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Flowering and shoot elongation of lychee in eastern Australia

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Abstract. We investigated the effects of the timing of shoot elongation on the flowering of lychee (*Litchi chinensis* Sonn.) in eastern Australia. Trees of cv. Kwai May Pink growing in Alstonville (lat. 28.9° S) were pruned during spring and summer, and subsequent shoot elongation was measured until the following spring. New shoots grew by discrete flushes, with the trees initiating 3, 2, or 1 vegetative shoots prior to winter, according to the pruning sequence. Shoots were vegetative when the mean temperature during early flush development was above 17–19°C, and floral at lower temperatures. Trees with successive flushes commencing in February (late summer) and June (early winter) were more likely to flower than trees with flushes commencing in April and August, because the weather conditions in June were cooler than those in August and more likely to favour induction. The importance of cool weather conditions during early flush development for floral determination was not significantly affected by the number of vegetative flushes to develop between pruning and winter.

Having shown that the phase of recurrent flushing affects flowering, we sought to model the process in order to recognise reproductive and non-reproductive cycles along Australia's north-eastern seaboard, and to develop a management strategy for the promotion of flowering. From the results of the Alstonville pruning trial, the interval between successive flushes was regressed against the mean product of daily irradiation and mean daily temperature (°C.MJ/[m².day]) during the interval. The regression was used in conjunction with long-term weather records to estimate the flush commencement dates required for the completion of 1 or 2 vegetative flushes by the winter solstice at different latitudes. The earliest date for the completion of 1 flush ranged from 16 February in northern New South Wales (lat. 30° S) to 13 March in northern Queensland (lat. 17° S). To test the model, a pruning trial was conducted near Mareeba (lat. 17° S). Trees pruned on 10 February, estimated to produce ≈1.5 flushes prior to winter (i.e. flushes in late autumn and early spring, but not in winter), flowered poorly and had low yields. In contrast, trees pruned on 11 March, estimated to produce 1 vegetative flush by winter, had good flowering and yields. Thus, strategic pruning after harvest can be used to manipulate flushing times, so that new, potentially flowering shoots emerge in winter. Cool temperatures are still required for successful flowering, and we provide estimates of the likelihood of such weather in the major growing areas by calculating the annual number of days with a mean temperature <20°C. For Cairns (lat. 16.9° S) the number of such days varied from 0 to 39 from 1888 to 1993, which is consistent with the irregular flowering of lychee in coastal northern Queensland.

Our work is the first demonstration for any species that the phase of recurrent flushing affects flowering, and emphasises the interplay between a plant's endogenous developmental cycle and seasonal variations in weather.

Additional keywords: tree, floral induction, recurrent flushing, pruning.

Introduction

Lychee (*Litchi chinensis* Sonn.; Sapindaceae) is an evergreen tree native to the rainforests of southern China, and grown commercially for its fruit in many subtropical climates (Batten and McConchie 1995). Shoots elongate by flushes of growth, either vegetative or floral. Each vegetative flush comprises several leaves and internodes; the floral flush is a terminal inflorescence (panicle). Successive flushes are separated by quiescent periods during which the expanded leaves of the vegetative flushes darken and thicken.

The interval between the start of successive flushes can be as short as 6 weeks, but is longer at low temperatures (≈12 weeks at 20°C; Batten and Lahav 1994). A new flush begins only when the leaves of the previous flush have matured or been removed (Menzel *et al.* 2000).

Temperature is the only factor known to induce flowering in lychee, with panicles forming at average daily temperatures <20°C (Menzel and Simpson 1995). Low temperatures induce flowering during early flush development, when buds are no more than a few millimetres in length, but not at later stages of shoot elongation (Batten

and McConchie 1995). Low temperatures are probably also ineffective during at least the greater part of the quiescent period, although the idea has not been rigorously tested.

It follows that lychee is most likely to flower when bud swelling occurs during winter. Trees with other patterns of development, such as successive flushes beginning in late autumn and early spring, are less likely to flower because bud swelling is less likely to coincide with cool weather.

To test this, we pruned 14 well-watered and well-fertilised trees at intervals over spring and summer to generate a range of flushing patterns. The patterns were followed through to the following spring, when the extent of flowering was recorded. We then modelled shoot development in order to predict reproductive and non-reproductive flush cycles for the commercial range of lychee production along Australia's north-eastern seaboard. Lastly, we tested the model at an orchard distant from the site where the model was developed.

Materials and methods

Flush development at Alstonville

The first experiment was conducted in the lychee orchard at the Tropical Fruit Research Station, Alstonville, northern New South Wales (28.9° S, 153.5° E). Fourteen trees of cv. Kwai May Pink were

randomly selected for pruning. Each tree received ample water from both rainfall and irrigation (≈ 30 kL/year), had leaf nutrient concentrations within industry standards (Greer 1995), and was sprayed with pesticides as needed.

The trees were pruned in pairs on 7 occasions: 11 September, 1 October, 14 October, 30 October, 19 November, and 10 December in 1996, and March 6 in 1997. Pruning was severe, involving the removal of major branches such that the tree heights were reduced from 7 to 2.5 m. All the remaining branches were tip-pruned to remove the most recent flush. The number of leaves per tree was reduced from several thousand to a few hundred.

Four tip-pruned branches were tagged on each tree, 1.5 m above the ground in the northern quarter of the canopy. The lengths of the new shoots of these branches were measured at intervals of 6–29 days (depending on how quickly the flushes grew) until 24 October 1997. On 13 October 1997, counts were made for each tree of the numbers of vegetative and floral branches. On 28 January 1998, counts were made of the fruit. New South Wales Agriculture provided hourly means of temperature and irradiation (400–1100 nm) for the research station (Fig. 1).

Each episode of shoot elongation is an s-shaped increase in length over time, that is, increasing rates of elongation at the beginning of the episode and decreasing rates towards the end. Menzel *et al.* (2000) described shoot elongation with the following s-shaped function, a modified sine curve that is asymmetrical when $t \neq 1$:

$$y = y_{\max} \cdot ([\sin(\pi \cdot r \cdot x - [\pi/2]) + 1]/2)^t \quad (1)$$

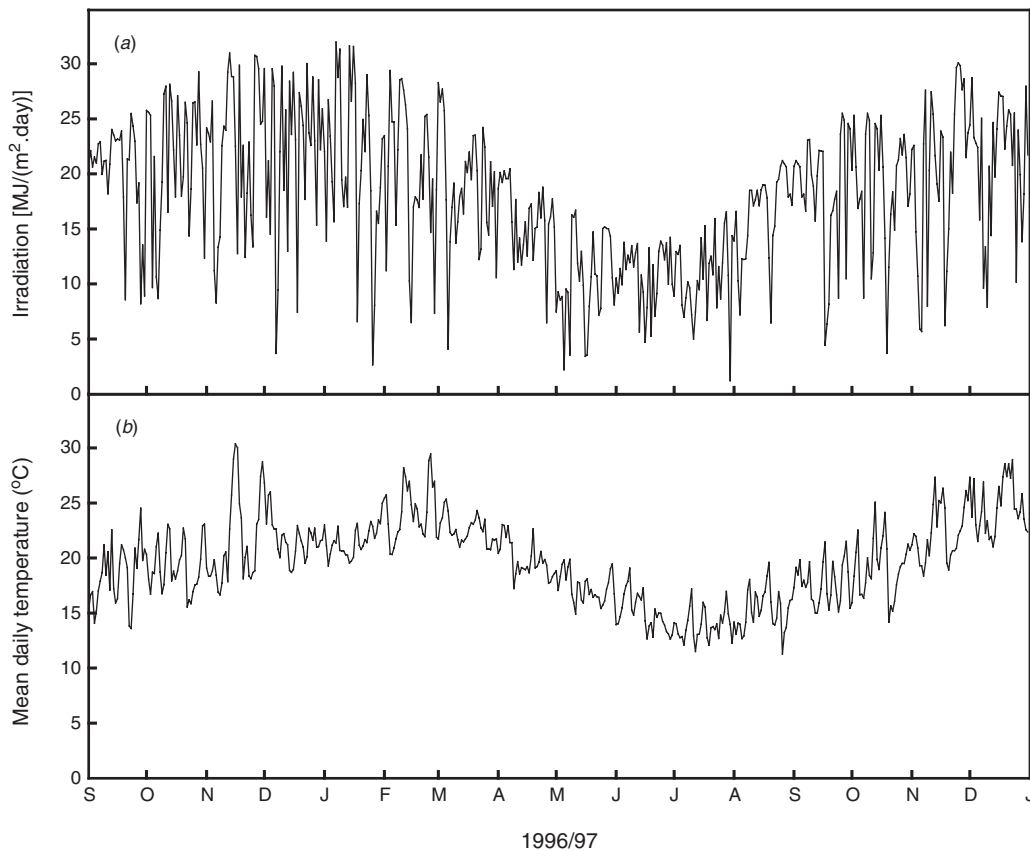


Fig. 1. Incident radiation (400–1100 nm) and air temperature at the Tropical Fruit Research Station, Alstonville (28.9° S), during the 1996–97 pruning trial.

where y is shoot length at time x , y_{\max} is the measured shoot length when elongation had ceased, x is the time from the start of the episode of shoot elongation, and r and t are form parameters related to the slope and symmetry of the curve; $x = 0$ was set at the date of the visit prior to the day on which the first sign of elongation was observed. The maximum increase in shoot length was taken as the measured value. Thus only 2 parameters were estimated (r and t). The function was further constrained by having the final day of shoot elongation no later than the day on which the maximum increase in shoot length was measured for the first time. All regressions were fitted using the Marquardt-Levenberg algorithm in *SigmaStat* (Jandel Corporation, San Rafael, CA). The branches of any one tree had only limited asynchrony in the development of flushes of new growth, with visually observable swelling of all tagged buds within the period of 2 visits. Curve-fitting was restricted to the tagged shoot with the longest extension during each whole-tree flush because there tended to be more measurements of intermediate lengths for this shoot.

Equation 1 was used to estimate the day on which shoot extension (for the shoot with the longest extension) was 2 mm in length. In this regard, the interpolated values were close to actual values in that approximately half of the first measured lengths of shoot extension were ≤ 2 mm. The day on which the shoot reached 2 mm in length was designated the commencement time for the whole-tree flush.

Bud determination (vegetative or floral) occurs when the buds are approximately 2 mm in length (Batten and McConchie 1995). The average temperature and daily irradiation at the time of bud determination were estimated from the weather records as the means of the 11-day block starting 5 days prior to the day on which the shoot with the longest extension reached 2 mm in length. An 11-day block was used for 3 reasons: firstly, uncertainty as to when buds reached 2 mm in length; secondly, uncertainty as to the length of the inductive window; thirdly, the 11-day averages reduced the day-to-day residual sums of squares for irradiation and temperature by approximately 80% and 40%, respectively (Menzel *et al.* 2000).

The dependency of the time between the commencement of successive flushes (based on the commencement times calculated above) on temperature and irradiation was described by a logistic curve fitted using *SigmaStat*. The fitted curve was used in conjunction with the long-term weather data of Meinke *et al.* (1995) to model the variation in flush development with latitude along Australia's north-eastern seaboard. The latitudes and longitudes of the weather station sites are given in Table 1, along with the periods of record.

Table 1. Long-term weather records at locations along the north-eastern seaboard of Australia

Location	Lat. (°S)	Long. (°E)	Years of record
Mossman	16.5	145.4	1911–1993
Cairns	16.9	145.8	1888–1993
Mareeba	17.0	145.4	1904–1993
Innisfail	17.5	146.0	1888–1993
Ingham	18.7	146.2	1893–1993
Ayr	19.6	147.4	1888–1993
Proserpine	20.5	148.5	1889–1993
Mackay	21.2	149.1	1891–1993
Nebo	21.7	148.7	1888–1993
Bundaberg	24.9	152.4	1888–1993
Gin Gin	25.0	152.0	1901–1993
Tiaro	25.7	152.6	1894–1993
Nambour	26.6	153.0	1894–1993
Murwillumbah	28.4	153.4	1891–1993
Harwood	29.4	153.3	1916–1993
Grafton	29.7	152.9	1880–1993

Test of model at Mareeba

The second experiment was a pruning trial on a commercial orchard near Mareeba in northern Queensland (17° S, 145.4° E). The trees were growing on a brown sandy loam overlying a clay, and were watered and fertilised as per industry recommendations (Greer 1995). Fifteen trees were randomly sorted into 3 groups of 5. One group was not pruned and acted as the control, another was pruned on 10 February, and the third group was pruned on 11 March. The pruning dates were chosen on the basis of predictions from the model of flush development, as will be explained below. Pruning involved the removal of approximately 0.5 m from each branch. The numbers of floral and vegetative branches per tree were scored in September. In November, each tree was scored for the number of fruit, and for the depth, breadth, and width of its canopy.

Results

Flush development at Alstonville

Phenology

All the trees budded shortly after pruning. Consequently, staggered pruning resulted in staggered bud release, and the stagger was perpetuated through successive episodes of shoot elongation (flushing), so different trees had different phases of flush development. An example for 2 trees is shown in Fig. 2a. Data from these 2 trees plus the other 12 trees were subsequently used to explore relationships between flowering and patterns of flush development (Fig. 2b,c), weather conditions during early flush development and floral determination (Fig. 2d) and relative yield and the start of panicle development (Fig. 2e). The data were also used to describe the dependency of the rate of flush development on the prevailing weather conditions (Fig. 3).

Trees with successive flushes starting in late summer and early winter were more likely to flower than trees with flushes commencing in mid-autumn and late winter (Fig. 2b,c). The winter shoots followed the pre-winter shoots by approximately 126 days (Fig. 2c).

The relationship between the phase of flush development and flowering was not significantly affected by the sequence of pruning. Nine trees had 3 vegetative flushes prior to winter, 3 trees had 2, and 2 trees had one. The flowering of the 5 trees with 1 or 2 flushes was indistinguishable from that of the other 9 trees (Fig. 2b).

Ambient temperatures at the time of bud break were higher for vegetative than for floral shoots (Fig. 2d). Incoming solar radiation also tended to be higher, although the separation was not as clear (Fig. 2d).

The earlier panicles produced more fruit (Fig. 2e). In addition, trees with 1 or 2 vegetative flushes between pruning and winter had fewer fruit per panicle than trees with 3 vegetative flushes (Fig. 2e; Tukey–Kramer $P < 0.05$).

Modelling

The interval between successive flushes was negatively correlated with the mean product of the daily irradiation and mean daily temperature during the interval (Fig. 3a). Its reciprocal, the rate of flush development, varied in an

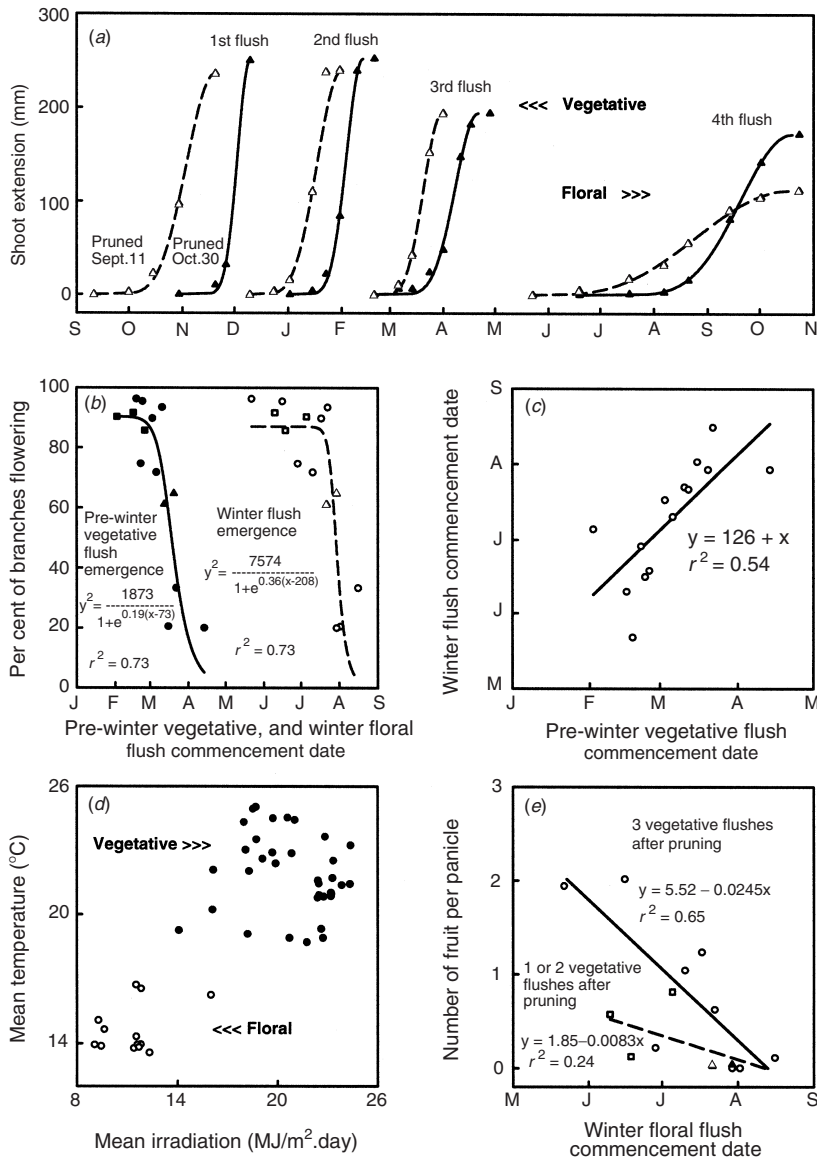


Fig. 2. The phenology of cv. Kwai May Pink pruned at various times in northern New South Wales. (a) Successive flush development for one tree pruned on 11 September (Δ data points for zero to maximum flush length, broken lines are fitted curves based on equation 1) and another pruned on 30 October (\blacktriangle , solid lines) 1996, based on the longest measured shoot to develop during each whole tree flush. From left to right, the parameter estimates \pm standard errors for Eqn 1 were $r = 0.0143$ (fixed), 0.0244 (fixed), 0.0219 ± 0.0009 , 0.0236 ± 0.0006 , 0.0253 ± 0.0007 , 0.0215 ± 0.0008 , 0.0067 ± 0.0002 , and 0.0081 ± 0.0001 ; and $t = 3.69 \pm 0.24$, 6.65 ± 0.67 , 6.75 ± 2.34 , 4.09 ± 0.53 , 2.77 ± 0.37 , 2.38 ± 0.40 , 1.70 ± 0.15 , and 3.53 ± 0.13 . (b) The proportion of branches flowering in spring 1997 against the starting date (flush = 2 mm in length) of the last vegetative flush before winter (closed symbols) and the starting date of the subsequent winter flush (open symbols). The starting dates were estimated from the fitted curves to the longest measured shoot to develop during each whole tree flush. Trees with 1, 2, and 3 vegetative flushes between pruning and winter are designated by triangles, squares and circles, respectively. (c) The starting dates of the winter flushes with respect to the starting dates of the previous vegetative flushes. (d) Average temperature and daily irradiation load at bud determination (vegetative buds, \bullet ; floral buds, \circ). (e) The number of fruit at harvest divided by the number of floral branches in the previous spring, expressed against the starting times of the floral flushes (symbols as per b). Solid line represents the principal axis of the correlation for the 9 trees with 3 vegetative flushes prior to winter. The broken line represents the principal axis for the 5 trees with 1 or 2 vegetative flushes prior to winter.

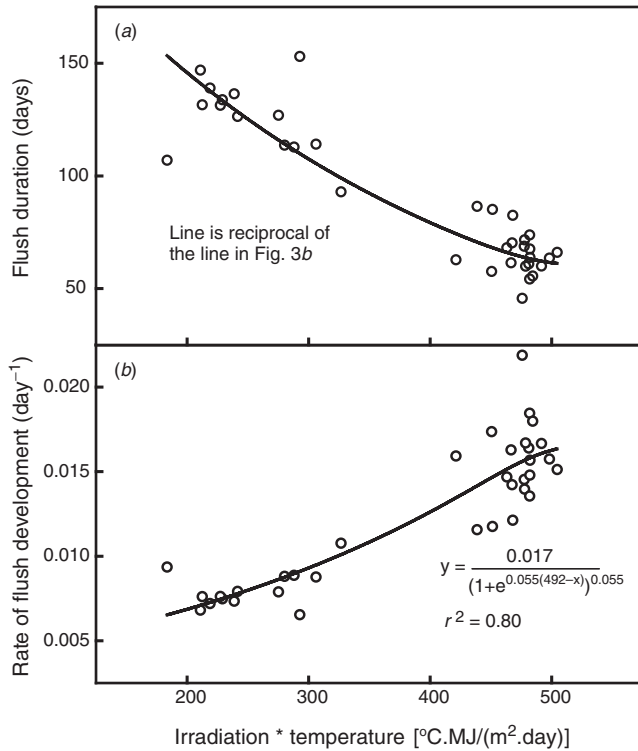


Fig. 3. (a) Variation in the time between successive flushes and the corresponding mean products of daily irradiation and mean daily temperature during flush development. (b) The reciprocal of the time between successive flushes, the flush development rate, also expressed against the irradiation-temperature product.

s-shaped fashion (Fig. 3b), with a significant upper asymptote (*t* statistic $P < 0.05$) corresponding to a minimum flush interval of 60 days.

The curve fitted to Fig. 3b was used in conjunction with long-term weather records (Meinke *et al.* 1995) from sites along Australia's north-eastern seaboard (Table 1) to estimate the dates on which bud swelling would need to begin for the completion of 1 or 2 vegetative flushes by the winter solstice (Fig. 4a). This was done by counting back the number of days from the winter solstice until the calendar rate (1/day) was equal to the flush development rate expected given the mean [daily irradiation by mean daily temperature product] for the interval. This gave the commencement date for the flush immediately prior to the solstice. For the penultimate flush, the process was repeated using the commencement date for the flush immediately prior to the solstice as the completion date.

There was considerable variation from one year to the next. For example, in Cairns (lat. 16.9° S) the earliest commencement date was 31 days earlier than the latest commencement date, while the difference at Murwillumbah (lat. 28.4° S) was 25 days. The regression line for the

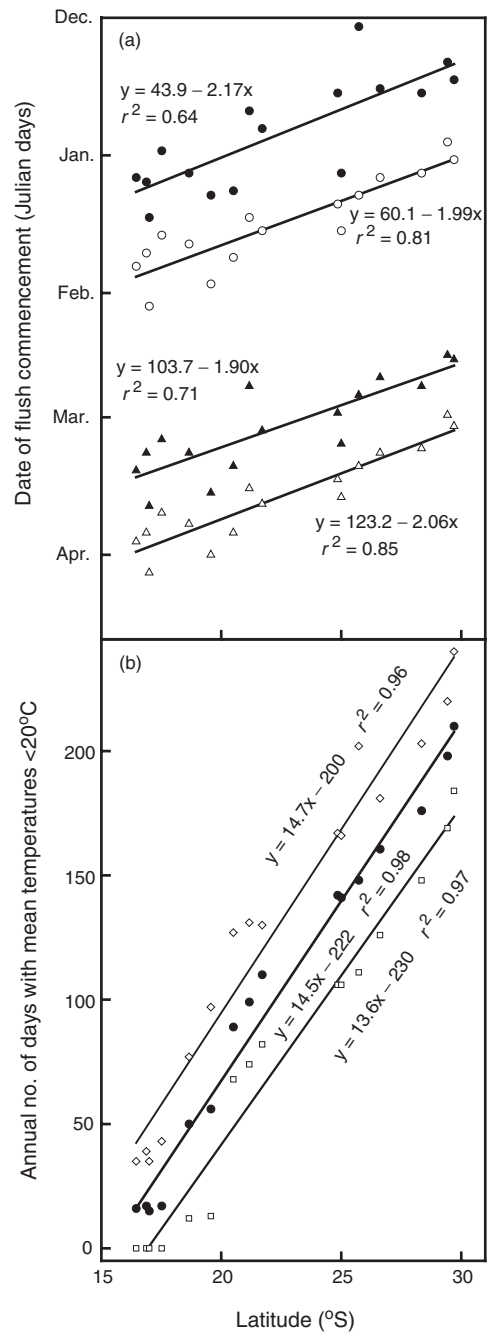


Fig. 4. (a) Variation in flush commencement dates with latitude for the completion of 1 or 2 vegetative flushes at the winter solstice (21 June). Estimates were made by applying the fitted equation in Fig. 3b to long-term weather records from the locations listed in Table 1, as outlined under *Modelling* in **Results**. Triangles designate 1 flush to the solstice, circles 2 flushes. Open symbols designate the median commencement date for all the years of record, closed symbols the earliest commencement date. (b) For the same records, the median (●), maximum (◇) and minimum (□) number of days per year with mean daily temperatures <20°C.

commencement time for 2 flushes prior to the winter solstice was essentially parallel to that for 1 flush (Fig. 4a) because the weather conditions at all sites during late summer and early autumn could support near maximum growth.

The long-term weather records were also used to estimate the number of days per year with mean daily temperatures $<20^{\circ}\text{C}$ as a guide to potential flowering (Menzel and Simpson 1995). There was a strong latitudinal gradient (Fig. 4b), with more than 100 inductive days in northern New South Wales (latitudes $>28.2^{\circ}\text{S}$), although some of these days may be too cold for growth, but a median of 17 days, and a minimum of 0 days, for Cairns.

Test of model at Mareeba

The estimate from Fig. 4a of the earliest commencement date for one vegetative flush prior to winter near Mareeba (lat. 17°S) was 13 March. Consequently, trees were pruned

close to this date (11 March) to stimulate bud growth. As expected, the trees completed one vegetative flush prior to winter, commenced a second, predominantly floral, flush in winter, and produced good crops (Table 2). The flowering and relative yields of the trees were equal to those of non-pruned controls (Table 2), which also initiated vegetative flushes in March and inflorescences in winter.

The estimate of the minimum flush duration at Mareeba was 60 days. Consequently, trees pruned 30 days prior to 13 March (i.e. 11 February) would be expected to produce approximately 1.5 flushes prior to winter (i.e. flushes in late autumn and early spring, but not in winter) and flower poorly. Trees pruned on 10 February had poorer flowering and relative yields than either the control trees or the trees pruned on 11 March (Table 2).

Discussion

The phase of recurrent flushing affects the extent of flowering of lychee (Fig. 2b,c). Trees with successive flushes commencing in February and June were more likely to flower than trees with flushes commencing in April and August, because June was cooler than August (Fig. 1b) and cool weather promotes panicle development (Fig. 2d). The details are essentially in accordance with the description of lychee development outlined in the **Introduction**.

Flush emergence was not haphazard, but dependent on irradiation and temperature (Fig. 3a,b). This is consistent with earlier work on the temperature-dependency of growth in lychee (Batten and Lahav 1994), and work on other evergreen tree species that has shown growth to be largely dependent on current photosynthate (Matsubara and Hiroki 1989; Sprugel *et al.* 1991).

The temperature around the time of bud commencement separated the fate of the buds, with flowering at cold temperatures and vegetative growth at warm temperatures (Fig. 2d). This is consistent with the work of Batten and McConchie (1995), who showed that cool weather during early bud development could induce flowering.

The buds seemed unresponsive to florally inductive weather during the greater part of the quiescent period. All trees were subject to a long, cold winter (Fig. 1b), but flowered differentially according to the winter flush commencement date (Fig. 2b).

Floral induction occurred at temperatures $<16.7\text{--}18.7^{\circ}\text{C}$ (Fig. 2d). This is slightly lower than the 20°C threshold suggested by Menzel and Simpson (1995) from work conducted in air-forced glasshouses.

Our work has implications for the management of lychee orchards in that strategic pruning can be used to correct non-productive flushing patterns. A first estimate of corrective pruning times is given by the equation for the earliest commencement date for one flush by the winter solstice given in Fig. 4a. This translates to pruning on 16 February at 30°S and 13 March at 17°S , with linear extrapolation for

Table 2. Results for the Mareeba experiment conducted in 1998

Control trees were not pruned. The other trees were pruned on 10 February or 11 March. The extent of flowering (%) was measured as the percentage of branches bearing panicles. The canopy surface area (m^2) was calculated from the canopy height, width, and breadth measurements assuming that the canopy was a semi-ellipsoid (Lang 1991). Yields were measured as whole-tree counts of fruit. The data, either raw or root-transformed, were tested using analysis of variance followed by Tukey pair-wise comparisons

	Flowering ^A	Canopy surface area	No of fruit per tree ^A	No of fruit per canopy surface area ^B
<i>Control</i>				
Tree 1	97	44	3363	76
Tree 2	92	46	3000	65
Tree 3	90	42	4058	97
Tree 4	85	42	2266	54
Tree 5	76	54	3497	64
Mean \pm s.e.	88 ± 4	46 ± 2	3237 ± 296	71 ± 7
<i>Pruned 10 February</i>				
Tree 1	96	33	3075	93
Tree 2	13	37	239	6
Tree 3	12	48	19	0
Tree 4	5	32	52	2
Tree 5	0	42	0	0
Mean \pm s.e.	25 ± 18	38 ± 3	677 ± 601	20 ± 18
<i>Pruned 11 March</i>				
Tree 1	96	36	3723	103
Tree 2	95	33	1703	52
Tree 3	90	35	2665	76
Tree 4	83	44	2525	57
Tree 5	51	45	174	4
Mean \pm s.e.	83 ± 8	39 ± 2	2158 ± 591	58 ± 16

^AControl = pruned 11 March $>$ pruned 10 February, $P < 0.05$.

^BControl = pruned 11 March; control $>$ pruned 10 February, $P < 0.05$; pruned 11 March $>$ pruned 10 February, $P = 0.06$.

other latitudes. The estimate was successful for our pruning trial in Mareeba in 1998 (Table 2), but needs refinement both at the broad geographic scale and in terms of the microclimates of individual farms.

The estimate is conservative in that it gives a high likelihood of flush maturation by the solstice in all years. One consequence of this is that undesirable late autumn vegetative flushes may develop in some years, although these can be chemically defoliated or tip-pruned to enhance flowering (Olesen *et al.* 1999; Menzel *et al.* 2000). In such cases, only the immature leaves or flushes should be removed as the crop is highly dependent on the leaves of the most recently matured flushes. The late autumn remedial measures (defoliation or tip-pruning) are also potential alternatives to post-harvest pruning for the correction of non-productive flushing cycles, for those orchards where the control of tree height is not a current priority.

Strategic pruning, involving the removal of 0.5 m from the canopy radius and the rejuvenation of the canopy by one vegetative flush prior to winter, had little effect on the relative yields of the trees (Table 2) and was sufficient to control tree height. The pruned trees had lower absolute yields than the controls (Table 2), although the difference was not significant.

Many sections of the Australian lychee industry have adopted strategic pruning because it allows for the maintenance of small, productive trees that are easy to pick, spray, and net.

There may be a parallel between our work and that of several Israeli authors (e.g. Stern *et al.* 1993) on the use of autumn drought to promote high yields. It is possible that such drought inhibits the development of late autumn flushes, which are unlikely to mature before the end of winter. Winter rains then promote flush development, with a high likelihood of flowering. However, a direct effect of drought on flowering remains a possibility.

This said, low temperature remains the only factor known to promote flowering in lychee. Strategic pruning can only work if there is winter weather cool enough to induce panicle development. Cairns (lat. 16.9° S) approaches the northern limit of lychee production along Australia's north-eastern seaboard (Fig. 4b).

Our work may have implications for other species. Mango (*Mangifera indica* L., Anacardiaceae) and longan (*Dimocarpus longan* Lour., Sapindaceae) are also evergreen trees that grow by repeated flushes, have terminal inflorescences, and can be induced to flower by low temperatures during early flush development (Batten and

McConchie 1995; Menzel *et al.* 2000; N. Jarassamrit, pers. comm.). It might also be related to the mast flowering of certain forest tree species.

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