and in 2019 for both WT ($P = 0.0005$) and for CC ($P < 0.0001$). CC in 2018 failed to recognize a maximum floral requirement. However, an estimate of 838 chilling units was identified in 2019 under CC conditions. The estimated chilling requirement of 696 chilling units (576 chilling units assuming hypothetical chilling negation) under WT conditions in 2019 was much less. The mean floral response of 2.59 for WT (compared with 3.76 mean floral response for CC the same year), along with reduced floral activity from 4 to 5 weeks of chilling, further implicate WT warm temperature interruption as an inhibitor of flowering in this cultivar. Although floral bud abortion was not surveyed extensively in our study, a greater incidence was generally observed with WT in this cultivar. The maximum floral chilling requirement of 1019 chilling units (the average between 2018 and 2019 for CC only) estimated here was slightly less than, but comparable to, the reported estimate of 1100 chilling units for 'AU Fitzgerald' by Wall et al. (2008) (Figs. 7 and 8).

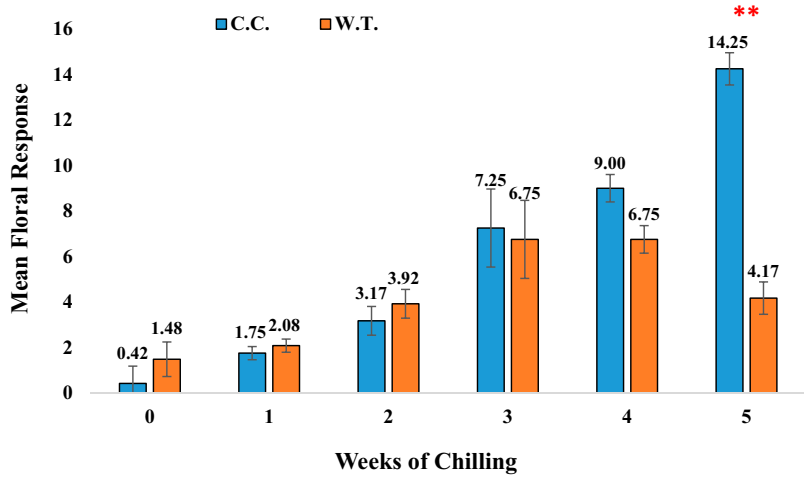

Fig. 3. 'AU Fitzgerald' kiwifruit mean floral response to warm temperature interruption (WT) during chilling exposure and continuous chilling (CC) exposure across six chilling levels for 1 year (2018–19). The mean floral response was based on the number of floral buds and flowers per 10-node cane sample (± standard error for error bars). The base chilling estimate of 360 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Pairwise comparison was completed for CC and WT for each level of chilling. ** $P < 0.01$ (n = 3).

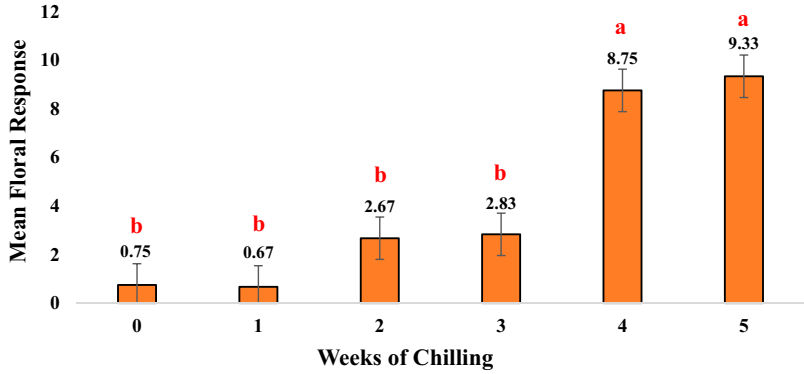

Fig. 4. 'AU Golden Dragon' kiwifruit floral response as the mean floral response to warm temperature interruption during chilling exposure across six chilling levels for 1 year (2017–18). The mean floral response was based on the number of floral buds and flowers per 10-node cane sample. The base chilling estimate of 334 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with the same lowercase letter are not significantly different using Tukey's honestly significant difference ($\alpha = 0.05$) (n = 3).

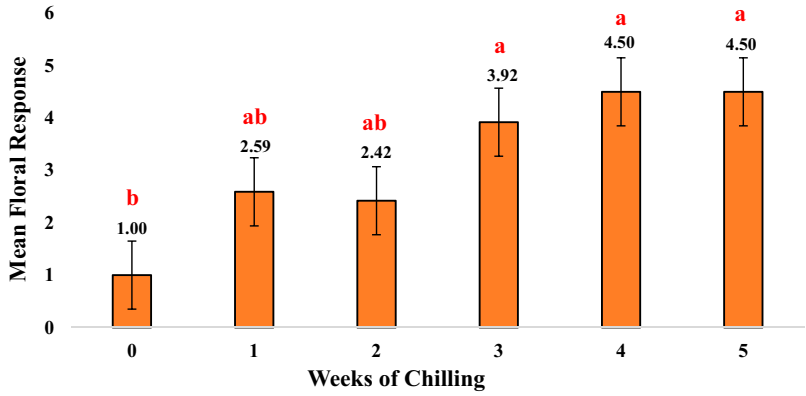

Fig. 5. 'AU Golden Dragon' kiwifruit floral response as the mean floral response to warm temperature interruption during chilling exposure across six chilling levels for 1 year (2018–19). The mean floral response was based on the number of floral buds and flowers per 10-node cane sample. The base chilling estimate of 360 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with by the same lowercase letter are not significantly different using Tukey's honestly significant difference ($\alpha = 0.05$) ($n = 3$).

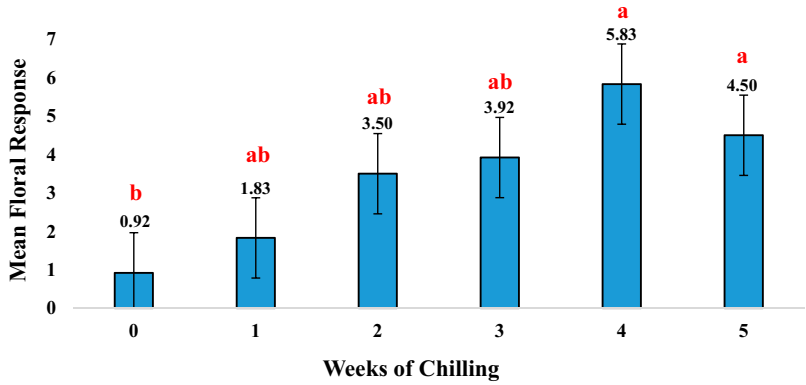

Fig. 6. 'AU Golden Dragon' kiwifruit floral response as the mean floral response to continuous chilling exposure across six chilling levels for 1 year (2018–19). the mean floral response was based on the number of floral buds and flowers per 10-node cane sample. The base chilling estimate of 360 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with the same lowercase letter are not significantly different using Tukey's honestly significant difference ($\alpha = 0.05$) ($n = 3$).

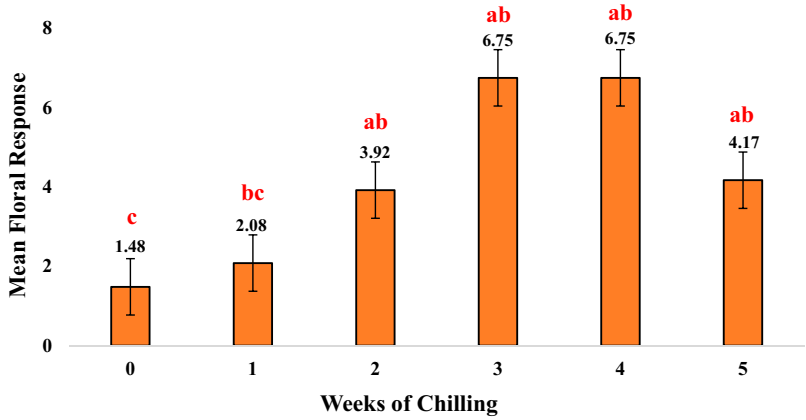

Fig. 7. 'AU Fitzgerald' kiwifruit mean floral response to warm temperature interruption during chilling exposure across six chilling levels for 1 year (2018–19). The mean floral response was based on the number of floral buds and flowers per 10-node cane sample. The base chilling estimate of 360 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with the same lowercase letter are not significantly different using Tukey's honestly significant difference ($\alpha = 0.05$) ($n = 3$).

In general, chilling generally had less of an impact on vegetative response in both cultivars, particularly 'AU Fitzgerald'. This was surprising, considering that a maximum vegetative requirement of 800 chilling units was reported for both cultivars (Wall et al. 2008). However, the vegetative chilling response and requirement appear to be much more flexible compared with floral development in kiwifruit, particularly before entering endodormancy, as evident when correlative inhibition is removed (Guerriero et al. 1991). Such responses have even led some researchers, such as Brundell (1976), to suggest that chilling is not required for rest termination and flowering in fuzzy kiwifruit. For 'AU Golden Dragon', chilling only had a significant effect in 2018 ($P = 0.0052$) and 2019 ($P = 0.0368$) on percent vegetative budbreak, and only under WT conditions, further supporting that warm temperature in association with chilling is not detrimental in this cultivar. Under this scenario, maximum vegetative budbreak was achieved at 1006 chilling units in 2018 and 1032 chilling units in 2019—both of which were higher than reported previously. However, 50% vegetative budbreak was achieved as early as ~685 chilling units compared with the maximum of 74% (over the 2 years) (Figs. 9 and 10).

Nodal position response to chilling type. Percent vegetative budbreak and floral response were both assessed on a per-node basis during the first year, with the results reflecting data from across all chilling levels. Floral response and, to a lesser degree, percent vegetative budbreak exhibited a strong basipetal trend in both cultivars across all treatments. In fact, the apical (10th) node accounted for an average of 48.6% of the total floral response and 26.8% of total vegetative budbreak per cane for the two cultivars altogether (data combined). This pattern may have been accentuated by the near vertical (60 to 90° angle) orientation of the fruiting canes in this experiment, which are typically tied down in a horizontal (0°) position (Snelgar et al. 1997). The length of the cane was also likely influential on both floral and vegetative development. A length of 10 nodes was chosen to simulate more completely the behavior of whole canes (Dennis 2003; Snowball 1997) and to avoid underestimation of chilling requirements through removal of correlative inhibition (Guerriero et al. 1991). However, these longer canes may have also experienced greater internode competition for carbohydrates. Nevertheless, exposure to WT chilling conditions tended to reduce the intensity of apical dominance in our experiment. For example, floral response relative to the entire cane at node positions 9 and 10 (combined) was 55.6% and 48.6% under WT conditions for 'AU Golden Dragon' and 'AU Fitzgerald', respectively, compared with 66% and 83.4% under CC for these cultivars, respectively (all chilling levels; data not shown).

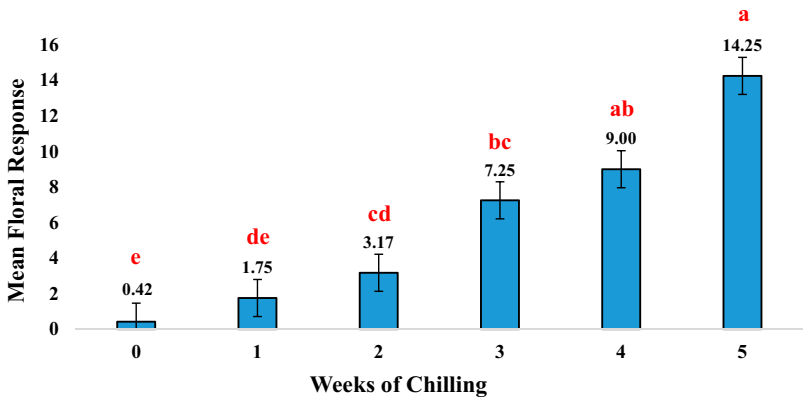

Fig. 8. 'AU Fitzgerald' kiwifruit floral response to continuous chilling exposure across six chilling levels for 1 year (2018–19). The mean floral response was based on the number of floral buds and flowers per 10-node cane sample. The base chilling estimate of 360 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with the same lowercase letter are not significantly different using Tukey's honestly significant difference (α = 0.05) (n = 3).

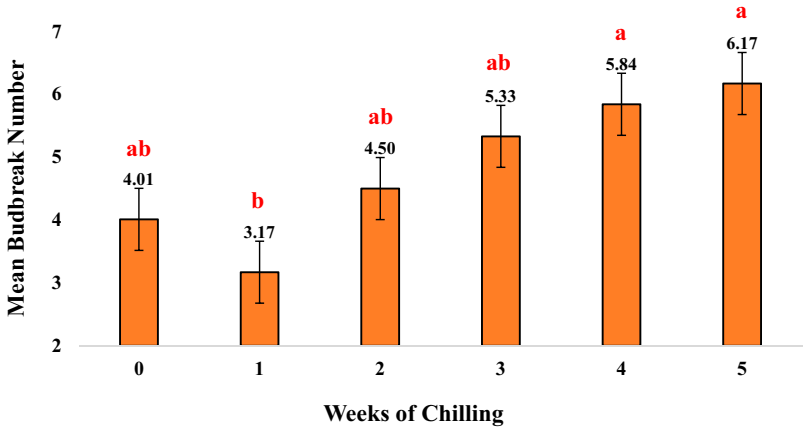

Fig. 9. 'AU Golden Dragon' kiwifruit mean vegetative budbreak number per cane vs. warm temperature interruption during chilling exposure across six chilling levels for 1 year (2017–18). The mean floral bud number per cane was based on a 10-node cane sample. The base chilling estimate of 334 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with the same lowercase letter are not significantly different using Tukey's honestly significant difference (α = 0.05) (n = 3).

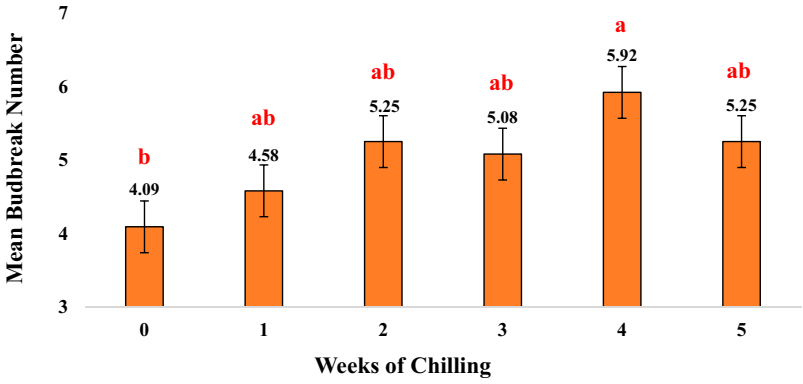

Fig. 10. 'AU Golden Dragon' kiwifruit mean vegetative budbreak number per cane vs. warm temperature interruption during chilling exposure across six chilling levels for 1 year (2018–19). The mean floral bud number per cane was based on a 10-node cane sample. The base chilling estimate of 360 units includes field-supplied and accumulation-during-storage values based on 0 to 7.2 °C and Richardson models. Treatment means (± standard error for error bars) with the same lowercase letter are not significantly different using Tukey's honestly significant difference (α = 0.05) (n = 3).

Conclusion

The objective of our study was to determine whether exposure to warm temperature interruption, as encountered during the winter in the southeastern United States, could result in negation of chilling in kiwifruit. Demonstrated at the highest two levels, the green cultivar AU Fitzgerald exhibited reduced floral activity under conditions of warm temperature interruption during chilling accumulation. Conversely, 'AU Golden Dragon' produced comparable and, in some cases, greater floral activity under these conditions, showing no indication of chilling negation in this gold cultivar. However, exposure to higher experimental temperatures during chilling interruption proved capable of floral inhibition in both cultivars.

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