Mathematical Foundations of Population Dynamics

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Development

Temperature-dependent organisms that develop under different temperature regimes generally exhibit significantly different process completion times. For example, boll weevil egg to adult emergence times change by 20 days as temperatures vary over a 15°C range. In addition to the developmental variation between temperature regimes, there are also significant variations among individuals under identical temperature regimes. For example, boll weevils from a single cohort emerge over a two- to three-week period under mid-season field temperatures.

The basic problem addressed in this chapter is the modeling of biological developmental times. As illustrated above, there are two basic components to the modeling problem: (1) the prediction of mean developmental times under arbitrary temperature regimes, and (2) the prediction of the variation about the mean time. The prediction of mean developmental times has a long history, dating back to the mid-nineteenth century. The incorporation of the stochastic aspects of development was not addressed in detail until the mid-1970s. The motivation for modeling the distribution of times as well as the means is of great practical interest. For example, an application of pesticide at the mean developmental time of an insect cohort would at best encompass 50% of the individuals. In addition, the early developers may have already dispersed, whereas the late developers may still be in a protected environment.

Our modeling approach is to make certain assumptions regarding the temperature response of the organism. Based on these assumptions and data from both laboratory and field experiments, a mathematical structure for development is derived. The practical importance of the resulting methodology is due to its demonstrated accuracy when applied to populations in the field. We begin this chapter by reviewing the mechanics of predicting developmental times. A general mean developmental rate function that is often utilized in predictive techniques is discussed in Section 3.2. Section 3.3 presents the methodology for in-
3.1 Predicting Mean Development Times

Historically, biologists and ecologists have noted that temperature-dependent processes correlate well with the summation of certain functions of temperature (Candolle 1855; Reibisch 1902). These observations led to the most commonly used method of developmental time prediction, the degree-day concept. The modeling of crop growth and development are typical areas where this concept has been applied. A plant such as cotton grown under field conditions exhibits different chronological maturation times in different years. However, if a degree-day as opposed to a chronological day scale is used, the processes have surprisingly consistent timings from year to year.

The degree-day method is based on summing (hourly, for instance) the number of degrees above a specified temperature threshold that occur during the day. This sum is then converted to degree-day units by dividing by the number of time increments utilized for the day (24 increments for an hourly computation). Developmental times measured on this degree-day scale are often independent of temperature; thus the mean number of degree-days can be utilized to predict mean completion times. Sometimes it is necessary to have a maximum as well as a minimum threshold, since certain processes slow down considerably above some optimal growth temperature. For example, nymphs of the spotted alfalfa aphid, *Theroaphis maculata* (Buckton), reach their peak development rate at 26°C and maintain approximately this rate through 32.5°C (Messenger 1964). Thus, an upper degree-day scale is used to approximate this organism's development rates. The numerical example below illustrates these concepts.

For consistency of presentation and comparison with other methods, the degree-day computation is modified slightly from the overview given above. If each degree-day unit is divided by the mean number required to complete the process (535°C-days for cotton flowering; Gutierrez 1975), then the summation at any instant is the fraction of the mean process time completed at that instant. Using this scale, the mean biological time for the process has elapsed when the summation reaches one.

3.1.1 Degree-Day Summation

For a process with total degree-day unit requirements of $r_0$ and discrete environmental temperature measurements $T_1, T_2, \ldots , T_n$, the developmental scale, $d_i$, at any time, $t$, in elapsed days is

$$d_i = \left( \frac{1}{nr_0} \right) \sum_{i=1}^{n} \max \{0, \min(T_i, UT) - LT\}.$$  \hspace{1cm} (3.1)

where $n$ is the number of time increments in a day, and $UT$ and $LT$ are the upper and lower temperature thresholds, respectively.

The degree-day summation, Equation (3.1), is an approximation, since the biological development process operates continuously, and the temperature function, $\psi(\cdot)$, is actually a continuous function of time. The proper value of development in degree-days is the integral from the start time, $t_0$, to time $t$ given by

$$d_t = \frac{1}{r_0} \int_{t_0}^{t} \max \{0, \min(\psi(x), UT) - LT\} dx.$$  \hspace{1cm} (3.2)

The degree-day summation approximation is illustrated in Figure 3.1.
Example. To illustrate the use of the degree-day formula, (3.1), the developmental status of a flowerbud of Acala cotton is to be computed for two days of growth. Temperatures (°C) are available at four-hour increments: 24, 27, 30, 36, 32, 29, 27, 25, 23, 21, 23, 27. Development at \( t = 2 \) days is computed (using lower and upper thresholds of 12°C and 35°C, respectively, and a mean total requirement of 535 °C-days) as

\[
d_t = \frac{1}{6(535)} \sum_{i=1}^{12} \max\{0, \min(T_i, 35) - 12\}
\]

\[
= \frac{1}{6(535)} \left( 12 + 15 + 18 + 23 + 20 + 17 
+ 15 + 13 + 11 + 9 + 11 + 15 \right)
\]

\[
= \frac{1}{3210} (179) = 0.05576.
\]

Under the specified temperature regime, the development process is approximately 1/18 complete in two days. If the environmental temperatures repeated themselves every two days, the mean developmental time would take a total of 36 days.

3.1.2 Rate Method

The degree-day concept, although it is used for many applications, has been shown to be applicable only over a narrow temperature range. The degree-day method assumes that the rate of development increases linearly with temperature. However, most biological processes appear to have a linear temperature response when plotted on a temperature scale, implying an exponential response over the midtemperature range. This exponential response is illustrated in Figure 3.2 for boll weevil egg to adult emergence in flowerbuds.

Biological researchers (e.g., Fye et al. 1969; Butler and Watson 1974) have noted that regressions utilizing constant temperature data showed better correlations when the reciprocal of the developmental times were used instead of the actual times. This observation furnished impetus to the development of the rate method for modeling processes under variable temperature regimes. The rate method is based on the concept that developmental rates are additive for changing temperature. The advantage of the rate approach over the degree-day method is that the rate function is not restricted to a linear temperature response. The concept of using rates for predictive purposes is not new. Johnson and Lewin (1946) used developmental rates when working with bacteria. However, until the 1960s, developmental rates were not commonly used in insect population studies.

The rate summation rule uses as the developmental rate the reciprocal of the mean developmental time for each constant temperature. If the developmental time at a given temperature is 20 days, then the process is assumed to develop at a rate of 1/20 per day. This method is applicable to variable as well as constant temperature regimes. For example, consider an environment that alternates every 12 hours between 20°C and 30°C. If these environments have developmental rates of 0.05 and 0.10, respectively, then in one day the development is

\[
d_t = \frac{1}{2} (0.05) + \frac{1}{2} (0.10) = 0.075.
\]
Under this regime, development would be completed in \((1/0.075 =) 13.33\) days. The rate summation rule can be summarized as follows.

**Rate Summation Method.** For a process with temperature-dependent developmental rate function \(r(t)\), in inverse days, and with discrete environmental temperature measurements \(T_1, T_2, \ldots\), the fraction of the mean development, \(d_t\), that has occurred after \(t\) days is

\[
d_t = \frac{1}{n} \sum_{i=1}^{n} r(T_i),
\]  

(3.3)

where \(n\) is the number of time increments in a day, and \(nt\) is the number of increments in \(t\) days. The mean time of process completion occurs at the time \(t\) for which \(d_t = 1\).

**Example.** For the greenbug, biotype C, *Schizaphis graminum* Rondani, an approximate developmental rate function is

\[
r(T) = 0.019 e^{0.0538T},
\]  

(3.4)

where \(T\) is °C. The environmental temperatures are available on a four-hour increment. For one day of temperatures of 15, 20, 23, 25, 31, and 24°C over the four-hour intervals, the developmental fraction is computed as

\[
d_t = \frac{1}{6} (0.0426 + 0.0557 + 0.0655 + 0.0729 + 0.1007 + 0.0691) = 0.068.
\]

Thus, after one day the process is 6.8% complete; under a repeating sequence of temperatures as given above, the mean development would be 14.7 days.

Like the degree-day summation procedure, the rate summation method is also an approximation because of the continuous nature of development and environmental temperatures. This summation rule uses discrete time steps to compute an approximation to the following integral.

\[
d_t = \int_{t_0}^{t} r(\psi(x))dx.
\]  

(3.5)

Equation (3.5) is the generally acknowledged method for computing development (Stinner et al. 1974; Allen 1976; Logan et al. 1976; Curry et al. 1978b). In practice, however, Equation (3.3) is most often used, given the simplicity of its computation and the problems associated with estimating continuous temperature regimes. Table 3.1 illustrates the accuracy of the discrete approximations to rate integra-

**Table 3.1** Accuracy Comparisons between Rate Summation Method and the Integration Method.

<table>
<thead>
<tr>
<th>Temperature Profile (Eq. 3.5)</th>
<th>½ Hour</th>
<th>1 Hour</th>
<th>2 Hour</th>
<th>3 Hour</th>
<th>4 Hour</th>
</tr>
</thead>
<tbody>
<tr>
<td>BOLL WEEVIL ((r = 0.0085157 e^{0.0736°C}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 15 18.229</td>
<td>18.229</td>
<td>18.208</td>
<td>18.167</td>
<td>18.375</td>
<td>17.833</td>
</tr>
<tr>
<td>GREENBUG ((r = 0.019 e^{0.0538°C}))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 15 13.75</td>
<td>13.75</td>
<td>13.75</td>
<td>13.75</td>
<td>13.875</td>
<td>13.667</td>
</tr>
</tbody>
</table>

\(^{a}\)Dates denote starting day for temperature profile for Spur, Texas, during 1966.

\(^{b}\)Development times.

\(^{c}\)Development times and % deviations from the integration method.
ation (Equation 3.3) for various time increments. The rate summation method is reasonably accurate up to a three-hour time increment.

3.2 Developmental Rate Functions

The previous section addressed the mechanics of predicting mean biological developmental times. The procedure used a general temperature-dependent mean developmental rate function, \( r(T) \), which is a continuous function of temperature and needs to be described as such. Normally, selected constant-temperature developmental rates are experimentally established to estimate the rate functions. The procedure for estimating these rates is straightforward. The experiments yield developmental times as opposed to developmental rates. However, assuming that rates are constant throughout the developmental period (see Section 3.4 for the relaxation of this assumption), the reciprocal of time determines the rate. With these estimated mean rates, a continuous rate function is then developed by curve-fitting techniques. Several functional forms for these rate functions are considered next.

3.2.1 Degree-Day Rates

The degree-day summation method (Equation 3.1) has the same form as Equation (3.3); therefore, it is actually a rate summation method. The degree-day rate function is linear with respect to temperature, \( T \), between the thresholds, and it is given for all \( T \) by

\[
r(T) = \frac{1}{r_0} \max\{0, \min(T, UT) - LT\},
\]

(3.6)

where \( UT \) and \( LT \) are the upper and lower temperature thresholds, respectively, and \( r_0 \) is the mean number of degree-day units for process completion. The graph given in Figure 3.3 for 12°C and 35°C threshold levels shows that for this linear rate function the threshold temperatures need to be estimated along with the total number of degree-day units, \( r_0 \), needed for mean development completion. However, given the threshold values, any temperature regime data (not necessarily constant temperature data) can be used to estimate \( r_0 \). Since the thresholds for many insects and plants are generally in the neighborhood of 12°C and 35°C, this method is frequently utilized without the aid of constant temperature experimental data. Often the organism operates in temperature regions which infrequently encounter the threshold limits. Thus, the upper threshold limit is commonly omitted. Using biologically reasonable estimates for the thresholds allows any temperature regime data to be used to estimate \( r_0 \). The minimal data requirement for estimating the degree-day rate function is one of the major advantages of this method and probably has contributed significantly to its popularity.

3.2.2 Interpolation

When the developmental time data for a number of constant temperature regimes is available, an interpolation of these data points can be used in lieu of an explicit form of the rate functions. This method utilizes linear interpolation for temperatures between the available experimental data. These extremes could be handled by estimating zero rate temperatures and including them in the rate data, such as the 35°C point in Figure 3.4. Another method would be to merely associate with any point outside the available data region the value of the associated limit point, such as the 10°C point in the figure. The interpolation procedure is summarized as follows.
these regions. In other words, the polynomial function may suddenly deviate significantly from the trend line. Thus, the estimated function should be compared to the data, and limits established on the temperatures for which the function yields acceptable values. The same procedure as with the linear interpolation function, Equation (3.7), could be used. Hence, the polynomial method is as follows.

**Polynomial Function.** For a set of constant temperature regime data, \((T_i, r_i)\), for all experimental observations, \(i\), the polynomial rate function of degree \(n\) for any temperature \(T\) is

\[
    r(T) = \begin{cases} 
           r_i, & \text{for } T < T_i; \\
           r_i + \frac{(T - T_i)(r_{i+1} - r_i)}{(T_{i+1} - T_i)}, & \text{for } T_i \leq T < T_{i+1}; \\
           r_{i+1}, & \text{for } T_i \leq T. 
        \end{cases} \tag{3.8}
\]

where \((T_i, r_i)\) and \((T_{i+1}, r_{i+1})\) are the lower and upper data pairs (temperature and associated rate) of the validity region for the rate function, and \(a_0, a_1, \ldots, a_n\) are the polynomial parameters obtained by the method of least squares (see almost any elementary statistics text for least-squares procedures).

### 3.2.4 Eyring Function

A function that has found considerable application in biochemistry is the Eyring rate equation (Eyring 1935) given by

\[
    r(T) = \frac{KT}{h} \exp\left(\frac{c_1 - c_2/T}{R}\right),
\]

where \(K\) is the Boltzmann constant, \(T\) is absolute temperature, \(h\) is Planck's constant, \(c_1\) is entropy of activation, \(c_2\) is enthalpy of activation, and \(R\) is the universal gas constant. The application of this equation to organism developmental rates requires the estimation of two parameters, \(c_1\) and \(c_2\). Since these parameters are to be estimated, the other constants can be absorbed in them, yielding the equation

\[
    r(T) = aT e^{-bT}, \tag{3.9}
\]

where \(a\) and \(b\) are parameters to be estimated. By a simple logarithmic transformation of the data, the polynomial (of order one) least-square
technique can be used to estimate these parameters. For each experimental data pair \((T_i, r_i)\), letting
\[
y_i = \ln(r_i) - \ln(T_i),
\] (3.10)
and
\[
x_i = -\frac{1}{T_i},
\]
the equation to be estimated is
\[
y = a' + bx,
\]
where \(a' = \ln(a)\). In summary, \(a'\) and \(b\) are found by a linear least-squares fit of the data pairs \((x_i, y_i)\). The original parameter \(a\) of (3.9) is obtained by setting it equal to \(\exp(a')\).

A variant of the Eyring equation frequently encountered in mathematical and statistical analysis is the exponential form
\[
r(T) = ae^{bT}.
\] (3.11)
The parameters of this function are found as they are for the Eyring equation, with the exception that Equation (3.10) is replaced by
\[
y_i = \ln(r_i).
\]

### 3.2.5 Poikilotherm Model

The final rate functional form to be considered was recently developed by Sharpe and DeMichele (1977). This function was demonstrated to fit a wide range of organisms, from bacteria to plants and insects. The basic concept underlying the rate equation is that the organism will have a rate-determining control enzyme or enzyme complex. The control enzyme is assumed to have three basic states: (1) active, (2) cold-temperature denatured (reversible) inactive, and (3) hot-temperature denatured (reversible) inactive. The organism is assumed to have a large quantity of the control enzyme, with a proportion in each of the three states. These proportions vary with temperature, since an Eyring function (3.9) for the activity rates in the active state is assumed. This assumption, along with an exponential probability assumption for passing between the states, yields the following poikilotherm rate function.

#### Poikilotherm Function

A biological organism has a poikilotherm response rate function if the constant temperature developmental rates have the form
\[
r(T) = \frac{T \exp(a - a/T)}{1 + \exp(a - a/T) + \exp(a - a/T)},
\] (3.12)
where \(T\) is absolute temperature, and the \(a\) are curve-fit parameters. A thermodynamic interpretation of these parameters as they relate to the organism's developmental control enzyme system is found in Schoolfield et al. (1981).

The parameters in (3.12) are difficult to estimate, since the standard linear least-squares method is not applicable, and nonlinear optimization methods must be used. A complicating aspect is that each parameter appears in the exponent of the exponential function and is thus quite sensitive to small changes in its value. Wagner et al. (1984) present an SAS-based parameter estimation algorithm (Helwig and Council 1979) utilizing Marquardt’s least-squares method.

The applicability of the poikilotherm rate model for describing constant temperature developmental rates has been demonstrated in Barfield et al. (1977), Sharpe and DeMichele (1977), and Sharpe et al. (1981). Figure 3.5 illustrates the accuracy of this approach for four different organisms.

#### Derivation

It is interesting to consider the derivation of Equation (3.12). The conceptual approach is to model the states of a “control” enzyme and hypothesize that this response captures the essence of the actual organism’s response. The developmental rate proceeds in proportion to the fraction of the enzymes in the active state. The temperature response for an active enzyme is assumed to follow the Eyring form (3.9). The length of time the enzyme remains in a state is assumed to be exponentially distributed. The transition rate of moving from one enzyme state to another is temperature dependent, and that dependency is also described by the Eyring response. To be explicit, the active, cold inactive, and hot inactive states are denoted by \(a\), \(c\), and \(h\). Four nonzero transition rates labeled \(\mu_a\), \(\mu_c\), \(\mu_h\), and \(\mu_s\) denote the transitions \(c\) to \(a\), \(a\) to \(c\), \(h\) to \(a\), and \(a\) to \(h\), respectively (Figure 3.6).
The exponential assumption implies that the probability of an enzyme moving from one state to another state is \( \mu_i \Delta t \) during a small time increment, \( \Delta t \), and thus the probability of not making that transition is \( (1 - \mu_i \Delta t) \). The probability of an enzyme being in state \( i \), for \( i = a, c, \) or \( h \), is denoted by \( p_i \). The equations defining these probabilities follow.

**ACTIVE**

\[
p_a(t + \Delta t) = p_a(t)[(1 - \mu_2 \Delta t)(1 - \mu_4 \Delta t)] + p_c(t)\mu_1 \Delta t + p_h(t)\mu_3 \Delta t,
\]

and

\[
\frac{p_a(t + \Delta t) - p_a(t)}{\Delta t} = -(\mu_2 + \mu_4)p_a(t) + \mu_1 p_c(t) + \mu_3 p_h(t) + \mu_2 \mu_4 p_a(t) \Delta t.
\]

Taking the limit as \( \Delta t \) approaches 0 yields

\[
\frac{dp_a(t)}{dt} = -(\mu_2 + \mu_4)p_a(t) + \mu_1 p_c(t) + \mu_3 p_h(t).
\]  \hspace{1cm} \text{(3.13)}

**COLD INACTIVE**

\[
p_a(t + \Delta t) = p_a(t)(1 - \mu_2 \Delta t) + p_c(t)(\mu_3 \Delta t),
\]
and
\[
\frac{p_i(t + \Delta t) - p_i(t)}{\Delta t} = -\mu_1 p_i(t) + \mu_2 p_a(t).
\]

Taking the limit as \( \Delta t \) approaches 0 yields the differential equation
\[
\frac{dp_i(t)}{dt} = -\mu_1 p_i(t) + \mu_2 p_a(t). \tag{3.14}
\]

HOT INACTIVE
\[
p_a(t + \Delta t) = p_a(t)(1 - \mu_3 \Delta t) + p_4(t) \mu_4 \Delta t,
\]
and
\[
\frac{p_a(t + \Delta t) - p_a(t)}{\Delta t} = -\mu_3 p_a(t) + \mu_4 p_a(t).
\]

Taking the limit as \( t \) approaches 0 yields
\[
\frac{dp_a(t)}{dt} = -\mu_3 p_a(t) + \mu_4 p_a(t). \tag{3.15}
\]

Equations (3.13) to (3.15) are differential equations describing the time-dependent behavior of the proportions of enzymes in each state. The mean rates \( \mu_i \) in these equations are also functions of time as given by the Eyring Equation (3.9). Thus, this system is extremely difficult to solve for the transient behavioral proportions \( p_i(t) \). Assuming, however, that the transient phase is of short duration relative to the total developmental time, the steady-state proportions can be obtained by recognizing that \( dp_i(t)/dt = 0 \) in steady state. This yields the three equations
\[
-\mu_1 p_i + \mu_2 p_a = 0;
\]
\[
(\mu_2 + \mu_4)p_a + \mu_3 p_i + \mu_3 p_h = 0;
\]
\[
-\mu_3 p_h + \mu_4 p_a = 0.
\]

where \( p_i \) is the asymptotic value of \( p_i(t) \), and \( p_i + p_a + p_h = 1 \). Solving for the proportion of the control enzymes in the active state yields
\[
p_a = 1/(1 + e^{\omega_1 \tau} + e^{\omega_2 \tau} + e^{\omega_3 \tau}),
\]

Substituting Equation (3.9) for each \( \mu_i \), and rearranging terms yields
\[
p_a = 1/(1 + e^{a_1 \tau} + e^{a_2 \tau} + e^{a_3 \tau}),
\]

where the \( a_i \) are aggregate constants incorporating the unknown parameters of (3.9). The developmental equation is completed by multiplying the developmental rate for active enzymes by the proportion of the enzymes in the active state. The final result (Equation 3.12) is equivalent to the equation derived by Sharpe and DeMichele (1977).

3.3 Distributions of Development Times

Poikilo therm developmental completion for a group of individuals of identical age (a cohort) and environmental conditions are distributed over a range of completion times. This dispersion of developmental times is frequently ignored, with only a mean-value rate function being utilized. For certain organisms the range of the variation is significant in comparison to the mean. For the boll weevil, the standard deviation of the egg to adult emergence time averages about 16% of the mean value. Thus, for a typical summer development time of three weeks, the weevils would emerge over a period from two weeks to one month from the time of oviposition. Such variations are normal among biological organisms and greatly increase the difficulty of selecting the timing of such control measures as insecticide applications.

Concern has recently centered on predicting the developmental completion time distribution. For constant temperature regimes, these emergence distributions appear to have similar shapes, though the actual values vary greatly with temperature. Figure 3.7 displays three constant temperature boll weevil egg to adult emergence distributions. For variable temperature regimes, the developmental distributions may have a totally different form from that of a constant temperature regime. This difference is illustrated by comparing the distributional forms in Figures 3.7 and 3.8. The multimodal aspect of the distribution in Figure 3.8 is an expression of the variable temperature responses. The number of modes in the distribution vary according to
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Examples are provided by the work of Friend et al. (1962, 1963) who found that floral initiation, heading and anthesis in Marquis wheat were earlier at higher temperatures (up to 30°C) and higher light intensities. Final plant dry weight was greatest at the low temperatures. Barley, grown by Power et al. (1970) at a constant air temperature with soil temperatures of 9, 15 and 22°C, reached maturity in 79 days at 22°C but needed 92 days with a soil temperature of 9°C. Once internode elongation starts, the temperature of the barley apex is controlled by that of the air, so it is not clear why the lower soil temperature delayed the attainment of maturity, unless development rate was reduced by decreased supplies of water and nutrients from the roots and by alteration of hormone balances.

The expression of the genetic potential of plants may be affected by water stress, and moderate levels of water stress may cause a shift towards the reproductive phase in plants; for example, summer drought often results in prolific flower bud development in apple trees (Luckwill, 1970). Landsberg and Thorpe (1975) suggest that this is a result of reduced gibberellin production. In grain crops, such as barley, water stress will delay inflorescence formation (Slattery, 1969). In a paper cited by Slattery, Whiteman and Wilson (1965) reported that the development of sorghum inflorescences was suspended by water stress, yet development was resumed on re-watering, leading to flowering heads not significantly different from those in control plants.

Hormones obviously play an important part in the regulation of plant development and a clear understanding of their role and manner of action in any given situation would greatly enhance the possibility of useful mathematical formulation of the developmental process under study. Warding (1971), discussing the role of hormones in differentiation, says that “it would appear possible that hormones affect gene activation and repression”, but the response to hormones depends upon the level of competence of the tissue affected by them, and the extent to which the pathway of differentiation of that tissue is already determined. Waring and Phillips (1970) suggest that hormones might play an important role at some step in enzyme synthesis, without determining which genes are activated at any given time or place, or they might affect the activity of an enzyme.

The concepts of “competence” and “determination” are useful in considering developmental processes. Before they can respond to a stimulus which shifts the genetic control, cells must be in a state in which they are competent to do so. Competence may be an “all or nothing” state or it may be quantiative. For example, if dormant buds of woody plants are transferred to warm conditions soon after becoming dormant, bud break will not occur, or at least not for a long time, but if the buds are kept in cold conditions before being transferred to warm conditions, bud break and subsequent development will occur and will proceed more rapidly (under the same warm conditions) if the cold period was long than if it was short. We might say that, in general, if progression towards competence is still going on when the stimulus, or switch which initiates a change in the direction of development is applied, the organism will respond, but not as efficiently as if the changes which lead to competence in the tissue or organ had been completed. In the example given there is, of course, a limit to the useful length of the cold period. The changes which take place in the bud during vernalization probably involve changes in the balance of hormones.

This process of progression towards competence has been described mathematically (Landsberg, 1974) for apple buds; vernalization in Lolium perenne (analysed later) provides another example. The end of the juvenile phase in trees appears to provide an example of a relatively abrupt transition to a state of competence, although different parts of the same plant body may be in different, stable, phases (Waring and Phillips, 1970). In an attempt to analyse a developmental process in terms of progression towards, and the attainment of, competence, we need to identify the factors which control such progression, the end point, and the stimulus which causes the switch into a new pathway of differentiation.

“Determination” of the direction of development implies that once an organ passes a certain stage of development it becomes irreversibly committed, and cannot be converted into any other structure.

**QUANTIFYING PLANT DEVELOPMENT**

One of the main problems in modelling developmental processes is that of choosing units. At the molecular and cellular levels development is a matter of enzyme synthesis and the differentiation of cells, at the plant level it is a matter of organ formation and growth. Plant growth models can be written in terms of the accumulation of mass, but we cannot put units to enzyme synthesis or numbers to cell divisions when we are dealing with whole plants. Therefore we must often work in terms of events or arbitrary “development units”.

A valuable, but unfortunately apparently little known, contribution has been made in this area by the work of Sarvas (1972, 1974). He divided physiological events into two categories:

- i. point events, i.e. events which have taken place or have not; and
- ii. segment or stage events, i.e. events or stages which either have not been reached, or have been reached but not passed through, or have been passed through.

Sarvas applied these concepts in his investigations on the annual cycle of development of forest trees, using them, essentially, as a means of overcoming the conceptual problems which arise with “heat units” or “day-degrees”.

The use of day-degrees normally involves starting from some arbitrary date or starting point and summing the daily mean temperature above some base value until a given event (P) occurs, e.g. flowering. It is generally possible to establish,
within limits, the number of day-degrees required for the event to occur, and for this reason the method, despite the fact that the units are physically and physiologically meaningless and the whole approach entirely empirical, has been widely used and has undoubtedly been useful. In effect the calculations are based on the equation

$$P_1 \to P_2 = c \cdot \sum_{i=1}^{n} (T_i - T_0) \Delta t_i$$  \hspace{1cm} (1)

where $c$ = constant, $T_i$ = temperature of the $i$th day, $T_0$ = a base, or limiting temperature and $\Delta t_i$ = time interval, in days.

Equation (1) is in fact an empirical estimate of

$$P(t) = \int_{t_i}^{t_f} f(T) \cdot dt$$  \hspace{1cm} (2)

(where $P(t)$ denotes the stage reached at time $t$) which follows from the fact that

$$\frac{dP}{dt} = f(T)$$  \hspace{1cm} (3)

Sarvas (1972) recognized this and wrote

$$P_1 \to P_2 = v(T)(t_2 - t_1)$$  \hspace{1cm} (4)

where $P_1$, $P_2$ = point events and $v(T)$ = the rate at which the physiological phenomena proceed at temperature $T$. Now, $v(T)$ (units/h) may be determined from careful studies in controlled environments, leading to the useful relationship

$$v(T) = v(T_P) \cdot \frac{b_p}{b_T}$$  \hspace{1cm} (5)

where $b_p$ = time (hours) required for the cycle to pass through a given cycle interval at some reference temperature $T_P$, and $b_T$ = the time required to pass through the same cycle interval at temperature $T$.

From equation (4) we may write

$$P(t) = \int_{t_i}^{t_f} v(T(t)) \cdot dt$$  \hspace{1cm} (6)

for fluctuating temperatures, or, in finite difference form,

$$P(t) = \sum_{i=1}^{n} v(T_i) \cdot \Delta t_i$$

These equations can be solved in practice, and furthermore the units of the process under study can be given some physiological meaning; Sarvas (1972) used cell division to define his point events but many other parameters could be envisaged.

In an independent approach to this problem of quantifying development (Landsberg, 1974) equations (2) and (3) were explicitly recognized, but arbitrary "development units" were used in a model in which apple fruit bud development was related to temperature. The form of $f(T)$ was assumed, whereas in Sarvas' approach it can be defined by experiment.

There are many developmental processes which can be quantified in terms of readily observed phenomena; in examples discussed later, tillering in barley is analysed in terms of the number of tillers which develop, flowering in ryegrass in terms of the rate of inflorescence development, which could be defined in terms of inflorescence size, number of florets etc., and apple bud morphogenesis is analysed in terms of the number of primordia in the bud. (The use of size as a developmental parameter must always be regarded with some suspicion—the line between development, involving differentiation, and growth is not always clear and equating development with the accumulation of mass may not clarify matters.) Point events which occur after some recognizable stimulus (e.g. daylength) causes a change in the direction of differentiation should be fairly easy to recognize; on the scale of a whole plant the production of floral primordia in buds or the activation of axillary meristems in grass, indicating the passage into flowering, provide some good examples.

In any particular study it will be necessary to consider all the factors which affect the developmental process(es), and how they affect it, i.e. is there a vernalization requirement (quantitative or absolute), does temperature affect the rate of development after vernalization, do radiant energy and nutrition play a role (competition?), what are the effects of water deficits, how do the various first-order factors interact, is there a switch, and if so what activates it and is the response abrupt or "fuzzy"? Point and segment events should be defined as clearly as possible. It will generally be useful to consider the mechanisms of the developmental process at the most basic practicable level; for example, if hormones are known to be involved, is there a balance of hormones which can be measured, or are there measurable changes in nucleic acid composition or enzyme complements? (These may be important and useful if enzyme complements are organ-specific.) If such changes can be identified they can be quantified and formulated.

In an attempt to illustrate some of the ideas discussed so far, the remainder of this paper will be devoted to the analysis of several "case histories" of plant development.

**ANALYSES OF SOME DEVELOPMENTAL PROCESSES**

**TILLERING IN BARLEY**

Aspinall (1961) showed the initiation and growth of tillers in barley to be very largely controlled by nutrient supply. His data provided the basic for...
hypotheses about genetic control of switching systems, but they do provide an illustration of the manner in which environmental factors control the expression of genetic potential, so that, with some unexceptionable assumptions, we can formulate the developmental pattern. Aspinall’s main results are shown in Fig. 1, where the variations in rate of tiller production, as influenced by the nutritional treatments, are illustrated.

The work was done in an open-sided glasshouse, so there is no information on the effects of temperature and light energy on the rate of tiller production, but some indication of their effects is provided by Aspinall and Paleg (1963) who found that the rate of production of floral primordia, on the apex of the main axis of barley plants, increased as both light intensity and daylength increased. Therefore, denoting the rate of tiller production as \( dS/dt \), we may write

\[
\frac{dS}{dt} = f(N, T, I)
\]

where \( t \) = time, \( N \) = nutrient concentration, \( T \) = temperature, and \( I \) = light intensity.

The equations which follow do not allow for interaction, and equation (7) can be written

\[
\frac{dS}{dt} = S_{\text{max}} \cdot f(N) \cdot f(T) \cdot f(I)
\]

where \( S_{\text{max}} \) is the maximum possible rate of tiller production, attained when all factors are at optimum levels, and \( f(N) \), \( f(T) \) and \( f(I) \) will have values varying between zero and unity. Now for the sake of the argument let us assume, on the slender evidence of the curves in Fig. 1, that \( dS/dt \) may be described by a Michaelis–Menten type relation, viz.

\[
f(N) = \frac{dS}{dt} = \frac{1}{1 + K/N}
\]

where \( K \) is the Michaelis constant. Let us also assume, from general knowledge, that the rate of tiller production is a function of temperature, which can be described by a normal curve, i.e.

\[
f(T) = \frac{dS}{dt} = \exp\left(-\frac{(T - T_{\text{opt}})^2}{\sigma^2}\right)
\]

where \( T_{\text{opt}} \) is the optimum temperature and the parameter \( \sigma \), which controls the width or spread of the curve, is in degrees Celsius. The rate of assimilate supply is a function of light intensity, hence

\[
f(I) = \frac{dS}{dt} = \frac{1}{1 + (I/b)}
\]

Equation (10) is, of course, the simple rectangular hyperbola often used to describe photosynthesis rate; \( S_{\text{max}} \) may depend on leaf area and plant volume, and the “constant” \( b \) of the hyperbola may change with time, but these are slowly varying parameters compared to \( I \).

Equations (8) to (10) may now be combined into a single expression to describe the manner in which environmental factors are likely to affect the expression of the genetic potential of barley in terms of tiller production:

\[
\frac{dS}{dt} = \frac{S_{\text{max}} \cdot \exp\left(-\frac{(T - T_{\text{opt}})^2}{\sigma^2}\right)}{1 + (K/N) \cdot (1 + b/I)}
\]