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Modelling Kiwifruit Budbreak as a Function of Temperature and Bud Interactions

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This paper presents two models of budbreak on canes of 'Hayward' kiwifruit (*Actinidia deliciosa*). A conventional 'chill unit' (CU) type model is compared with an alternative 'loss of potential' (LOP) approach, which assumes that the number of buds developing in spring depends on climate and node position-dependent bud-to-bud interactions that vary in duration and intensity. Both models describe how temperature, and application of a dormancy-breaking chemical, determine the overall amount of budbreak for whole canes. However, the LOP model does so by describing patterns of budbreak along canes. To do this, the cumulative influence of distal neighbours is assumed to cause a progressive fall in the capacity for bud development over the autumn–winter period, an influence that gets stronger as temperature rises. The LOP model also assumes that the rate of decline varies along the cane, as a function of some inherent bud property. These two factors mean that buds towards the base of the cane break less often under the suppressive influence of distal neighbours, while low temperature ('chilling') increases budbreak by diminishing the intensity of suppression relative to bud development rate. Under this scenario, dormancy-breaking chemicals (such as hydrogen cyanamide, HC) enhance budbreak by diminishing the duration of suppression. Models were calibrated using daily temperature series and budbreak proportion data from a multi-year regional survey, and were then tested against independent data sets. Both models were run from a fixed start date until the time budbreak was almost complete, or until a standard date. The fitted models described 87 % of variation in amount of budbreak due to site, year, HC and node position effects in the original data set. Results suggest that the correlation between chilling and the amount of budbreak can be interpreted as a population-based phenomenon based on interaction among buds.

Key words: *Actinidia deliciosa*, kiwifruit, 'Hayward', dormancy, chilling, budbreak, models, temperature, hydrogen cyanamide.

INTRODUCTION

A model is presented that describes how climatic variation (mainly in temperature) may influence the pattern of budbreak (i.e. branching) along overwintered shoots of perennial plants, by altering correlative interactions among buds. The plant examined is kiwifruit, *Actinidia deliciosa* C.F. Liang et A.R. Ferguson and *A. chinensis* Planch., which requires an autumn–winter period of low temperatures above 0 °C ('chilling') for budbreak and flowering (Brundell, 1976; Lionakis and Schwabe, 1984; Warrington and Stanley, 1986). Budbreak is high (>50 %) when winters are cool, but can fall below 20 % in warm-temperate regions, with flower numbers below economic levels for crop production (McPherson *et al*., 1994).

Importantly, budbreak is not uniform along overwintered kiwifruit shoots ('canes'), but displays distinct, and climatically dependent, patterns. These patterns are typical of shoot branching in a variety of species (Guédon *et al*., 2001). Budbreak typically rises from near zero at the cane base, to near 100 % at the tip of pruned canes (McPherson *et al*., 1994). The frequency of budbreak near the cane base is lower under warm winter conditions, and when growing shoots are trained upwards to favour apical dominance (Snelgar and Manson, 1990). These trends are not entirely accounted for by developmental variation during shoot growth, exhibited by leaf area (Seleznyova and Greer, 2001), and axillary bud size (Snowball, 1996). Rather they suggest that in kiwifruit, the intensity of apical dominance is influenced by the environment, as in other species (Moe, 1988; Faust and Heins, 1996; Cook and Jacobs, 1999). Thus, the trends in budbreak within pruned canes may reflect a temperature influence on apical dominance, either during dormancy or as growth is initiated in spring.

A possible role for bud interactions is also suggested by the effect of node number on budbreak of excised kiwifruit cuttings. These have been used to study environmental requirements for budbreak and flowering (Snelgar *et al*., 1997; Snowball, 1997*a*), but do not behave as intact plants (Stanley *et al*., 1995). Less chilling exposure is required for budbreak on single node kiwifruit cuttings than for intact plants (Guerriero *et al*., 1990) and the final proportion of budbreak is greater. This is may be because apical buds on cuttings are freed of the influence of other more distal buds,

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since buds below a node appear to have little influence on budbreak (Grant and Ryugo, 1984; Stanley *et al*., 1995; Snelgar *et al*., 1997; Snowball, 1997*a*).

More generally, much attention has been given to competition as a factor determining growth patterns in plants. Resource partitioning during active growth of kiwifruit has been described (Greer and Jeffares, 1998; Greaves *et al*., 1999; Henton *et al*., 1999), showing relationships between allocation patterns and reproductive effort. An apical bias is characteristic of such partitioning, and it is reasonable to expect such patterns to remain during dormancy and renewal of growth in spring. However, the ideas of plant structure inherent in such studies have not been used to describe development during dormancy for a deciduous species such as kiwifruit.

There is a need for ecophysiological models that afford understanding of how plant structure and environment interact to determine patterns of plant development. Single-clone studies under multiple or controlled environments provide an obvious tool by which to achieve this objective. However, the possibility of architectural interactions with environmental effects is largely absent in horticultural studies on responses to winter chilling. 'Chill unit' (CU) models (Richardson *et al*., 1974; Shaltout and Unrath, 1983; Fishman *et al*., 1987) are used to describe the temperature response of budbreak on deciduous fruit species, but these models treat dormant buds as physiologically independent entities. They typically assume that the CU indices represent a primary impact on bud 'endodormancy', and not an effect on correlative interactions *among* buds. Likewise, the environmental contribution to patterns of shoot formation is not widely considered in the literature on quantitative plant architecture.

Models incorporating information about bud position, budbreak patterns and possible interactions among buds would provide a more comprehensive basis for describing climatic impacts on bud development (spring budbreak and flowering) in kiwifruit. Kiwifruit provides a useful test system since budbreak and flowering have a close phenological connection. Initiation of floral parts occurs in bud axils as they begin new development in spring (Brundell, 1975; Grant and Ryugo, 1982; Polito and Grant, 1984). Interaction among apices is clearly shown in kiwifruit by, for instance, the sharp decline in floral potential at budbreak under the influence of actively growing shoots (Grant and Ryugo, 1982). Grant and Ryugo therefore suggested that 'flower development is controlled by interactions among different meristems at the time of shoot elongation in spring'.

Here we extend this idea of interaction between meristems to the probability of budbreak along kiwifruit canes, and use it as a framework to describe how various factors can influence the proportion of buds breaking. Thus, the simulative effect of chilling is interpreted as a reduction of these interactions at low temperature. This approach has not been used previously to describe the environmental impacts on bud dormancy. If successful, it could offer a means to integrate understanding and quantitative modelling of structural factors that influence budbreak and reproductive potential of deciduous plants.

MATERIALS AND METHODS

Chill unit model

A modified chill unit model was used as a basis to evaluate alternative models, using a CU-type index to quantify low temperature exposure (Richardson *et al*., 1974). Key differences from the original 'Utah' CU phenology model were: (1) CU accumulation is used to predict *proportion* of budbreak, P, rather than *time* of budbreak; (2) a different chilling temperature optimum was estimated by the fitting procedure; and (3) CU values were accumulated to a fixed day (1 August), at which point the proportion of budbreak was calculated from accumulated CU.

CU values were calculated using the function:

$$\mathrm{CU} = \frac{4}{T_c^2} T(T_c - T) \tag{1}$$

where T_c is the intercept with the x-axis (beyond which the CU index is negative), and T is daily mean temperature. This quadratic function passes through 0 °C, giving an implicit intercept parameter, T_b = 0·0 °C (Fig. 1A). Accumulation of CU began when the CU total ceased to decline further, as is standard practice for CU-type models. This start date, t_0, lay between mid-February and late March under New Zealand conditions.

The predicted mean budbreak proportion for a site, P, was calculated as:

$$P = \begin{cases} c_1 \sum_{t=t_o}^{t_{end}} \mathrm{CU} & \text{Non-HC treated vines} \\ c_1 \sum_{t=t_o}^{t_{end}} \mathrm{CU} + \dfrac{1}{c_2 \sum_{t=t_o}^{t_{end}} \mathrm{CU}} & \text{HC-treated vines}, \sum_{t=t_o}^{t_{end}} \mathrm{CU} > 0 \end{cases} \tag{2}$$

where c_1 determines how budbreak changes with increasing CU accumulation, c_2 determines how HC application increases budbreak, an effect more pronounced as winter temperature conditions become warmer, and t_{end} is 1 August in a given year (in New Zealand).

Parameter values for this modified CU model were estimated using data describing mean budbreak proportion on pruned canes of 'Hayward' vines at three sites in a multi-year field survey (see below).

Loss of potential (LOP) model concepts

The alternative budbreak model also relied on a distinction between the *proportion* of budbreak and its timing (i.e. date of 50 % budbreak), which here was provided as part of the input data set (or else would need to be independently predicted). This model was based on the following assumptions: (1) Budbreak is a binary event (i.e. 1 = bud

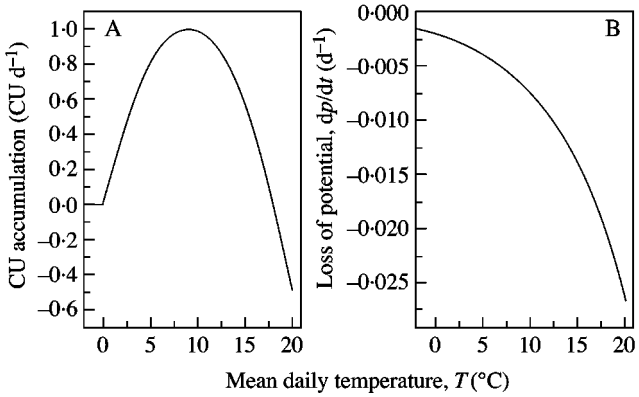

FIG. 1. Temperature response functions for daily chill unit accumulation and for loss of budbreak potential on 'Hayward' kiwifruit canes. A, CU index based on daily mean temperature: T_c = 18·0 °C; B, LOP model, k_p = 0·0021, k_T = 0·13.

growth; 0 = no growth), with the budbreak proportion p, ($0 < p < 1$) varying with node position. (2) The observed proportion results from changes to budbreak potential, an empirical variable reflecting relative competitive strength. This variable shows the proportion of buds that would break at a node if the bud population to which they belonged had reached a nominated stage of budbreak at that time. (3) Budbreak potential at a node *declines* from an initial maximum with a rate proportional to current potential and bud position. (4) The positional effect has two aspects: a 'structural effect', assumed to reflect variation in size or development state between buds; and a 'neighbour effect', related to correlative interactions among buds. (5) Bud interactions are polarized, so that loss of potential is a function only of the influence of more distal bud neighbours. (6) The influence of distal bud neighbours, represented by the cumulative budbreak potential, declines with intervening number of nodes between buds. (7) Budbreak potential is lost more rapidly at high temperature, and more slowly at low temperature. (8) Dormancy breaking chemicals, such as hydrogen cyanamide (HC), affect budbreak proportion indirectly via their effect on timing of budbreak.

These assumptions mean that warm conditions, which delay budbreak, induce more loss of budbreak potential at basal nodes, leading to the distally biased budbreak patterns observed under these conditions. Conversely, any factor that advances the time of budbreak will limit loss of potential, and increase budbreak proportion.

Several alternative models for changes in p, particularly in relation to how buds might interact while emerging from dormancy, were investigated using positional budbreak data from a multi-year regional survey (see below). These data described budbreak along pruned canes of 'T-bar'-trained vines. However, while canes had been pruned to equivalent length (approx. 2 m), variation in internode length meant that the number of nodes on a cane, I, varied widely (from 13 to 40) between site/year/treatment combinations. To examine position effects, the set of canes in each site/year/treatment set was therefore allotted to two subsets relative to the median cane node count, I_{50}, for the set: those with $I > I_{50}$ (the longer canes), and those with $I < I_{50}$ (shorter canes).

Node position budbreak averages for each subset were calculated after mapping the initial node position index (relative to the cane base), i, onto a standardized position index, j, for an 'average' cane with I nodes, the mean number of nodes for that subset. The mapping method adopted ensured that the relative position of buds at the five final nodes at both ends of the cane remained fixed, whereas bud positions in the middle of canes were subject to localized displacement. Nodal displacement was calculated in three steps: (1) A standardized position index, z, was calculated for each cane, relative to the cane midpoint, M, and an arbitrarily defined positional 'standard deviation', S. This index was given by:

$$z_i = \frac{(i - M)}{S} \tag{3A}$$

where i is the initial non-displaced position index, and $M = (I + 1)/2$, and $S = I/6$.

(2) The cumulative normal probability function was used to calculate a displacement quotient, q, corresponding to the z value:

$$q_i = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{z_i} e^{\frac{-z_i^2}{2}} \mathrm{d}z \tag{3B}$$

(3) This value was used to map nodes to new positions on a standardized -node index:

$$j = \mathrm{round}(i + (\bar{I} - I)q_i) \tag{3C}$$

where j is the new node position and the 'round' function adjusts node positions to the nearest integer value, and I is the nearest integer value greater than the subset mean for I. All model calculations relate to this standard index, and use it to describe how dp_j/dt, the loss of potential for budbreak at each node j, varies with respect to time, position and factors such as temperature.

In kiwifruit, the beginning of the decline in p is presumed to occur in autumn or early winter, at which time bud interactions are assumed to begin to affect dp/dt. The basis for this onset of sensitivity is uncertain: it might be related to leaf-fall or completion of a low-temperature requirement for bud development (i.e. the end of endodormancy). A later date appears more consistent within the LOP model framework if loss of budbreak potential is a phenomenon that strengthens as buds become more physiologically active. Whatever the case, $p(0)$, the initial potential for budbreak potential, was given by:

$$p_j(0) = p^* = 1 \tag{4}$$

where p^* is an initial estimate of budbreak potential at node j before the onset of any position-related bud interactions causing the loss of potential. A fixed value of 1·0 is suggested by observations that terminal buds of short-

pruned canes (two to five node 'stubs') will almost always break (P. T. Austin, unpubl. res.), even though they do not break when canes are left with more nodes.

Loss of potential at any node was described as a function of temperature, the current potential at that node, position relative to the cane base (a bud size effect, based on an approximate allometric relationship with leaf size) and position relative to the cane tip (a 'neighbour' effect, based on correlative influences). Thus, dp/dt at the j^{th} node from the base of a cane was given by:

$$\frac{\mathrm{d}p_j}{\mathrm{d}t} = k_p e^{k_T T} f(j) g(J,j) \qquad (5)$$

where k_p and k_T are parameters, T is daily mean temperature, p_j is the current potential for budbreak at the jth node from the base of the cane and J is the total count of nodes on the cane, while $f(j)$ and $g(J, j)$ describe the 'allometric' and 'neighbour' effects, respectively. The resulting temperature response for dp_j/dt decreases monotonically (Fig. 1B), compared with the optimum of the CU response curve (Fig. 1A).

The allometric effect was expressed in terms of j by a relationship that reflected variation in bud size (Snowball, 1996), and changes in leaf size along kiwifruit canes (Seleznyova and Greer, 2001). Thus,

$$f(j) = p_j(1 - (e^{-A(j-1)})(1 - e^{-B(j-1)})) \qquad (6A)$$

where A and B are parameters whose values are estimated independently from trends in leaf size along 'Hayward' canes (A = 0·025 and B = 0·25) (Fig. 2A).

The neighbour effect (Fig. 2B) was calculated as the cumulative sum of the distance-weighted influence of buds more distal to a given node j on a cane of J nodes. Thus,

$$g(J,j) = D + \sum_{k=j+1}^{J} p_k \frac{e^{C(j+1-k)}}{2} \qquad (6B)$$

where p_k is budbreak potential at nodes more distal than the j^{th} node, C is a parameter determining how sensitive the distal effect is to the nodal separation between buds and D determines how fast budbreak potential is lost at any node position, independent of the distal effect (recognizing the possible influence of other plant parts).

These equations produce a model of budbreak potential related to node position and cane node count, as seen when they are integrated at two constant temperatures for up to 160 d (Fig. 3). Overall, at 16 °C, p_j declines rapidly, whatever the cane size, especially at nodes towards the base of the cane, whereas loss of budbreak potential is limited at the tip. By comparison, at 6 °C, the decline in p_i is less marked, and the peak at node 10 less prominent.

The final aspect of the model concerned the beginning and end of the period over which the equations were integrated (i.e. that period during which buds lose potential to initiate development). For simplicity, a single global start date, t_0, was fixed at 1 June for all site/year combinations. This meant that decline in p_j started at the same time at all sites and years, and possible regional/seasonal effects on developmental phenology are ignored. There were three reasons for this choice: (1) an assumption that loss of potential begins later in the season as buds emerge from endodormancy; (2) the inherent correlation between t_0 and k_p, which increases parameter value uncertainties; and (3) for convenience when using the model for practical predictions. Shoot extension on canes used for next year's production terminates well before 1 June, while leaf fall occurs between May and June (Snowball, 1997*b*). Pruning normally occurs during June and July.

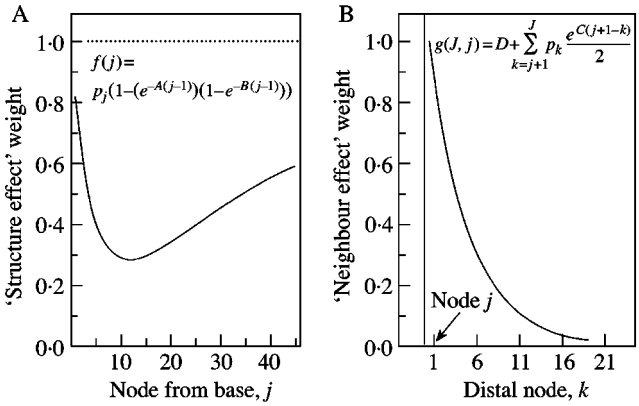

FIG. 2. Functional forms specified for nodal weights used to calculate loss of budbreak potential under the LOP model. (Parameter values are those estimated by fitting to 1996–1998 regional survey data)

The integration end time, when budbreak estimates were made, corresponded to the time when the majority of buds that finally developed had reached a size of approx. 1 cm in length (i.e. BB stage; Brundell, 1975). This date was calculated from observed phenology data as:

$$t_{\text{BB}} = t_{\text{BB50}} + \sigma_{\text{BB}} \qquad (7)$$

where t_{BB50} is the time of 50 % budbreak (days after 1 January), and σ_{BB} is the standard deviation (days) of a cumulative normal distribution fitted to observed budbreak data. Hence, $t_{\text{BB}} \approx t_{\text{BB85}}$, where t_{BB85} is the date at which approx. 85 % of buds finally breaking had broken (i.e. if only half of all buds broke, then estimates were made when budbreak reached approx. 42·5 %). The delay of one standard deviation presumes that potential budbreak at nodes where development is less advanced continues to diminish as budbreak progresses, under the influence of more advanced buds. Since budbreak is both later and more drawn out in warmer conditions, this approach lengthened the period over which p declined under warmer conditions. Other delays are possible, but were not investigated.

Model parameter estimation and validation

For both models, non-weighted least squares estimates of parameter values were calculated by numerical integration within PROC NLIN (SAS Institute Inc., 1987), using NLIN's multivariate secant (DUD) method. The primary

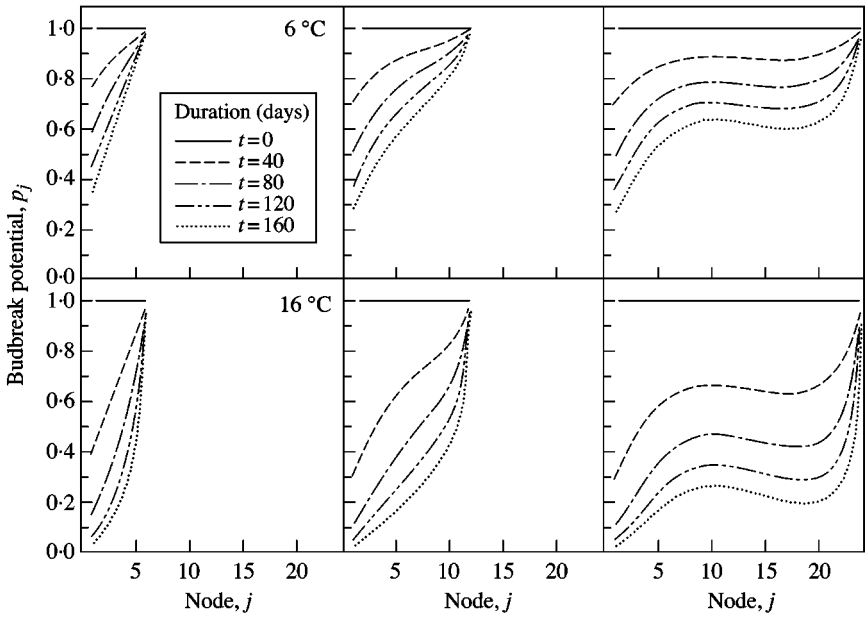

FIG. 3. Change in budbreak potential, p_j at nodes along 'Hayward' kiwifruit canes of varying length, simulated by the LOP model at two constant temperatures (6 and 16 °C) over 40, 80, 120 and 160 d.

data set used came from a survey of vines in three major New Zealand kiwifruit production regions, conducted between 1996 and 1999. Survey sites were located at Kerikeri (35·1°S, 173·5°E, 73 m asl), Te Puke (37·5°S, 176·2°E, 91 m asl) and Riwaka (41·1°S, 172·6°E, 8 m asl). Hydrogen cyanamide had been applied to ten of the 20 vines surveyed at each site in each year to increase budbreak. Budbreak on one cane had been recorded on each vine, which had been trained to a standard 'T-bar' support structure. Canes were pruned and were mostly non self-terminating. The proportion of budbreak was recorded near the time of bloom so that numbers of shoots and flowers at each node were counted simultaneously. This approach may mean that some very small buds at the base of canes, which typically do not break, may have been overlooked.

For the CU model, the fitting procedure minimized differences among cane budbreak data for each site/year/treatment combination (i.e. positional budbreak data were averaged to give overall means). For the LOP model, the fitting procedure minimized the difference between mean observed budbreak at each node along the cane and model output.

Survey data from years 1996–1998 were used to calculate parameter estimates for the models, while 1999 regional survey data were used to validate parameter estimates. Additional validation was provided by prediction against data from a 1986 survey. This information consisted of positional data describing budbreak along canes at five orchards located in three NZ regions: Calver and Dicey orchards in Katikati (37·5°S, 176·2°E, 50 m asl), Honnor and Larmer orchards near New Plymouth (39·1°S, 174·1°E, approx. 100 m asl), and the Carson orchard at Wanganui (39·8°S, 175°E, 50 m asl). Daily mean temperature time-series were derived from the nearest meteorological station.

A third validation data set tested how well models described the effect of temperature in early winter. These data came from a controlled environment (CE) experiment using containerized vines at NZCEL, New Zealand's CE laboratory (McPherson *et al*., 1995). Data described average budbreak proportion for sets of two or three plants exposed to one of 14 treatments in which the temperature and duration of an artificial 'winter' were varied prior to forcing at 21/11 °C (day max./ night min., 12 h linear ramps). Three winter temperature regimes were used: 18/8 °C, 15/5 °C and 11/3 °C, selected to reflect winter conditions in Kerikeri, Te Puke and Riwaka. The duration of the artificial winter before forcing was 1, 2, 3 and 4 months. Plants were placed in the CE chambers on 25 May 1987. Two additional 'delay' treatments were also included in the design, in which plants were first exposed to 2 months at 21/11 °C before being exposed to chilling at 15/5 °C and 11/3 °C. Experience at NZCEL suggests that budbreak and flowering on containerized vines is generally lower than on equivalent standard vines. Hence, the data were used to test the possibility that this could be accounted for by a sharper decline in budbreak potential along canes, in an manner analogous to the way defoliation reduces bud size (Snowball, 1996).

RESULTS

The modified CU model and LOP model proved similarly effective as descriptions of variation in the cane budbreak proportion observed in the 1996–1998 regional survey calibration data set (Fig. 4). The three sites of this data set span the climatic range of the New Zealand kiwifruit industry: Te Puke being the main production region, with Kerikeri being relatively warm and Riwaka relatively cool. The impact of these climatic differences is seen in the cane

budbreak proportion for non-HC treated vines: 35–40 % at Te Puke, much lower (18 %) at Kerikeri after the warm winter of 1998, and around 50 % at Riwaka. The differences between sites are less pronounced when HC is applied, though the relative rankings do not change.

The non-positional CU model, which assumes that budbreak is a function of modified CU accumulated from 1 June to a standard date (1 August), accounted for 87 % of variability due to site, year and HC treatment effects (Table 1). Parameter values were relatively well estimated and did not show high inter-correlation. By comparison, the LOP model, which was integrated from 1 June to the time when budbreak was 85 % complete (latest in 1998 at Kerikeri, earliest at Riwaka in 1996), accounted for the same variation in P (87 %), but its parameters were not as well estimated. The largest error for both models was for HC-treated vines at Te Puke in 1996, which had the highest cane budbreak (61 %) of all site/year/treatment combinations.

Calculated LOP values for p_j approximated the general trend in budbreak along canes under all site/year combinations with similar accuracy (Fig. 5). However, the noise in the non-smoothed node-wise data was considerable, the model accounting for 55 % of total variation (Table 1). Mean node count of the cane subsets varied between sites (fewest nodes at Kerikeri, most at Riwaka, especially in 1998), but the LOP model represented the effect of node count with reasonable accuracy (Fig. 5). It also indirectly accounted for the effect of HC application via the advancing effect of HC on time of budbreak. The success of this implicit approach for the effect of HC on budbreak is a distinctive result for this model, and a point of difference with the CU model. Importantly, the LOP model also represented the pattern of budbreak after the warm winter at Kerikeri in 1998 well. Accuracy under these conditions is an important model evaluation criterion, given the significance of warm winters for kiwifruit production.

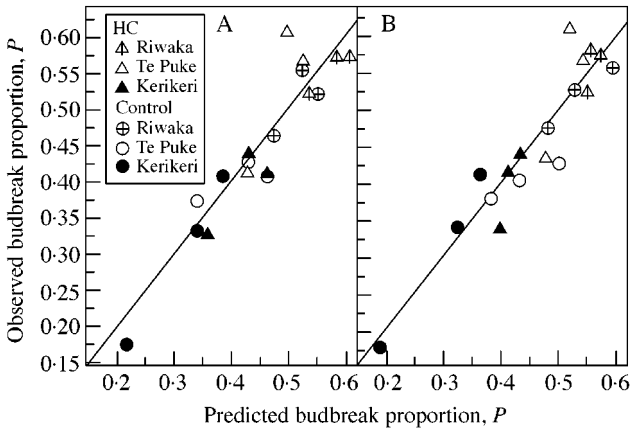

FIG. 4. Comparison of simulated cane budbreak proportion, P, with that observed on control and HC-treated 'Hayward' kiwifruit canes at Riwaka, Te Puke and Kerikeri in 1996–98 predicted using a modified CU model (A) or an alternative LOP model (B). (Budbreak proportion, P, averaged over all nodes for standardized canes of both length subsets.)

Both models had similar precision when predicting mean cane budbreak (Fig. 6; Table 2) against observations in 1999 (same vines in the following year) and 1986 (different sites). These data showed the normal differences in budbreak between New Zealand regions (Kerikeri < Te Puke < Riwaka). The 1986 data were intermediate between Kerikeri and Riwaka. This is as expected since, being coastal, the orchards in which the 1986 date were collected have similar climates to Te Puke. Observed cane budbreak was therefore in a similar range: 44 and 38 % for Calver and Dicey near Te Puke, 36 and 42 % at Larmer and Honnor and 45 % at Carson. Both models predicted higher budbreak on 1999 HC-treated vines than on 1999 controls. However, the mean error for the CU model was smaller than that for the LOP model, which tended to overpredict budbreak by 6 % on average (Table 2). The CU model, which underpredicted cane budbreak by an average of 4 % in 1999, showed little error in 1986.

Node-wise plots of predicted budbreak against 1986 and 1999 observations show a possible reason for overprediction by the LOP model (Figs 7 and 8). Average cane node count again varied between sites in 1999 (19–31 nodes), with vines being longer at Riwaka than at Kerikeri, but varied less between the 1986 sites (22–27 nodes). This variation did not appear to be the primary cause of model inaccuracy, though data were noisy (n = approx. 10 at each node). General trends were adequately represented by the LOP model, with budbreak rising from near zero at the lowest

TABLE 1. *Parameter estimates and precision for all models, fitted to 1996–1998 regional survey data*

	Parameter estimates ± s.e.							Model precision			
Model	c_1	c_2	T_c (°C)	T_b (°C)				σ_{err} P	R^2		
CU	0·0041 ± 0·0002	0·14 ± 0·03	18·2 ± 0·4	0				0·040*	0·87	–	–
	t_0	k_T	k_p	A	B	C	D	σ_{err} P	R^2	σ_{err} p_j	R^2
LOP	1 June†	0·13 ± 0·13	0·002 ± 0·003	0·025†	0·25†	0·21 ± 0·16	1·15 ± 0·40	0·041	0·87	0·16‡	0·55

σ, Standard deviation of prediction errors, for individual predictions of p_j, and for prediction of P on canes of each site/year/treatment combination.
* No. of observations = 18 (site/year/treatment combinations).
† Fixed parameter value. A and B chosen to represent trend of number of leaf initials per bud.
‡ No. of observations = 360 (20 nodes, 18 site/year/treatment combinations).

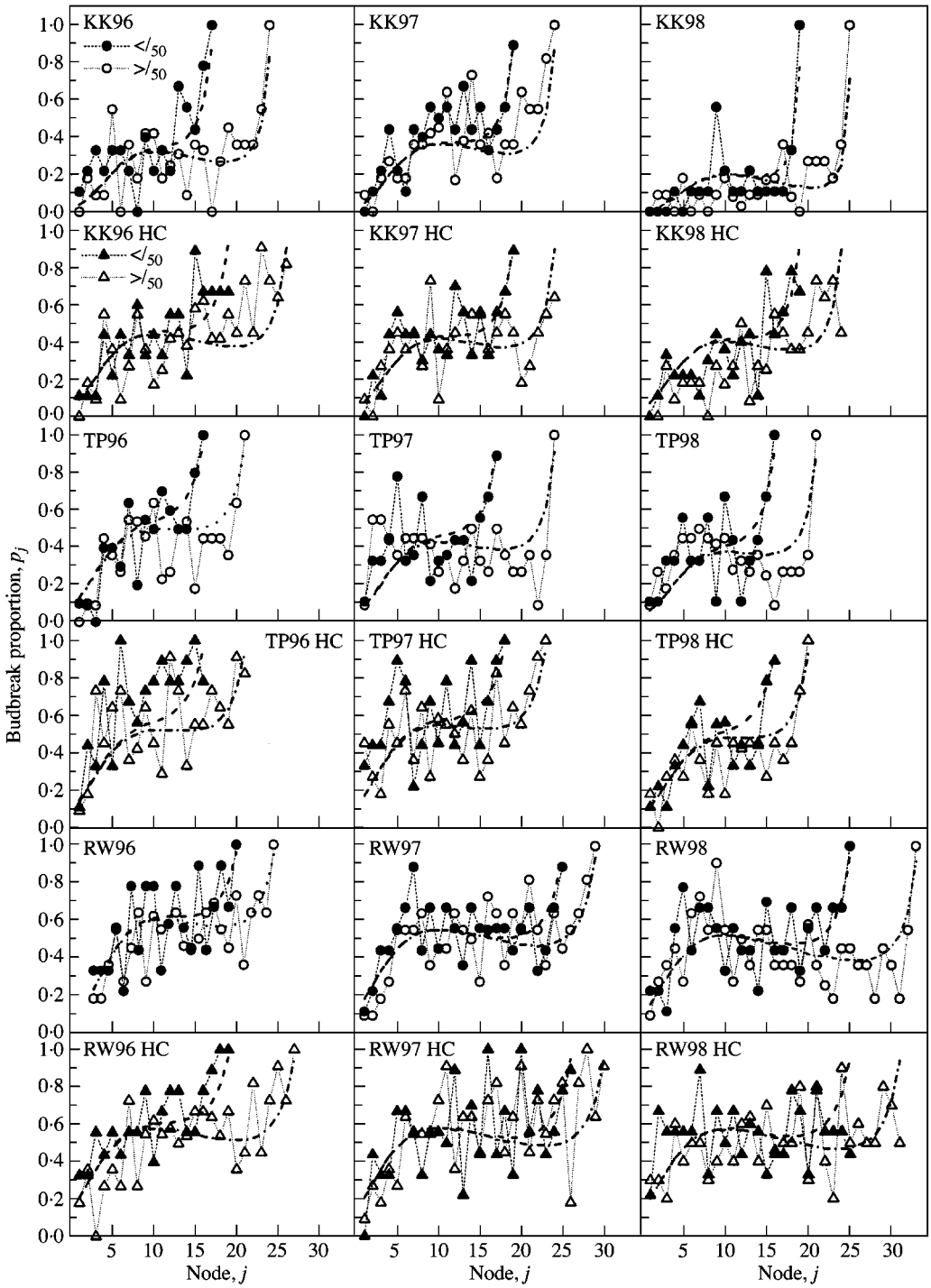

FIG. 5. Observed budbreak proportion on control and HC-treated 'Hayward' kiwifruit canes at Kerikeri (KK), Te Puke (TP) and Riwaka (RW) in 1996–98, compared with that calculated using the LOP model. (Observations: n = 10, canes, grouped into two node count classes: < I_{50} = < median count; > I50 = > median count.)

nodes to a local peak around nodes 10–15, reaching a maximum at the tip in all cases. What appeared more significant was that budbreak sometimes declined more sharply towards a sub-terminal minimum than was typical of the 1996–98 data. Examples include non-treated canes at Kerikeri and Te Puke in 1999 (Fig. 7), and canes at Honnor in 1986 (Fig. 8). Reproduction by the LOP model of the budbreak pattern along canes was poorest for HC-treated vines at Kerikeri, although the error for cane budbreak was greater (approx. 10 %) for Riwaka.

A greater difference between the LOP and CU models was seen when both were used to predict cane budbreak averages on containerized vines exposed to chilling treatments in controlled environments (Fig. 9). This data set was selected to test how well the models described experimental manipulation of the natural sequence, timing and level of temperature conditions. In this case, the CU model underpredicted *P* (Table 2), and did not discriminate well between treatments (Fig. 9A). In contrast, the LOP model overpredicted *P* but more accurately ranked budbreak levels, except for the very short/warm treatment (1 month at 18/8 °C), and the delayed chilling treatments (Fig. 9B). Neither model adequately predicted budbreak for these treatments. Increasing the slope for the 'allometric' component for dp_j/dt (A = 0·025 arbitrarily increased four-fold to A = 0·1) improved the fit of the LOP model to this data set (Fig. 9C). This is consistent with the idea that low budbreak on containerized CE vines reflects a more rapid loss of budbreak potential at distal nodes on containerized vines.

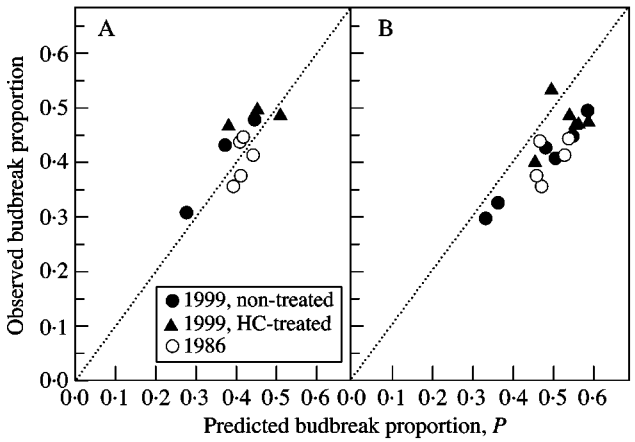

FIG. 6. Observed and predicted cane budbreak proportion, *P*, on 'Hayward' kiwifruit vines under natural orchard conditions in 1986 and 1999: predicted using CU model (A) or LOP model (B) (1999 data are pairs for $<I_{50}$ and $>I_{50}$ subsets).

DISCUSSION

The model comparison presented here was designed to test the idea that interactions among buds (e.g. apical dominance) need to be considered to describe the response of kiwifruit budbreak to climatic variation. However, CU-type models tend to be associated with idea of bud-level endodormancy, distinguishing a period of sensitivity to 'chilling' from a subsequent growth period (Richardson *et al*., 1974). Hypotheses regarding the physiological basis for this response underlie a dynamically oriented model of budbreak in peach (Fishman *et al*., 1987), which assumes budbreak levels reflect the interplay between processes driving release from endodormancy and which occur at different rates under diurnal temperature cycles.

This endodormancy-oriented approach to modelling bud development seems ecologically justified for species native to cool temperate regions with high-amplitude seasonal temperature cycles. This is because, in theory, individual bud temperature should provide a reliable control of development where its variation provides a seasonal signal directly related to survival. Under these conditions, temperature-dependent release from endodormancy could be expected to be a significant regulator of both phenology and probability of growth. However, this argument appears less strong for taxa from warmer regions where temperature less directly affects plant survival. In these regions, environmental variation, and seasonal temperature cycles in particular, appear less significant as signals for controlling growth flushes. Thus, chilling appears unimportant for timing budbreak in the Mediterranean species *Planatus acerifolia* (Chiune, 2000), while correlative phenomena appear more important in some tropical plants (Borchert, 1999; Okubo, 1999).

The LOP model therefore follows from a suggestion that endodormancy in kiwifruit is weaker than in other deciduous species (Guerriero *et al*., 1990), and observations that a Richardson ('Utah') CU index did not describe budbreak well (McPherson *et al*., 1995). This could be consistent with the warm-temperate origins of *Actinidia*, under which the seasonal temperature cycle might not provide as strong a signal for synchronizing growth with seasons as it does at

TABLE 2. *Model accuracy predicting cane budbreak proportion (*P*) and for individual nodes (*p_j*) for three independent data sets: (1) 1999 regional survey; (2) 1986 orchard survey; (3) CE data from NZCEL*

	Model performance							
	1999 regional survey*			1986 orchard survey†			CE experiment‡	
Model	Mean error	σ_{err} P	σ_{err} p_j	Mean error	σ_{err} P	σ_{err} p_j	Error, $P \pm \sigma_{err}$ A = 0·025	Error, $P \pm \sigma_{err}$ A = 0·1
CU	+0·04	0·04	–	–0·01	0·03	–	+0·05 ± 0·10	–
Node position	+0·07	0·01	0·12		–0·03 ± 0·02		+0·11 ± 0·09	+0·11 ± 0·09
LOP	–0·06	0·03	0·18	–0·06	0·03	0·18	–0·15 ± 0·10	–0·02 ± 0·10

Error = Obs. – Pred.
* 12 site/year/treatment/node count combinations.
† No. of site observations = 5.
‡ No. of. CE treatments = 14.

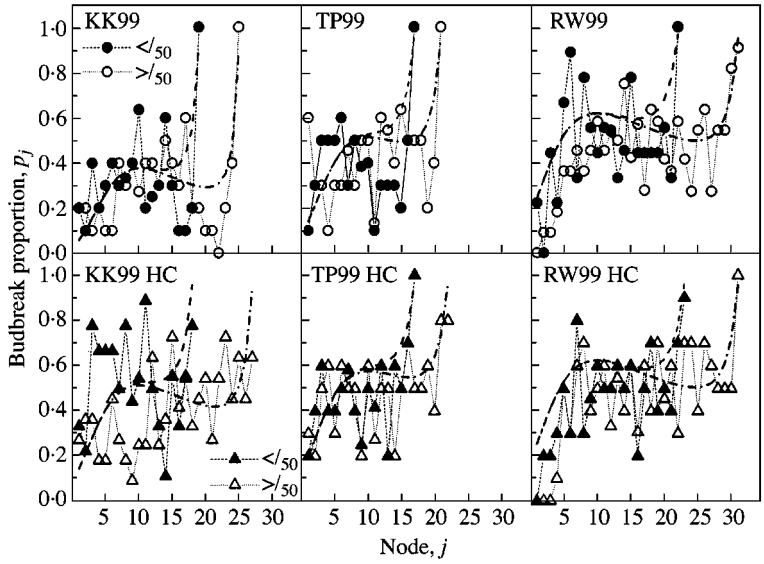

FIG. 7. Observed budbreak at nodes on control and HC-treated 'Hayward' kiwifruit canes at Kerikeri (KK), Te Puke (TP) and Riwaka (RW) in 1999, compared with that predicted using LOP model. (Observations: n = 10, canes grouped by node count: < I_{50} = below median count; > I_{50} = above median count. See Fig. 6 for cane budbreak.)

higher latitudes. Hence, seasonal growth flush regulation in *Actinidia* might differ from that in cold-temperate species, much as the origins of phenological control in tropical species have been shown to have a whole-plant basis, reflecting correlative growth phenomena (Borchert, 1999).

The accuracy and precision of the modified CU model was better than expected. The improvement is probably due to a re-fitted optimum CU temperature: around 10 °C for this model *vs*. approx. 7 °C for the standard Richardson model. This change appears reasonable given the growing conditions of New Zealand kiwifruit production regions, and the original provenance of *Actinidia*, both of which are warmer than the continental climate winter conditions for which the original index was developed. Other CU-type indices estimated under warmer regions also have higher optima (e.g. Shaltout and Unrath, 1983).

The similar precision of the CU and LOP models in describing average budbreak was also not expected given the intended differences in structure, timing of environmental sensitivity and temperature response functions. For instance, the LOP model assumes that variation in budbreak reflects a position-dependent process whose rate increases with rising temperature. This response type was chosen for consistency with 'normal' physiological processes, which generally accelerate as temperature rises. In contrast, typical CU responses display a distinct optimum. Also, the CU model begins accumulation in early autumn (March) and ends at the start of August, whereas the LOP model begins on 1 June and ends when budbreak is almost (85 %) complete (this can be as late as mid-November for non-HC treated vines in Kerikeri).

These similarities might be attributed to several causes. First, seasonal temperatures are inherently correlated, relatively warm winters often being followed by warmer spring conditions. Secondly, few periods with daily mean

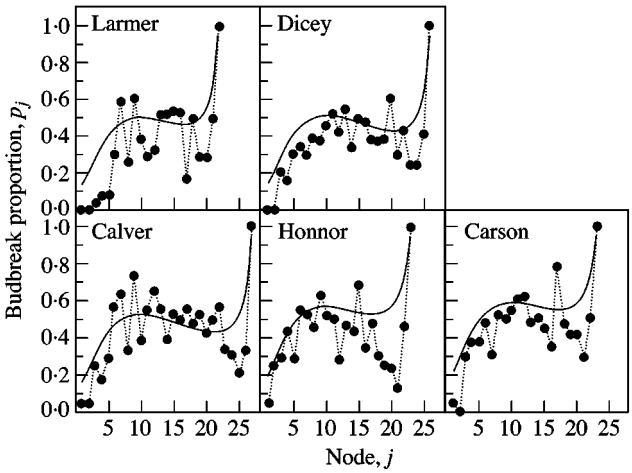

FIG. 8. Observed budbreak along 'Hayward' kiwifruit canes in the Bay of Plenty (Larmer, Dicey), Taranaki (Calver, Honnor) and Wanganui (Carson) regions of New Zealand in 1986, compared with that predicted using the LOP model. (Observations: n = 24. See Fig. 6 for cane budbreak.)

temperatures much below 10 °C are experienced in New Zealand kiwifruit production regions, so there is little to distinguish between the functions below 10 °C. Thirdly, the effect of autumn temperature is entered implicitly into the LOP model via the date of budbreak. If chilling during this period delays budbreak, then a warm autumn period will extend the period over which the LOP model simulates loss of budbreak potential. Fourthly, it is possible that the CU model describes a positive correlation of mean temperature with a low level, but persistent, correlative effect occurring over the winter period. Thus, the focus of CU accumulation

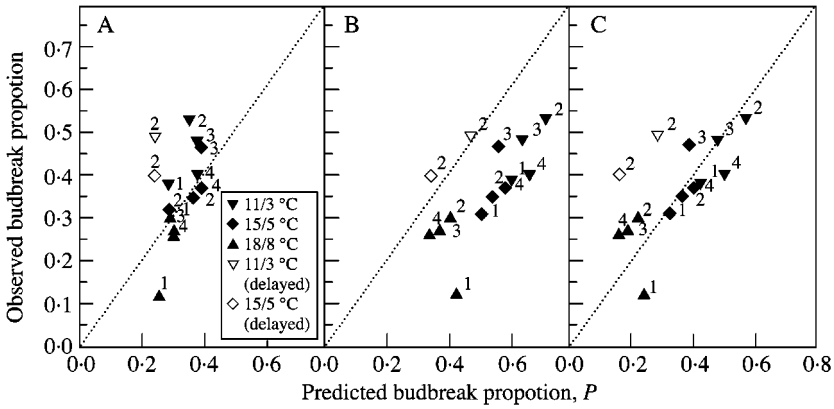

FIG. 9. Observed and predicted cane budbreak proportion, *P*, on containerized 'Hayward' kiwifruit vines subjected to artificial 'winters' under controlled environment conditions: predicted using CU model (A); LOP model with $A = 0{\cdot}025$ (B); LOP model with $A = 0{\cdot}1$ (C). (Numbers indicate duration of artificial chilling, delayed vines transferred to chilling 2 months after other vines.)

is shifted from the physiological processes operating *within each* bud to processes operating *among* buds.

These characteristics point to the limitations of field data, and to the value of CE studies, which allow conditions that depart from the climatic norm. The CE results (Fig. 9) did suggest that the LOP model may better describe the effect of temperature on budbreak, particularly if it is valid to assume that the decline in budbreak is steeper along canes of containerized vines. However, LOP predictions still differed strongly from observations where CE conditions departed markedly from climatic norms. Thus, the largest error was due to a much higher than predicted budbreak observed after the shortest warm-winter treatment (Fig. 9, 1 month at 18/8 °C treatment: $P = 0{\cdot}42$ vs. $0{\cdot}12$ observed), while budbreak after delayed chilling also did not fit the trend of the other predictions. This might result if the initial rate with which potential is lost is related to the removal of endodormancy (i.e. slower until dormancy is fully alleviated).

The prediction error against the CE data suggests inaccuracy in the developmental dependence of the LOP model. One option explored to correct this was to vary the start date, t_0. This seems reasonable if t_0 is associated with leaf fall or the onset of bud growth (i.e. potential is lost in late winter and early spring). However, climatically dependent start dates, either as a fixed duration before budbreak, or a fixed 'temperature sum' (i.e. growing degree-days; GDD), did not improve performance for the field data sets, possibly because of month-to-month correlation between field temperatures. Another option, that of changing the state dependence of dp/dt, also did not improve performance against field data. Data from a range of CE chilling treatments, combined with defoliation treatments, manipulation of cane length by pruning, girdling and excision of cuttings, might show when, and how, budbreak potential begins to change. Ideally, such data should describe the time and proportion of budbreak at individual nodes, rather than cane budbreak averages.

The effect of different levels of HC application on budbreak along canes of different length could also show the relative importance of bud level *vs*. correlative factors. The LOP model assumes no *direct* influence of HC on budbreak proportion. Rather, by accelerating growth re-initiation, HC increases budbreak by shortening the period of interaction among buds. This is not inconsistent with hypotheses concerning the effect of HC application (Walton *et al*., 1991), but means the effectiveness of chemicals, such as HC, depends on the advancement of budbreak, and probably also its synchrony. This indirect action of HC may explain its occasional inconsistency (Sale, 2000), since its effect then depends on time of application and stage of development. Late application will have less effect than earlier application. It is not clear whether this approach is valid for other dormancy-breaking compounds and growth stimulants, but if valid, earlier budbreak should correlate with higher budbreak.

What might be the basis of influence by bud neighbours? It does require physiological activity by buds, which do show a low but rising level of respiration over winter (McPherson *et al*., 1997). One possibility is that apical dominance is maintained even when buds are not visibly growing (i.e. when they are dormant). Temperature does affect apical dominance (Moe, 1988; Faust and Heins, 1996; Cook and Jacobs, 1999) in other species. Its importance for kiwifruit could be tested using growth regulators (e.g. cytokinins), or by altering physical relationships between buds, by girdling or removing terminal buds ('tipping'). Simulations suggested that the LOP model could reproduce patterns of budbreak induced by tipping (Manson and Snelgar, 1995), but only if parameter values were substantially altered.

Another possibility is competition among buds for a limiting resource (e.g. carbon or nitrogen), since manipulating vine and cane carbohydrate status has an impact on budbreak consistent with resource limitation. Thus, buds on canes shaded the previous season break less frequently and bear fewer flowers (Grant and Ryugo, 1984; Morgan *et al*., 1985; Fabbri *et al*., 1992; Snelgar *et al*., 1992). Rootstocks affect budbreak in a way that suggests an effect on vine

carbohydrate and transport characteristics (Wang *et al*., 1994*a*, *b*), and budbreak is generally higher on larger, more vigorous canes (Volz *et al*., 1992).

If buds do compete, then the isolation of terminal buds (absence of distal neighbours) may offer an advantage if translocation can overcome localized depletion (Greaves *et al*., 1999). This is especially so under warm conditions, which may increase competition for reserves. Under these conditions shoot growth from the terminal bud is enhanced and the percentage of shoots bearing flowers is reduced (Snelgar *et al*., 1988). Conversely, removal of terminal buds at budbreak can increase flower numbers (Manson and Snelgar, 1991*a*), although growth of the apical shoot is only weakly correlated with flower numbers on remaining shoots (Manson and Snelgar, 1991*b*).

However, there is presently little to suggest that kiwifruit buds compete intensively for reserves. For instance, nitrogen reserves in bark and wood are readily hydrolysed in spring (Ferguson and Turner, 1981), and the highest concentrations of free amino acids occur around budbreak (Clark and Smith, 1991). Mineral ions such as K, Mg and P are mobile (Ferguson and Turner, 1981), while storage carbohydrate levels are also high in stems surrounding buds over winter (Smith *et al*., 1992). Rates of respiration remain low throughout the winter period until immediately prior to budbreak (McPherson *et al*., 1997). Testing whether reserves are a significant factor in determining patterns of interaction should be possible if the relative accessibility of buds to reserves is manipulated by excision of buds and cuttings, and by girdling.

We conclude that the LOP approach may provide a useful integrative framework for practical models of kiwifruit budbreak, and flowering. Such models would ideally describe the impacts of climate and management techniques on both budbreak and flowering, and may also help with developing replacements for HC. The value of effective predictive tools will also increase should global trends towards warmer winter temperatures reduce budbreak and flowering on both 'Hayward' and newer plantings of *A. chinensis* 'Hort16A'.

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