Apple Fruit Bud Development and Growth; Analysis and an Empirical Model

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ABSTRACT

Analysis of the information available on apple bud development and growth after dormancy leads to an empirical model of growth to full bloom. The analysis and model are set in the framework of the physiological mechanisms considered to be responsible for dormancy and subsequent bud growth. It is necessary to introduce an arbitrary 'growth unit' scale to describe these processes quantitatively, which is done by the equation

$$G = A/(1 + be^{-k(I) \cdot P})$$

where G and A are in growth units, the value of k is controlled by a dormancy index I and P is a temperature summation. The model fulfils the main requirements laid down for it and the values of P at full bloom, derived from controlled environment work and field observations, are very similar.

INTRODUCTION

This analysis is concerned only with fruit buds (i.e. those which produce leaf and floral primordia and hence can lead to blossoms) although much of it probably applies equally to vegetative buds.

We may divide the process of apple bud development into three phases:

(1) morphogenesis and development to dormancy;
(2) dormancy;
(3) subsequent growth to full bloom.

If we take the term 'development' to mean changes with time in the structure or internal situation of the bud, and 'growth' to denote an irreversible increase in dry matter content, whether by cell division or expansion or both, then phases 1 and 2 are basically developmental phases and phase 3 is largely a growth phase.

Morphogenesis commences in late spring to early summer. Primordia are laid down in the bud at a rate which appears to be determined largely by physiological factors (Fulford, 1965); in those buds which have formed about 20 nodes the initiation of floral primordia usually begins at about the time shoot growth ceases (D. L. Abbott, personal communication). The length of the autumn development period, which depends on temperature and general growing conditions, affects the rate of growth of the buds in spring. Smith and Kefford (1964) contend that development towards dormancy is a positive process leading to a temporarily terminate condition. Leaf primordia are initiated in a manner qualitatively different from the development of leaves in extension growth, and quantitatively retarded. In its final form the bud consists of outer scales, leaf and bract primordia and flower initials (see Abbott, 1970). The stage at which the bud enters the dormant state is determined by environmental conditions, and until dormancy is broken the bud has the characteristic of being unable to grow under conditions of temperature and nutrition normally suitable to growth.

Dormancy may be induced by the accumulation of growth inhibitors in the bud, as described by Eagles and Wareing (1963, 1964) and by Walker (1970) for other woody

plants, or it may be due only to the depletion of a growth promoting hormone, as Abbott (1970) maintains, although the inhibitor abscisic acid has been found in dormant apple buds (Hoad, Healey, Bull and Abbott, 1973). Before growth can commence the balance between inhibitor(s) and promoter(s) must presumably be restored by the release of promoters and disappearance of inhibitors. In a number of woody plants the level of gibberellins in buds and seeds has been found to increase during winter chilling (Frankland and Wareing (1962), in hazel buds; Eagles and Wareing (1964) in sycamore seeds, and Badr, Hartmann and Martin (1970), in olive buds). In apples Pieniążek (1964) and Williams and Stahley (1968) have shown that dormancy can be broken by cytokinins and Luckwill and Whyte (1968) found that the levels of a cytokinin and another (unidentified) growth promoter in the xylem sap reached a peak at the time of full bloom. The accumulation of a growth promoter provides an adequate explanation for many of the processes involved in bud development and growth, but there are certain facets, such as the duration of the flowering period, the difference in flowering behaviour of blossoms on wood of different ages, and stock-scion interactions, which are better explained by invoking a balance of hormones (ratio between inhibitor and promoter). Although this explanation is not essential as a basis for this model I consider it to be the more probable one.

Given suitable conditions apple buds may start growing slowly when the onset of dormancy is followed by even a short cold period; in other words dormancy, as defined above, is broken. This may happen as soon as there is some restoration in the depleted level of the growth promoter substances, but since the inhibitor(s) remain dominant, growth is slow. As the length of the cold period increases the promoter/inhibitor balance improves and the rate of growth, under favourable conditions, increases. When the full chilling requirement has been met bud growth will proceed at a rate restricted only by the prevailing conditions. Inhibitor substances in growing tissue may be broken down by metabolic processes. Data in support of the changing bud growth rates are presented later.

When endogenous conditions are optimum bud growth in the first part of phase 3 is characterised by the exponential pattern usually associated with cell division (see Fig. 3) which is ultimately replaced by cell enlargement as the dominant process in the later stages. Full bloom may be regarded as a terminal point for the flower, though it may be followed by the development of a fruitlet, and leaves which formed part of the bud may continue to grow. We may therefore consider bud growth in phase 3, at least as far as the flower is concerned, as an asymptotic process. The commonly-used stages defining progression to full bloom in apples and pears (e.g. bud break, mouse ear, green cluster, etc.) are of no real physiological significance, although they serve as useful markers; they are the natural consequence of the enlargement of pre-formed parts of the bud which force their way out of the enclosing (dead) scales.

The above brief survey provides the background for the mathematical analysis of the process of bud development and growth to full bloom which follows. The analysis leads to an empirical model which has some analytical and some predictive value, although the latter, as in any model which uses weather data as an input, is limited by our present inability to predict future weather conditions for more than a short time ahead.

EXPERIMENTAL RESULTS AND OBSERVATIONS

The data presented in this section include many unpublished results and observations generously supplied by Mr. D. L. Abbott, who has for many years been studying various facets of apple bud development and the processes that are involved. Subsequent undated references to Abbott denote personal communications.

In general it appears that buds must complete a certain definite amount of development and growth before flowering. If dormancy is induced by adverse climatic conditions

before development is complete the cycle must be completed later and progress towards full bloom will be delayed.

The optimum chilling period

In an experiment in 1955/6 Abbott brought potted trees of several apple cultivars from plunge beds into a greenhouse, at weekly intervals, starting on 22 November 1955. Records were kept of the dates at which the various stages (bud swelling to full bloom) were reached. In another experiment, in 1966/7, batches of potted trees were brought
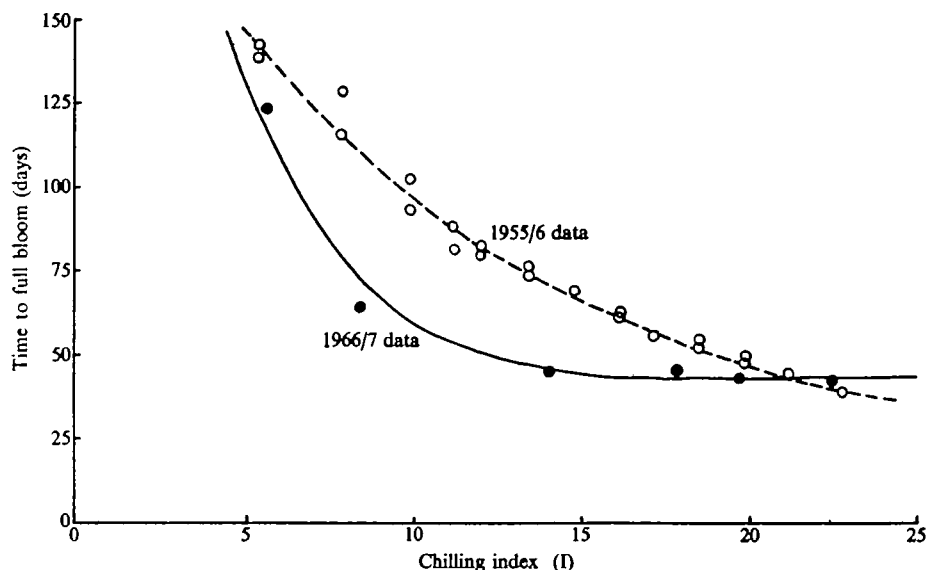

FIG. I. Time taken by apple buds to reach full bloom after being brought into warm conditions, plotted against a chilling index (*I*) based on average daily temperature (*T*) and the number of days spent in cold conditions (*n*): 1955/6 data are for individual trees; 1966/7 data are means for batches of four trees.

into a cold store (5 °C) for periods ranging from 14 to 112 days after leaf fall. Each batch was then transfered to standard 'spring' conditions (average temperature 11 °C) for 4 weeks and then into 'summer' (15 °C) conditions; progress towards full bloom was recorded.

Data from both these experiments have been analysed in the same way, i.e. by plotting (see Fig. 1) the time taken to reach full bloom, after plants were brought into warm conditions, against a chilling index, or dormancy integral, (*I*) (which may be taken to represent the accumulation of growth promoters), defined as

$$I = \int_0^t 1 \Big/ T(t) \cdot dt$$

where $T(t)$ is the temperature at time t, taken as the mean daily temperature (°C). This is based on the assumption that the chilling requirement is satisfied more rapidly at low temperatures, down to 5 °C. If $T(t) < 5$ °C, $T(t) = 5$ °C, in recognition of the fact that, beyond a certain point, lower temperatures cannot be advantageous to the physiological processes leading to the condition in which growth can proceed at the maximum rate allowed by prevailing conditions. The 5 °C limit is arbitrarily chosen as a convenient

value at about the level below which growth is usually assumed to cease. There is some evidence for this (Maclagan, 1933; Pearce and Preston, 1954; Lake, 1956). The chilling index for the 1955/6 data was calculated in finite difference form from daily meteorological records.

The analysis has been confined to the cultivar *Cox's Orange Pippin*. There was little evidence of differences between this and *Worcester Pearmain* (1955/6) or *Lord Lambourne* (1966/7), nor is there much varietal difference in other data published by Abbott (1962), although Lake (1956) observed significant differences in the effects of winter temperatures on *Cox* and *Worcester Pearmain*.

In view of the differences in experimental procedure the two curves in Fig. 1 are remarkably similar, illustrating clearly that the time taken for buds to reach full bloom after the onset of favourable growing conditions (i.e. the growth rate in warm conditions) is strongly dependent on the length of the chilling period to which they have been subjected since entering dormancy. Furthermore the two curves indicate approximately the same optimum value for I, suggesting that little subsequent advantage is conferred by time spent in cold conditions after I has reached a value of about 20, equivalent to 100 days at 5 °C or less. As might be expected this is more clear-cut for the controlled environment data than for those obtained in the uncontrolled conditions of plunge beds and greenhouse. The optimum I value is in good agreement with results presented by Eggert (1951), who found that about 2000 h at temperatures below 0 °C and about 3000 h below 7 °C were necessary to induce 50 per cent bud activity in a number of apple varieties, brought into warm conditions after varying periods in the cold. (These data suggest that the choice of 5 °C as the optimum chilling temperature may not be correct, but Eggert's results were based on thermograph records of field temperatures, which fluctuate, and this fluctuation may be important.)

Pearce and Preston (1954) found that June temperatures in the summer prior to flowering (i.e. during phase 1) affected the date at which apple buds reached full bloom in the following spring, a conclusion which they found difficult to accept but which was supported by Lake (1956). This effect may be due to increased vegetative growth in warm June conditions, with consequent inhibition of flower bud morphogenesis. They also found that temperatures after mid-March, i.e. at the later stages of progress to full bloom, had progressively less effect on the date of full bloom. Abbott (1962) demonstrated that the date of bud break is more strongly influenced by the time when winter chilling occurred than by its intensity, and he suggested that a mild autumn allows further pre-development of flower primordia than does a cold one. This is supported by the results of an experiment which Abbott did to assess the effects of bud age on subsequent growth in spring. Batches of young trees were brought into 'autumn' (11 °C) and then 'winter' (5 °C) conditions from mid-May onwards, so that the age of buds (then in phase 1) at the time of imposition of cold conditions was gradually increased. After a standard 4 weeks of 'autumn' and 8 weeks of 'winter' the trees were brought back into 'spring' (11 °C for 4 weeks) and then into 'early summer' (15 °C) conditions. The time required to reach full bloom after transfer to spring conditions decreased as the age of the buds increased. The trend was asymptotic to about 45 days (spring plus summer). When transfer to cold conditions was delayed for longer the buds continued to grow slowly in size but did not break until after chilling, when they opened directly to the green cluster stage, i.e. flower buds could be seen as soon as the scales loosened with little evidence of leaf growth. Although the relationship is asymptotic, within the range of conditions likely to be met in nature the number of days required to reach full bloom in spring/early summer can be closely approximated by a linear equation. This is presented later.

In some potted trees left in a cold store for almost a year after morphogenesis was complete the buds eventually reached full bloom, almost simultaneously. As in the case of old buds the flowers were 'strong' with relatively little leaf development.

REQUIREMENTS FOR A MODEL

The results and observations discussed above indicate that a model of bud development and growth must fulfil several conditions:

   (i)   if calculations are commenced from the time when buds enter dormancy the equation(s) must, almost immediately, allow some growth to be made at subsequent favourable temperatures, at rates that increase at any given temperature as the time spent in cold conditions approaches the optimum;

   (ii) once the chilling requirement has been satisfied the rate of subsequent growth is a function of temperature, exponential at first and hyperbolic towards full bloom;

  (iii) there must be some allowance for the stage of development reached at the onset of dormancy.

Units

Since there is no readily available, or generally accepted, parameter which can be used to express bud growth in quantitative terms the choice of units for an empirical model poses a problem. Bud weight is unsatisfactory since we have no information on the relationship between bud weight and growth stage, and there seems no *a priori* reason why a definitive relationship should exist. Ideally hormone concentrations, reaction rates and rates of cell division should be used, but there is no information on any of these phenomena in connection with bud development and growth. Consequently, for lack of a better criterion, an arbitrary growth unit scale has been adopted, allocating approximately 100 units to the process of bud opening from the onset of dormancy to the attainment of full bloom.

THE MODEL

Denoting the number of growth units as G and time as t we may write

$$\frac{dG}{dt} = f(I, T)$$

which, to fulfil the requirements of the model, may be expanded to

$$\frac{dG}{dt} = k(I)f(T) \tag{1}$$

where k is a rate coefficient. The requirements laid down for the model suggest that the integral from equation (1) should be a logistic of some sort, so the equation

$$G = \frac{A}{1 + be^{-kt}}$$

where A is the asymptote and b is a constant, provides a good starting point, which satisfies the exponential requirement of equation (1), and has therefore been adopted as the basis for the model. Now since the analysis must be in terms of temperature, not time, some function of temperature must be substituted for t in the logistic equation, so we set $P = f(T)$ (cf. equation (1)) and re-write the logistic equation as

$$G = \frac{A}{1 + be^{-k(I).P}}. \tag{2}$$

The linear from of equation (2) is

$$\ln\left(\frac{A-G}{G}\right) = \ln b - k(I).P \tag{3}$$

and the dependence of bud development and growth rate on P is shown by the derivative

$$\frac{\mathrm{d}G}{\mathrm{d}t} = \frac{\delta G}{\delta P} \cdot \frac{\delta P}{\delta t} = k(I)\,\frac{G(A-G)}{A}. \tag{4}$$

To fulfil requirement (i) $k(I)$ must be allowed to increase as $I \rightarrow I_{\mathrm{opt}}$. The relationship

$$k(I) = k_{\mathrm{max}}(1 - e^{-I/I_{\mathrm{o}}}) \tag{5}$$

provides a reasonable approximation to the shape of the curves in Fig. 1 (taking time to full bloom as an analogue of k), and since $I_{\mathrm{opt}} = 20$, if we set $I_0 = 6 \cdot 7$ then $k \simeq 0 \cdot 95\,k_{\mathrm{max}}$ when $I = I_{\mathrm{opt}}$. The exponential requirement is therefore only fulfilled after k becomes constant.

The simplest possible assumption about the functional form of P is that

$$P = \int_0^N T(t)\,.\,\mathrm{d}t$$

where N is the number of days between the onset of dormancy and full bloom. There must be a temperature limit below which no growth will be made, and since the assumption has already been made that $5\,°C$ is an optimal temperature for dormancy, it is consistent to assume that no growth occurs at temperatures below this, so we write P in finite difference form as

$$P = \sum_1^N (T - T_0)\,\Delta t$$

where $\Delta t = 1$ day and $T_0 = 5\,°C$. To avoid the absurdity of negative growth it is also necessary to stipulate that if $T < T_0$, $T - T_0 = 0$. Requirements (i) and (ii) are now completely satisfied.

The value of b in equation (2) is obtained from equation (3); when P is small and $G \simeq 1$ then $b \simeq A$. By definition $A \simeq 100$; it is to be allowed to vary with stage of development in autumn, but it is convenient to set $b = 100$. Referring to Fig. 1, the shortest period to full bloom (after chilling) was 40–5 days, at about $15\,°C$. In this situation $I > 20$, $k = k_{\mathrm{max}}$ and $P = 400$. We specify that full bloom is reached when $G = 0 \cdot 95A$, and with $A = 100$, $P = 400$ and $b = 100$ obtain $k = -0 \cdot 0189$, say $-0 \cdot 02$.

Referring back to Abbott's data on bud ages, if we assume that morphogenesis and development in the field are unlikely to be checked by weather conditions earlier than 20, or later than 100, days after the initiation of the first flower primordium, we may approximate Abbott's results by equation (2) with A given by

$$A = 102 - 0 \cdot 1 t_D \tag{6}$$

where t_D is the time in days, after the initiation of the first flower primordium, during which conditions are such that development can continue. In practice this correction could be made by noting when shoot extension stops and taking t_D as the number of days from then until the first frost (see below). Equation (6) gives $A = 94$ when $t_D = 80$, which would be the result obtained if flower initiation began in early August and development was halted by environmental conditions at the beginning of November.

ASSESSMENT IN TERMS OF FIELD DATA

Meteorological records and observations of flowering dates of *Cox* at Long Ashton, for the seasons 1967/8 to 1972/3, have been used to evaluate the model for field conditions. Commencing at the beginning of October I and P were calculated, on a daily basis for each season, until the actual date on which full bloom was recorded in each year, based on visual estimates of the time when 50 per cent of flowers were open. Examination of the data to see whether there was any common factor which might identify a definitive starting point showed that the value of P reached at full bloom was remarkably constant if the

calculations were started from the day of the first air frost in autumn. From this starting point the dates at which important values of the parameters I and P were reached are given in Table 1.

TABLE 1. *Starting dates (first air frost) for the calculations of I and P; dates when the chilling requirement was satisfied ($I = 20$) and dates of full bloom, with the P values reached*

Data from Long Ashton Research Station

Start date	Date when $I = 20$	Date of full bloom	Value of P at full bloom
17 November 1967	10 March 1968	18 May 1968	363
5 November 1968	2 March 1969	16 May 1969	389
5 November 1969	3 March 1970	16 May 1971	355
16 November 1970	17 March 1971	10 May 1972	368
6 November 1971	23 February 1972	9 May 1972	388
14 November 1972	14 March 1973	15 May 1973	353

Although the temperature patterns of these seasons did not vary greatly there is suffi-cient variation to give confidence in the results, especially in view of the fact that the final value of P corresponds so closely to that estimated from the experiments with potted trees. The criterion taken for choice of starting date is not, of course, completely satis-factory; in some years there may be an unusually early frost, not followed by a significant cold spell, while in others there may be a spell of cold weather without frost; an isolated early frost may not halt bud development and growth and should probably be ignored, the latter weather pattern may do so. A subjective decision would have to be made in each individual case, but a sharp drop in air temperatures, without recovery, accom-panied by frost, may safely be taken to define the onset of dormancy. With the values of A, b and G used previously the average value of P at full bloom ($\sim$370) does not signifi-cantly alter the value of $k = -0.02$ derived earlier.

A further assessment of the model is provided by Figs. 2 and 3. The calculated bud development/growth curves ($A = 95$) for 1970/1 and 1971/2, based on meteorological records, are presented in Fig. 2. These curves quite closely reflect observations; for example we noted in March, 1972, that the buds appeared to be several weeks ahead of the stage reached on the same date in 1971. However the second half of March and all of April 1972 were exceptionally windy (average wind speeds were around 5 m s^{-1}) and this undoubtedly had a detrimental effect on bud growth, which was held back so that full bloom eventually occurred at about the same date as in 1971. The calculated curves for 1972 deviate from observation during April (see Fig. 3).

The data in Fig. 3 are bud weight ratios. Each week in the early spring of 1971 and 1972 five buds were cut from each of seven trees in an orchard of *Cox's Orange Pippin*, weighed, oven dried and weighed again. The ratios W/W_1, where W_1 is the average dry weight on the last date before significant increases began, are plotted against time on log-linear scales. The 1971 data fall on a straight line until after the green cluster stage; when significant leaf area is displayed the bud growth pattern, which up to this time depends on stored carbohydrate, is probably altered by the contribution of photosynthesis. The 1972 data are not so well behaved, presumably because of the adverse environmental conditions. Nevertheless the expected exponential pattern is not completely obscured.

To compare calculated and measured growth rates the ratios G/G_1, derived from Fig. 2, are plotted on Fig. 3, G_1 being the value of G at 1 March. The comparisons are restricted to the period before green cluster. The correspondence in both cases is good, and this fairly rigorous test provides confirmation that the model is a realistic and reasonably
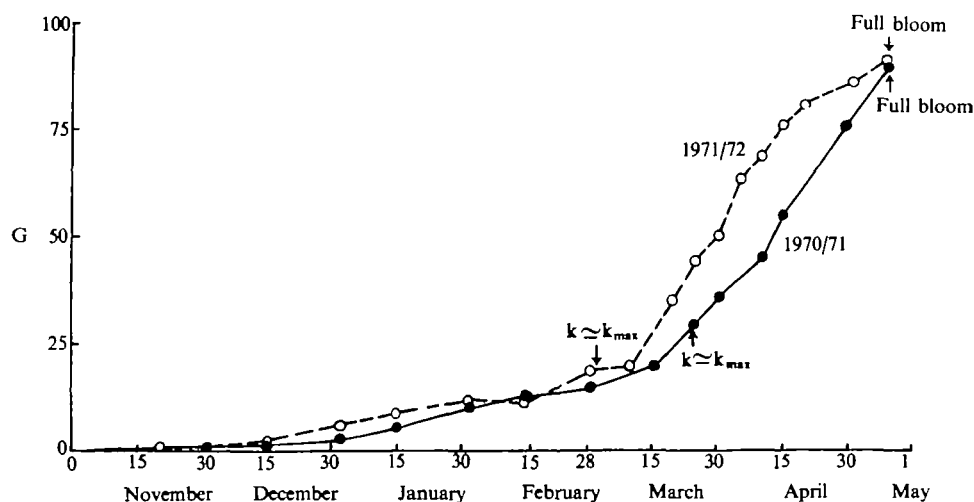
FIG. 2. Apple bud development and growth curves at Long Ashton calculated for 1970/1 (solid circles) and 1971/2 (open circles). The ordinate is an arbitrary unit scale, but from about the beginning of March to the end of April the curves represent bud weight increase.
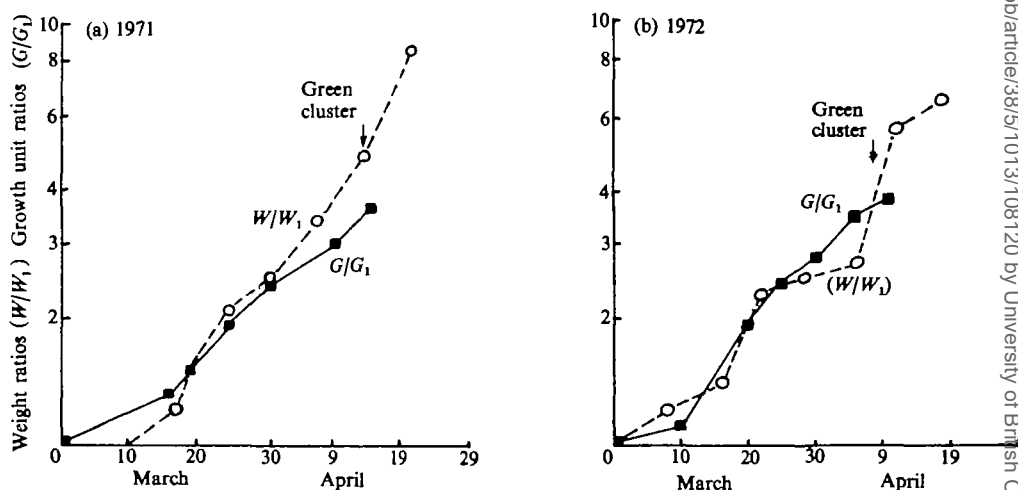
FIG. 3. Apple bud weights, obtained from field samples, plotted as ratios (W/W_1, where W_1 is the average dry weight on the last date before significant increases began) on log-linear scales against time for (a) early spring 1971 and (b) early spring 1972. Open circles joined by dashed lines denote measured points, black squares joined by full lines show the calculated ratios (growth units) for the same years over the same period.

accurate tool. However, it must be emphasised that the curves in Fig. 2 do not represent total bud weight changes except for the period from about the time $k = k_{max}$ to the green cluster stage. After this G may represent flower weights only.

DISCUSSION

The model presented here fulfils the specified requirements; the values of the rate constant derived from controlled environment studies and from field observations are essentially the same, and the calculated pattern of spring growth corresponds closely to

measured bud weight increments. It is therefore, in many respects, satisfactory. However there are unsatisfactory aspects, not least of which is the use of arbitrary growth units. There is an obvious need for research into the processes of bud development and growth with a view to establishing meaningful quantitative parameters by which to measure these processes.

If we use the model to simulate the behaviour of buds on a tree kept at a constant temperature of, say, 6 °C, we find that full bloom is reached about a year after the onset of dormancy. This is in accordance with observation, but if we simulate the behaviour of buds kept at a temperature of say 15 °C (no chilling period), full bloom is apparently reached after about 70 days (at which time $k \simeq 0.5 \, k_{max}$). This is not in accordance with observation. In Abbott's bud age experiment trees kept continually at 15 °C only reached full bloom about nine months after leaf fall, and then the flowering period was very long. Clearly some part of the model is not correct—probably the term controlling the value of k. It may be that above a certain temperature the accumulation of growth promoters is very slow, so that I would increase very slowly. This, and the pattern of change in inhibitor levels, can be tested experimentally or by measurement, but lacking any basic background information there is little merit in adjusting the model to induce it to behave properly in this extreme situation.

If the balance of hormones hypothesis is correct then application of gibberellins plus cytokinin should reduce the chilling requirement and hence increase the value of k, so that response to increased temperature will be more rapid. Similarly the application of a suitable inhibitor would delay flowering and also probably result in a longer flowering period—flowering in trees given inadequate chilling tends to be extended over a longer period than those subject to prolonged chilling. This model provides no information on duration of flowering, which may well depend on some aspect of the chilling process, for example the time spent at optimal temperatures, which may be around 0 °C or 1 °C. Temperature limits and the real form of the chilling index, or dormancy integral, require investigation. Lake (1956) suggested that minimum temperatures have important effects on the rate of development to full bloom.

Besides its value in indicating the extent of our ignorance, the model has practical value as a tool to assess the effects of site microclimate on the date of flowering in apple, given data on the microclimate in given topographical situations.

TABLE 2. *Average weeekly temperatures (°C) in southern England and the Po Valley (northern Italy) in spring*

Date	March					April				May		
	1–7	8–14	15–21	22–8	29–4	5–11	12–18	19–25	26–2	3–9	10–16	17–23
S. England	5·5	6·2	6·9	7·3	7·8	8·2	9·0	9·3	9·7	10·0	10·5	11·7
N. Italy	6·7	8·2	9·6	10·5	11·5	12·5	14·0	14·5	15·7	. .	. .	. .

It is also interesting to apply the calculations to regional data, and I have used mean temperature data from an apple growing region in southern Europe (the Po valley) and southern England to calculate bloom dates and to provide some insight into bud development and growth at these places. In both regions the average air temperature rises above 5 °C about the beginning of March; the European Winter temperatures are well below those of England but the spring temperature rise is much faster and spring temperatures considerably higher. Approximate weekly temperatures for the two areas are given in Table 2.

Based on the Long Ashton data analysed in this paper P has a value of about 150 at the beginning of March, so G will have reached a value of about 16 if, by then, $k \simeq k_{max}$. Because of the very cold winter temperatures we can probably assume that in Europe, $P \simeq 0$ at the beginning of March, with $k \simeq k_{max}$. On these assumptions G has been calculated for both areas and the results plotted in Fig. 4. They indicate that bud growth in southern England is in advance of that in southern Europe until about mid-April, but
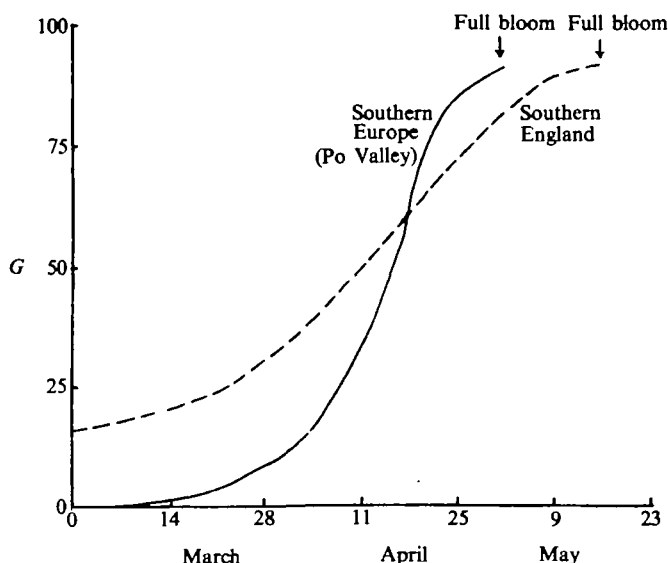
FIG. 4. Comparative patterns of apple bud growth in southern England and southern Europe (the Po valley in northern Italy) based on average weekly air temperature data.

that full bloom occurs in southern Europe at least two weeks before southern England, which is approximately correct. It seems likely that flowering in the continental areas is a much more abrupt process than in England, i.e. the flowering period will be shorter and the flowers stronger, with fewer leaves. It is possible that differences in flowering time may be quite seriously underestimated, because the bud temperatures in the two regions are likely to be even more different than air temperatures. All calculations with this or similar models should in fact be based on bud, not air temperatures (see Landsberg, Butler and Thorpe, 1974).

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