Scientia Horticulturae 205 (2016) 106–111

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Temperature model of litchi flowering—From induction to anthesis

Po-An Chen [a,b,*], Su-Feng Roan [c], Chin-Lung Lee [a], Iou-Zen Chen [a]

[a] Department of Horticulture, National Taiwan University, No. 1, Sec. 4, Roosevelt Road, Taipei, Taiwan
[b] Plant Technology Laboratories, Agricultural Technology Research Institute, No. 1, Ln. 51, Dahu Rd., Xiangshan Dist., Hsinchu, Taiwan
[c] Department of Horticulture and Biotechnology, Chinese Culture University, 55, Hwa-Kang Road, Yang-Ming-Shan, Taipei, Taiwan

ARTICLE INFO

Article history:
Received 25 November 2015
Received in revised form 8 April 2016
Accepted 12 April 2016
Available online 28 April 2016

Keywords:
Chilling requirement
Flowering phonological stage
Growth degree hour
Thermal requirement

ABSTRACT

To study the effect of air temperature on the physiological stages of flowering in litchi (*Litchi chinensis* Sonn.), we pruned the two apical buds of 'Yu Her Pau' litchi to release the axillary buds into inflorescence induction. We used three years of flowering performance data, including 14 pruning episodes, along with temperature data from the field, to develop three different growth models: an "inflorescence induction model" (IIM), a "floret anthesis model" (FAM), and an "inflorescence length model" (ILM). Using the regression relationship between assumed temperature and the coefficient of variation in "chilling-degree-hours" (CDHs), and the "thermal-degree-hours" (TDHs) of all treatments, we estimated the base temperatures of inflorescence induction and floret anthesis to be 23.42 °C and 19.32 °C, respectively. Furthermore, using the IIM, we divided inflorescence induction into "pre-induction" and "induction" phases, and these had chilling requirements of 4030 and 3343 CDHs, respectively. Florets entered anthesis when they reached 2397 TDHs after inflorescence emergence. The length of the inflorescence flush can be deduced from the CDHs between inflorescence emergence and floret flowering, and the ILM indicated that the length of the inflorescence flush was positively correlated with the CDHs during this period. However, the FAM showed that the timing of anthesis was positively correlated with the speed of thermal temperature accumulation. This finding indicates that the process from inflorescence emergence to floret anthesis results from a competition between the chilling requirement for inflorescence flush elongation and the thermal requirement for floret anthesis.

1. Introduction

Low temperature is essential for inflorescence induction in litchi (*Litchi chinensis* Sonn.) (Menzel, 1983). Each cultivar has a unique temperature and quantum threshold (Menzel and Simpson, 1988; Sethpakdee, 2002; Singh and Babita, 2002). The inflorescence induction period depends on the air temperature, and a faster accumulation of air temperature below the threshold during induction leads to faster inflorescence emergence (Chang, 1999; Menzel and Simpson, 1991, 1995; Shen, 1992; Teng, 1996). After inflorescence initiation, florets flower sooner and shorter inflorescences are formed in warm environments, but abortion occurs at high temperatures (Chang, 1999; Huang and Chen, 2003; Wei et al., 2013); whereas anthesis occurs later and longer inflorescences are developed at lower temperatures (Chang, 1999; Chen et al., 2013; Menzel and Simpson, 1991, 1995; Teng, 1996). These findings indicate that the requirements for inflorescence induction differ from those required for inflorescence development and anthesis in litchi. However, most of these studies considered the whole period of flowering, so the specific temperature requirements for induction and development could not be distinguished. Moreover, these studies evaluated temperature effects only at fixed points rather than along whole temperature gradients. As a result, the effect that temperature exerts on the induction and development of inflorescences is still unclear.

Litchi vegetative flushes cease to grow in autumn and then apical buds undergo inflorescence induction by low temperature in winter. After inflorescence induction, buds emerge, and then the next stage of flowering—inflorescence development—begins. Finally, anthesis of inflorescences occurs in early spring. The entire process of litchi flowering includes several stages and each stage is defined differently by different researchers. In the present study, we define "inflorescence induction" as the bud undergoes the period of chilling temperature that starts after pre-induction (Huang and Chen,

* Corresponding author at: Plant Technology Laboratories, Agricultural Technology Research Institute, No. 1, Ln. 51, Dahu Rd., Xiangshan Dist., Hsinchu, Taiwan.
E-mail addresses: pachen0603@yahoo.com.tw, chenpoan@mail.atri.org.tw (P.-A. Chen).

http://dx.doi.org/10.1016/j.scienta.2016.04.012
0304-4238/

2003); pre-induction is also called "vegetative dormancy" (Lin, 1987; Menzel et al., 1989). Inflorescence induction continues until inflorescence initiation, which corresponds to the time when inflorescence emergence is visible to the naked eye (visibility of "white granules"). Then, we define "inflorescence development" as the period from which white granules are formed, to floret flowering. In Taiwan, inflorescence induction in litchi begins in October, when the plants cease continuous vegetative growth, and floret anthesis occurs from February to April.

Litchi vegetative dormancy buds can be released into the inflorescence induction condition under suitable temperatures. In mango, pruning off the apical buds after exposure to low temperature may release the later axillary buds to form inflorescences (Davenport, 2006; Shu and Sheen, 1987), but tip pruning does not affect the chilling requirement of inflorescence induction (Nagao et al., 2000; Stern et al., 2005). Pruning does not affect the induction requirement of inflorescences in litchi, either (Lin et al., 1998; Stern, 1992). Hence, we could gather a series of axial inflorescence buds with different inflorescence induction starting points by pruning off the apical buds in winter. In this study, we recorded flowering performance after several rounds of tip pruning during the winter, for three years, to measure the critical base temperature of flowering in litchi. We used the statistics calculated include the regression coefficient and coefficient of variation in hours, modified from Arnold (1959) to establish the chilling requirement, which is the sum of total degrees under the chilling base temperature (CBT), and the thermal requirement, which is the sum of total degrees higher than thermal base temperature (TBT), to develop flowering models to explain the morphological changes that occur during the flowering period.

2. Materials and methods

2.1. Plant material and experimental method

The data for the statistical models were collected from 10-year-old "Yu Her Pau" litchi plants grown in the Niaosung District (22°65′ N, 120°34′ E) (2011–2013), and 10-year-old and 11-year-old litchi plants grown in the Dashu District (2013–2014) (22°70′ N, 120°43′ E) in Kaohsiung County, Taiwan. The average monthly temperatures from 1981 to 2010 ranged from 19.3 °C (January) to 29.2 °C (June). The average monthly temperatures from October to March, which is the time of inflorescence induction and development, were 26.7, 24.0, 20.6, 19.3, 20.3, and 22.6 °C, respectively.

The branches of all the experimental trees were pruned after the previous harvest (mid-June) in order to maintain the tree shape. All branches produced three leafy flushes before mid-October and were well maintained for the experiment. Fertilization and irrigation were discontinued when the branches matured in October. All of the plants ceased growing after October in our experiments. Two buds on the branches were pruned off from the top (Fig. 1) to restart the accumulation of temperature units for inflorescence induction. The tip pruning treatments were conducted between 2011 and 2014 at one-week to one-month intervals, depending on the vegetative dormancy and inflorescence induction conditions of the trees. The tip pruning dates during 2011–2012 were from November 19, 2011 to December 31, 2011, while the pruning dates during 2012–2013 were from November 16, 2012 to January 18, 2013. The pruning dates during 2013–2014 were from October 28, 2013 to January 12, 2014. Control groups without tip pruning were chosen after the leafy flushes matured in 2012 and 2013 in Dashu District. For each treatment, five trees randomly selected from the orchard were used, and 20 branches from each tree were randomly pruned at heights of approximately 1.5–1.8 m above the ground.

Fig. 1. Procedure of tip pruning in 'Yu Her Pau' litchi. The arrow indicates the apical vegetative dormancy bud.

2.2. Data collection

Flowering performance data were collected from all branches selected for the experiment during each week after pruning in order to ascertain date of inflorescence emergence (visibility of white granules), date of the first floret flowering in each inflorescence, and inflorescence length at the onset of anthesis in the first floret.

Air temperature data were collected with HOBO data loggers (Onset Computer Corporation, Bourne, MA) at each site from October to April. The data loggers were set under a shed cover at 1.5 m above the ground, with data recorded every hour.

2.3. Statistical analysis

2.3.1. Data quantification

The ratio of inflorescence emergence was calculated as the number of visible inflorescence primordia divided by 20 (the number of branches selected from each tree); the ratio of floret anthesis was given by the number of inflorescences undergoing anthesis divided by the total number of inflorescences on each tree; and the length of the inflorescence was calculated as the average length of the flowering inflorescences of each tree. The stages "inflorescence primordium becomes visible" and "floret anthesis" were recognized according to the description used in a previously study (Wei et al., 2013).

2.3.2. Model building

The inflorescence induction model (IIM) is given by:

$$IIM_i = \begin{cases} 0 & T_{bi} - T(i) < 0 \\ T_{bi} - T(i) & T_{bi} - T(i) \geq 0 \end{cases}$$

$$IIM_t = \sum_{i=leafmatured}^{t=cumulatingtime} IIM_i$$

and inflorescence emergence occurs when:

$$IIM_t \geq IIM_{cri}$$

where IIM_i is the induction quantum of each hour, T_{bi} is the base temperature of inflorescence induction (i.e., CBT), $T(i)$ is the air temperature of each hour, IIM_t is the sum of chilling-degree-hours (CDHs) from the leaf maturation date or pruning date to the time of cumulation (i.e., the amount of accumulated inflorescence induc-

tion at a specific time), and IIM_{cri} is the critical threshold amount of CDHs for inflorescence induction.

The floret anthesis model (FAM) is given by:

$$FAM_i = \begin{cases} 0 & T(i) - T_{ba} < 0 \\ T(i) - T_{ba} & T(i) - T_{ba} \geq 0 \end{cases}$$

$$FAM_t = \sum_{i=inflorescenceemergence}^{t=cumulatingtime} FAM_i$$

and floret anthesis occurs when:

$$FAM_t \geq FAM_{cri}$$

where FAM_i is the anthesis quantum of each hour, T_{ba} is the base temperature of anthesis (i.e., TBT), FAM_t is the sum of the thermal-degree-hours (TDHs) from inflorescence emergence to the time of cumulation (i.e., the accumulated amount of anthesis at a specific time), and FAM_{cri} is the critical threshold amount of TDHs for floret anthesis.

The inflorescence length model (ILM) is given by:

$$ILM_i = \begin{cases} 0 & T_{bi} - T(i) < 0 \\ T_{bi} - T(i) & T_{bi} - T(i) \geq 0 \end{cases}$$

$$ILM_t = \sum_{i=inflorescenceemergence}^{n=floretsanthesis} ILM_i$$

$$LI = \alpha \times ILM_t + \beta$$

where ILM_i is the induction quantum of each hour, T_{bi} is the base temperature of inflorescence development, ILM_t is the sum of the CDHs, (i.e., the total quantum of inflorescence development), LI is the length of the inflorescence, and α and β are the parameters of the LI linear relation equation.

The flowering model (FM) is given by:

$$FM_t = \left(\frac{IIM_t}{IIM_{cri}} - ILM_t\right) * 50 + \frac{FAM_t}{FAM_{cri}} * 50$$

and inflorescence flowering occurs when:

$$FM_t \geq 100$$

where FM_t is the degree level of the flowering, i.e., the accumulated amount of flowering in a specific time.

All base temperatures and growing-degree-hours (GDHs) in the models were estimated through (1) the regression coefficient, and (2) the coefficient of variation (CV) in degree hours. We first used a series of candidate base temperatures at 1 °C intervals, modified from the recommendations of Arnold (1959), and we then plotted CV values against temperature in intervals of 1 °C within the range of the induced temperatures from previous studies (15 °C to 26 °C) to calculate a set of GDHs and CV values for each temperature. Second, we used the base temperature and CV for the quadratic regression equation. Third, the minimum CV was calculated by the quadratic regression equation, and the temperature corresponding with the minimum CV was selected as the base temperature. Finally, we calculated the GDHs under the selected base temperature of each model. In this study, each base temperature and GDHs was calculated from 60 observed data sets.

3. Result and discussion

3.1. Effect of tip pruning on flowering

Tip pruning affected the timing of inflorescence emergence and anthesis in all three seasons (Fig. 2). The order of the timing of inflorescence emergence was consistent with the sequence order of pruning. However, the periods between pruning to inflorescence initiation and inflorescence emergence to floret anthesis were different for each treatment because of the temperature conditions. The control groups were no different from the earliest pruning, suggesting that the requirement for inflorescence induction was not affected by tip pruning, and induction started just after tip pruning.

The temperature was coldest in January at our experimental site, and lower temperature can accelerate the accumulation of inflorescence induction. Hence, the buds that were pruned before January reached maximum inflorescence emergence at the end of the third week of January. However, the buds that were pruned after January reached maximum inflorescence emergence after February. Because the temperature was getting cooler from October to January, the accumulation of inflorescence induction would take place during a shorter-day period. For this reason, the interval of our pruning treatment was shorter after mid-December.

3.2. Inflorescence induction model

The CBT of induction calculated from all experiments was 19.25 °C, which corresponds to the minimum value calculated by the regression equation (Fig. 3). However, the corresponding CV was 26.41%, which is high for a model with good predictive capacities. We divided the pruning treatments into two groups according to pruning date and the state of vegetative dormancy. The early group was pruned on November 19, 2011, December 3, 2011, November 16, 2012, December 14, 2012, October 28, 2013, December 1, 2013, and control groups which without pruning in 2012–2013 and 2013–2014. The late group included all other treatments, including December 17, 2011, December 31, 2011, January 4, 2013, January 18, 2013, December 15, 2013, December 22, 2013, January 5, 2014, and January 12, 2014. The CBTs of induction estimated from the early and late groups were 21.36 °C and 23.42 °C, respectively, and their corresponding CVs were 20.40% and 5.94% (Fig. 3). These results represent an improvement with respect to the estimates made from all treatments taken together, the late group especially so. However, the base temperature was considered consistent among cultivars (Menzel, 1983, 1984, 1985). We fixed the CBT of inflorescence induction at 23.42 °C as the parameter of T_{bi} because of its smaller CV and because of the physiological reason discussed below. Although the CBT we found is a little higher than that of other cultivars (Menzel and Simpson, 1988; Sethpakdee, 2002; Singh and Babita, 2002), the critical inflorescence induction temperatures of "Yu Her Pau" (an early season cultivar) was also found to be about 20–25 °C in previous studies that conducted in a phytotron at a fixed temperature (Chang, 1999; Chen and Wang, 2012; Shen, 1992; Teng, 1996). The number of hours under 15 °C before inflorescence emergence during each of the three winters was 40, 157, and 253, respectively. The number of hours under 10 °C before inflorescence emergence during the three years was 0, 13, and 50, respectively. These weather data showed that if 15 °C was chosen as a CBT, the chilling requirement could not be met. This supports that the base temperature of above 20 °C that we found in our model is reasonable.

The CDHs of the early pruning and late pruning group were well separated in our IIM. Using this model, we can observe that stimulation of inflorescence induction occurs under a specific range of CDHs (Fig. 4). We term this model-derived separation line the "watershed", as it not only divides the early and late groups but also

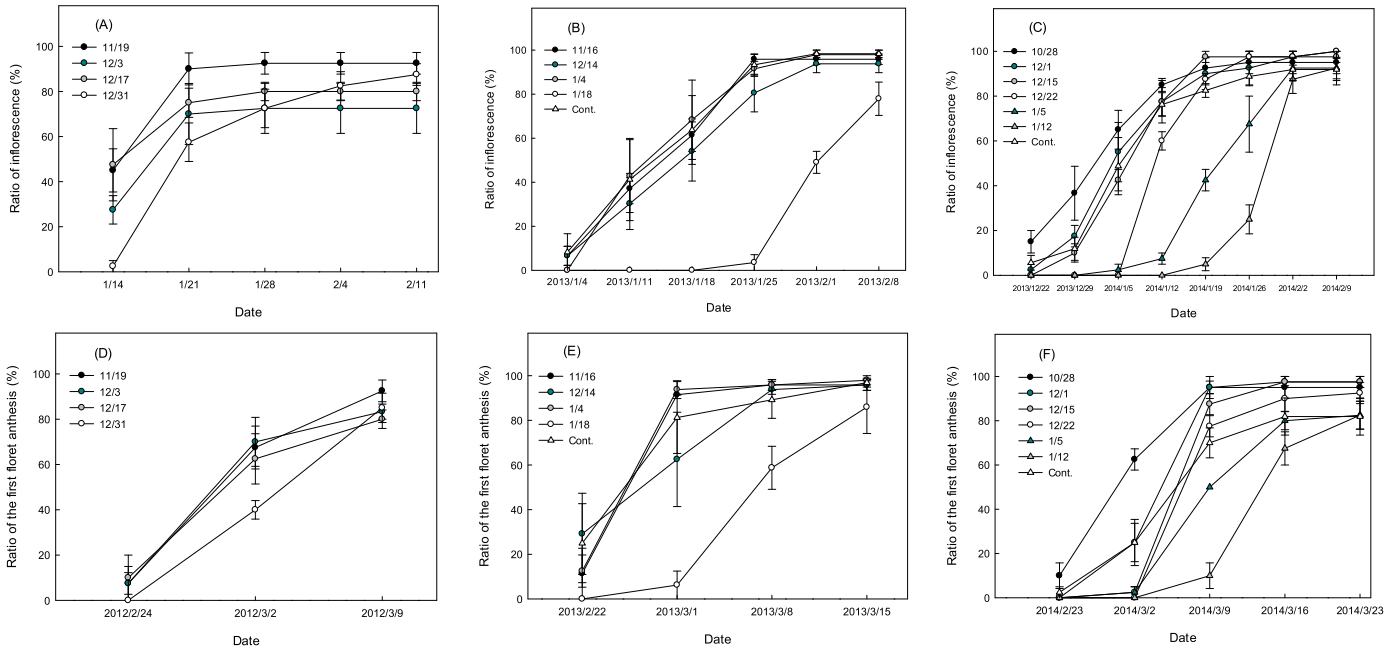

Fig. 2. The influence of pruning timing on the time of inflorescence emergence of 'Yu Her Pau' litchi in (A) 2011–2012 (B) 2012–2013 (C) 2013–2014; and anthesis time in (D) 2011–2012 (E) 2012–2013 (F) 2013–2014. Two buds on the top of flush were pruned off in each treatment. Control treatment (Cont.) means which was without pruning. The ratio of inflorescence emergence was calculated as the number of visible inflorescence primordia divided by 20; the ratio of floret anthesis was given by the number of inflorescences undergoing anthesis divided by the total number of inflorescences on each tree. Bar means ± SE. (n = 5).

divides the pre-induction and true-induction stages of the inflorescences. Below the watershed (the early group), about 7373 CDHs (the average CDHs of 2012–2013 cont., 2012/11/16, 2013–2014 cont. and 2013/10/28) are required for whole inflorescence induction, and this requirement decreases with time (Fig. 4). Across the watershed (the late group), only 3343 CDHs (the average CDHs of late group) were required for inflorescence induction, and this requirement does not change over time (Fig. 4). We therefore define this watershed as the line that distinguishes the conditions that are characteristic of pre-induction from those of true-induction (induction). This watershed period occurred around mid-December in Kaohsiung, Taiwan. Tip pruning only eliminates the effects of chilling requirement, which accumulate during pre-induction. Once pre-induction is completed, the plant enters vegetative dormancy. However, inflorescence induction is initiated when the axially bud is able to sense low temperatures, i.e., when it was released by pruning off its apical bud. These results suggest that pre-induction is beneficial for whole trees, while true induction is required for each bud. The division time is also the specific time for leafy inflorescence by gibberellic acid treatment (Chen et al., 2014). This implies that this was the inflorescence induction period for litchi, and therefore the division characterized by the model was appropriate. Before the watershed, the whole CDHs were used to overcome pre-induction and true-induction. Pre-induction is a period of cessation of growing before inflorescence induction in litchi, and it can be reached not only by low temperature but also by other factors such as drought or girdling (Huang and Chen, 2003; Menzel, 1983). Although pre-induction can brought about by other factors, low temperature is the most common and natural factor. However, no clear distinction has been recognized between the two parts of induction. We believe that our results identify this line of distinction and shed light on other differences in the physiological mechanisms of pre-induction and induction.

Across the watershed, only true-induction needs to be achieved. Pruning after the watershed, chilling requirement had been met had no effect (Fig. 4). This observation indicates that tip pruning does not affect true induction of the inflorescence; it only affects the onset of accumulation of CDHs at low temperatures. However, the chilling required may decrease with the delay before watershed. This finding implies that the requirements of the early group not only included inflorescence induction but also included pre-induction. Hence, it is a supportive proof that the watershed represents a line that is the characteristic of a stage between pre-induction and true-induction. The amount of vegetative dormancy induction depends on the environment and the condition of the tree. Therefore, the amount of chilling required by the early group was much more variable than in the late group (Fig. 4). However, in the same field and under the same cultivation conditions (e.g., soil moisture, light, and fertilization), the chilling requirement for pre-induction may not vary significantly. Our study indicated that approximately 4030 CDHs (7373−3343 = 4030) were needed.

3.3. Floret anthesis model

We estimated the TBT and quantity of anthesis using the same concepts and statistical methods used in the IIM. The only difference was that the thermal requirement was calculated here whereas the chilling requirement was calculated in IIM. The TBT of anthesis was 19.32 °C when the minimum value of the regression formula was 8.83% (Fig. 3). When using 19.32 °C as T_{ba}, the critical threshold amount for floret anthesis was 2397 TDHs. No grouping of the pruning times was required to estimate the FAM as was the case with the IIM model. This finding suggests that the physiological thermal requirement of anthesis is simpler in the FAM than in the IIM. According to the FAM model, warmer temperatures may lead to early flowering; this result is consistent with the results of previous studies (Chang, 1999; Menzel and Simpson, 1991; Teng, 1996). However, florets may abort and fail to reach anthesis when development occurs at high temperatures (Chang, 1999; Menzel and Simpson, 1991; Teng, 1996). The model developed in our study can identify the lower temperature limit, and this will aid in ascertaining flowering time; however, the upper temperature threshold that causes abortion could not be determined.

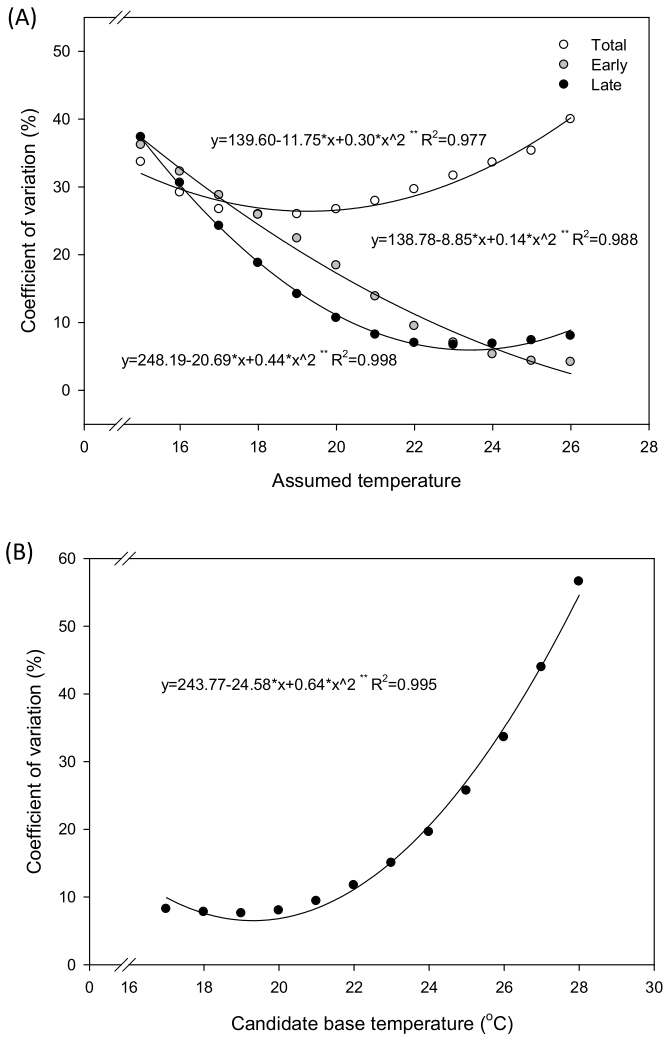

Fig. 3. Coefficient of variation in growing degree hours for the period between (A) pruning and inflorescence emergence and (B) inflorescence emergence and anthesis at various candidate base temperatures of 'Yu Her Pau' litchi during 2011–2014. Data are the coefficients of variation between 14 treatments, each treatment is the average of 20 branches per tree, with 5 trees each treatment.

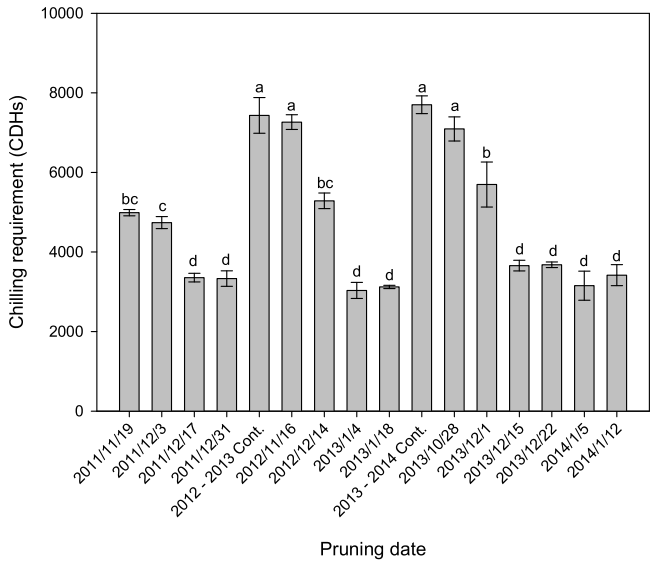

Fig. 4. The chilling requirement for inflorescence induction of 'Yu Her Pau' litchi of each pruning timing in 2011–2014. 2012–2013 cont. and 2013–2014 cont. means which were without pruning in 2012–2013 season and 2013–2014 season, respectively. Data are the average of 20 branches per tree, with 5 trees each treatment. Bar means ± SE. Different alphabets represent the application difference reaching Student-Newman-Keuls <0.05.

3.4. Inflorescence length model

We used the amount of CDHs during inflorescence development to predict inflorescence length (Fig. 5). The results show that the length of the inflorescence is positively correlated with the chilling amount, and there is no significant relation between the number of days between emergence and anthesis. However, there were two linear regressions (Fig. 5). The two regression peaks were separated by 6000 CDHs, and each regression could predict the inflorescence length in each group. Some previous studies have suggested that inflorescence at low temperatures can inhibit or prevent elongation (Chang, 1999; Menzel and Simpson, 1991; Stern et al., 2003). We believe this is the main reason why the slope of the regression decreased when the ILM was higher than 6000 CDHs.

The number of fruits among an inflorescence has been associated with the length of the inflorescence. We propose a way to predict the length of the inflorescence in this study, and a model to predict the number of fruits set according to the length of the inflorescence has been proposed earlier (Chen et al., 2013). These two models can be used to predict the yield of "Yu Her Pau" litchi.

3.5. Flowering model

The IIM model predicts when inflorescence emergence will occur. After inflorescence emergence, the tip meristem of the inflorescence keeps dividing and florets initiate. We can predict the end time of inflorescence development and anthesis using the FAM model. Once we know the anthesis time, we can estimate the length of the inflorescence by using the ILM model. All three models together represent the FM of litchi.

The inflorescence was initiated during inflorescence emergence and growth was observed even after initiation, and it ended at anthesis. During this period, inflorescence meristem (primordia) and floret meristem may develop together. Induction, initiation, and elongation occurred at the same time but not in the same place. Owing to its complexity, this period was not easy to segregate. Many studies have tried to describe the flowering stages, but

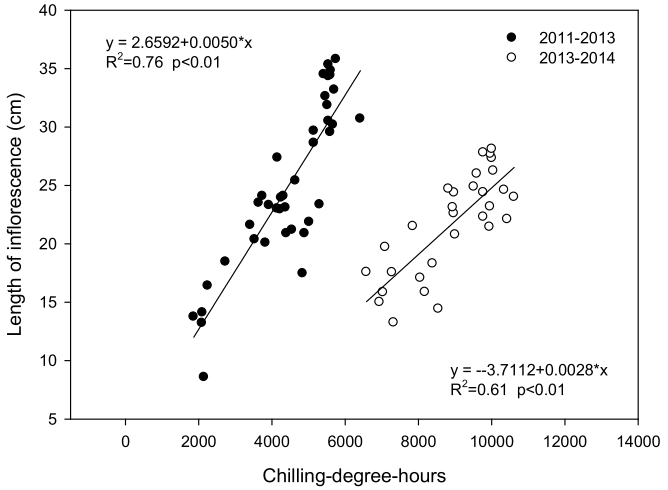

Fig. 5. The relationship between the amount of chilling-degree-hours during inflorescence emergence to anthesis and the length of inflorescence of 'Yu Her Pau' litchi in 2011–2014. Data are the average of 20 branches per tree, with 5 trees each treatment.

discrepancies continue to exist after inflorescence emergence and up to anthesis (Huang and Chen, 2003; Lin, 1987; Menzel, 1983).

Our three models, IIM, FAM, and ILM, were able to explain inflorescence development. IIM described the base temperature for induction. We hypothesize that the induction requirement of the inflorescence primordia is almost the same. All paracladia of the same inflorescence flower together when the inflorescence stops elongating and branching (Lee, 2004; Lin, 1987). Hence, each paracladium can be considered as a smaller version of an inflorescence. The paracladia stop differentiating once vegetative capacity decreases below a certain threshold (Prusinkiewicz et al., 2007). Warmer temperatures stop inflorescence development and elongation of inflorescences in litchi, whereas lower temperatures promote greater inflorescence lengths (Chang, 1999; Menzel and Simpson, 1991, 1995; Teng, 1996). Warmer temperature can be seen as the factor that stops inflorescence development. In contrast, lower temperature can be seen as the factor that promotes floret induction of the paracladium. Therefore, competition between warm temperature (stop code) and low temperature (promoter) determines anthesis time and the length of the inflorescence.

It appears that inflorescence elongation, floret initiation, and anthesis are intricately linked. However, the factors affecting each phase are quite different. The FAM and ILM suggest that the florets are induced by low temperature. New florets kept initiating on paracladia until the accumulation of thermal growth degrees reached its threshold. This was at the same time as when the top meristem of the inflorescence ceased to divide. When the meristem of the inflorescence ceased to divide into more primordia, the inflorescence stopped elongating.

T_{bi} (the CBT of IIM) and T_{ba} (the TBT of FAM) can also help describe the development of inflorescence in more detail. Our results showed that T_{bi} (23.42 °C) was higher than T_{ba} (19.32 °C). This means that floret and inflorescence development occur simultaneously. Only under these conditions can inflorescences can reach a certain length once florets are at anthesis time. If T_{bi} is lower than T_{ba}, litchi will not flower at a constant temperature. Because of this situation, the constant temperature could only satisfy CDHs or TDHs. However, litchi can flower well in a fixed temperature environment (Menzel and Simpson, 1995; O'Hare, 2002; Shen, 1992). Therefore, our results are consistent with those obtained by previous studies.

4. Conclusions

We generated different models for inflorescence induction, floret anthesis, and inflorescence length, in order to describe the flowering of litchi in detail. The base temperature of the IIM was 23.42 °C, and IM_{cri} was 3343 CDHs. By using the IIM model, we identified that pre-induction required 4030 CDHs, and it needed 7373 CDHs to satisfy all requirements from leaf maturation to inflorescence emergence. The base temperature of FAM was 19.32 °C, and AM_{cri} was 2397 TDHs. In the ILM model, the CDHs used 23.42 °C as the base temperature and was able to predict inflorescence length by linear regression. These models, as well as models to predict the actual state, were evaluated and validated with statistical indexes. These models can help describe in detail the physiology of flowering in litchi and how temperature affects various processes. The results of the present study suggest that understanding the physiological basis separating the stages of floral induction and floral development is important in order to develop models with predictive power.

References

Arnold, C.Y., 1959. The development and significance of the base temperature in a linear heat unit system. Proc. Am. Soc. Hortic. Sci. 74, 430–445.

Chang, J.W., 1999. Regulation of Flowering in Litchi (*Litchi Chinensis* Sonn.). Department of Horticulture. National Taiwan University, Taipei, Taiwan.

Chen, L., Wang, J., 2012. The relationship between blooming of Feizixiao Litchi cultivar with meteorological factors. Trop. For. 40, 26–28.

Chen, P.A., Roan, S.F., Lee, C.L., Chen, I.Z., 2013. The effect of temperature during inflorescence development to flowering and inflorescence length on yield of 'Yu Her Pau' litchi. Sci. Hortic. 159, 186–189.

Chen, P.A., Lee, C.L., Roan, S.F., Chen, I.Z., 2014. Effects of GA $_3$ application on the inflorescence and yield of 'Yu Her Pau' litchi. Sci. Hortic. 171, 45–50.

Davenport, Thomas L., 2006. Pruning strategies to maximize tropical mango production from the time of planting to restoration of old orchards. HortScience 41, 544–548.

Huang, H.B., Chen, H.B., 2003. A phase approach towards floral formation in lychee. Acta Hortic. 665, 185–194.

Lee, S.R., 2004. The Enabling Technology of the Flowering and Fruit Seeting of 'Yu-Her-Pao' Litchi (*Litchi Chinensis* Sonn.). Kaohsiung District Agricultural Research and Extension Station, Pingtung, Taiwan.

Lin, X.D., Wu, D.Y., Ye, Q.H., Wang, W.H., 1998. Effects of panicle pruning on litchi (*Litchi chinensis* Sonn. cv. Feizixiao) flower quality and fruit setting. J. South China Agric. Univ. (China) 19, 124–125.

Lin, T.S., 1987. Evocation, initiation, and development of flower and morphology of inflorescence in *Litchi chinensis* Sonn. Hortscience 22, 1125 (1125).

Menzel, C.M., Simpson, D.R., 1988. Effect of temperature on growth and flowering of litchi (*Litchi chinensis* Sonn) cultivars. J. Hortic. Sci. 63, 349–360.

Menzel, C.M., Simpson, D.R., 1991. Effects of temperature and leaf water stress on panicle and flower development of litchi (*Litchi chinensis* Sonn). J. Hortic. Sci. 66, 335–344.

Menzel, C.M., Simpson, D.R., 1995. Temperatures above 20 °C reduce flowering in lychee (*Litchi chinensis* Sonn.). J. Hortic. Sci. 70, 981–987.

Menzel, C.M., Rasmussen, T., Simpson, D., 1989. Effects of temperature and leaf water stress on growth and flowering of litchi (*Litchi chinensis* Sonn.). J. Hortic. Sci. 64, 739–752.

Menzel, C.M., 1983. The control of floral initiation in lychee: a review. Sci. Hortic. 21, 201–215.

Menzel, C.M., 1984. The pattern and control of reproductive development in lychee: a review. Sci. Hortic. 22, 333–345.

Menzel, C.M., 1985. Propagation of lychee—a review. Sci. Hortic. 25, 31–48.

Nagao, M.A., Hoa, E., Nishina, M.S., Zee, F., 2000. December pruning of vegetative flushes affects flowering of Kaimana Lychee in Hawaii. J. Hawaiian Pacific Agric. 11, 17–21.

O'Hare, T.J., 2002. Interaction of temperature and vegetative flush maturity influences shoot structure and development of lychee (*Litchi chinensis* Sonn.). Sci. Hortic. 95, 203–211.

Prusinkiewicz, P., Erasmus, Y., Lane, B., Harder, L.D., Coen, E., 2007. Evolution and development of inflorescence architectures. Science 316, 1452–1456.

Sethpakdee, R., 2002. Lychee Production in Thailand. Lychee Production in the Asia-Pacific Region. Food and Agriculture Organization of the United Nations, Regional Office for Asia and the Pacific, Bangkok, Thailand, pp. 106–113.

Shen, S.M., 1992. Effect of Temperature, Leaves, Ethylene and Light on Flower Cluster Formation of Litchi (*Litchi Chinensis* Sonn.). Department of Horticulture. National Taiwan University, Taipei, Taiwan.

Shu, Z.H., Sheen, T.F., 1987. Floral induction in axillary buds of mango (*Mangifera indica* L.) as affected by temperature. Sci. Hortic. 31, 81–87.

Singh, H.P., Babita, S., 2002. Lychee production in India. In: Papademetriou, M.K., Dent, F.J. (Eds.), Lychee Production the Asia-Pacific Region. Food and Agricultural Organization of the United Nations, Regional Office for Asia and the Pacific, Bangkok, Thailand, pp. 55–77.

Stern, R.A., Goren, M., Gazit, S., 2005. The effect of shoot pruning during the fall and winter on lychee flowering and yield. Acta Hortic. 665, 331–335.

Stern, R.A., Naor, A., Bar, N., Gazit, S., Bravdo, B.A., 2003. Xylem-sap zeatin-riboside and dihydrozeatin-riboside levels in relation to plant and soil water status and flowering in 'Mauritius' lychee. Sci. Hortic. 98, 285–291.

Stern, R.A., 1992. Elucidation of the Factors Affecting Litchi Productivity in Israel, and the Development of Methods to Improve its Yield. PhD Diss. Faculty of Agr., Hebrew Univ., Jerusalem, Israel.

Teng, Y.H., 1996. Pruning and Regulation of Blooming Time in High Density Planting of Lychee (*Litchi Chinensis* Sonn.) Cv. Yu Her Pau. Department of Horticulture. National Taiwan University, Taipei, Taiwan.

Wei, Y.Z., Zhang, H.N., Li, W.C., Xie, J.H., Wang, Y.C., Liu, L.Q., Shi, S.Y., 2013. Phenological growth stages of lychee (*Litchi chinensis* Sonn.) using the extended BBCH-scale. Sci. Hortic. 161, 273–277.