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Plant Growth Analysis: a Program for the Fitting of Lengthy Series of Data by the Method of *B*-splines*

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ABSTRACT

A method is presented for fitting curves to lengthy and/or complicated series of data on plant growth. A computer program which derives the usual plant growth analytical quantities, and their errors, from these fitted curves is also described and offered for circulation. The fitted curves are splined cubic polynomial exponentials. Examples of their application are given, employing both real and artificial data. In any set of data the number of splines, and the position of the knots joining them, may be determined either by objective statistical tests or by the experimenter himself, who thus retains a considerable degree of control over the process but can call on the assistance of the program if required. The value of this method is considered in relation to other curve-fitting approaches to plant growth analysis and it is concluded that, provided sufficient primary data are available, the method is free from many of the problems which beset earlier work in this field, and also provides new possibilities of its own.

Keywords: growth curves, approximating functions, empirical models, regression analysis, growth analysis.

INTRODUCTION

The use of fitted curves in describing plant growth has itself become a growth industry. Hunt (1979) cited over 20 recent publications concerned with methodology alone. It was suggested that curve-fitting chiefly provides the experimenter with a clearer perception of the reality of plant growth when a series of observational data is disturbed by random errors. Among 12 secondary advantages identified were the possibility of interpolation and a sounder statistical basis for the estimation of errors. In most cases the curve is needed not only to provide a convenient redescription of the primary data but as an instrument for the derivation of the quantities involved in plant growth analysis (Radford, 1967; Květ, Ondok, Něcas and Jarvis, 1971; Evans, 1972; Hunt, 1978).

The present paper is particularly concerned with the analysis of lengthy and/or complicated series of data. Its immediate links are with the more general work of Hughes and Freeman (1967) who advocated the use of the third order polynomial exponential (a cubic polynomial fitted to logarithmically transformed data, Causton, 1967, 1970), with that of Nicholls and Calder (1973) and Hunt and Parsons (1974) who stressed the importance of the greatest possible simplicity in the choice of polynomial exponential, and with that of Causton, Elias and Hadley (1978) and Venus and Causton (1979) who advocated the use of the Richards function (Richards, 1959). Important adjuncts such as the balance between the experimenter's 'biological expectation' and statistical exactitude have been dealt with by Hurd (1977), Hunt (1979) and Venus and Causton

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(1979) and the influence of data variability in determining the 'best' statistical model by Elias and Causton (1976).

The methods to be described here, which were foreshadowed by those of Hunt and Parsons (1977), were designed to form the ultimate in a series which progresses, according to the nature of the data in hand, from the methodology of Hunt and Parsons (1974) through that of Venus and Causton (1979) to that presented here. We give a general account of the approach, with a limited number of examples. For a fuller series of applications see Hunt and Evans (1980).

SPLINE FUNCTIONS

The spline function has been likened by Erh (1972) to the more familiar draughtsman's spline, a long, flexible strip used for drawing smooth curves through a set of specified points. In the mathematical spline, the flexible strip is replaced by a chain of separate polynomial functions, each of degree n. Although discrete, neighbouring functions meet at so-called knots. Here they fulfil continuity conditions both in the function themselves and in their first $n-1$ derivatives (Wold, 1974). The root source of this device was the work of Schoenberg (1946); since, it has been developed extensively in the mathematical literature (Ahlberg, Nilson and Walsh, 1967; Greville, 1969). An excellent appraisal of the general value of spline functions in data analysis has been given by Wold (1974). Comparisons with the related technique of sliding polynomials have been made by DuChateau, Nofziger, Ahuja and Swartzendruber (1972) and the applications of the spline function to soil science (Erh, 1972) and to the study of tree geometry (Max and Burkhart, 1976) have also been explored.

The methods of splines was first introduced as an alternative to polynomial curve-fitting, or more complicated methods using non-linear least squares, where the data to be fitted are obviously beyond the reach of a simple polynomial. Rather than raise the order of polynomial to such a degree that spurious over-fitting took place, with a breakdown in the method of least squares, the original workers in the field considered that a well ordered set of low-order polynomials would be a more effective approach. They encountered two problems: firstly, that of positioning the polynomials so that they would best reflect the underlying trends in the data and, secondly, that of using apparently disjointed and somewhat unrelated polynomials to represent arbitrary subsets of the data. The first was solved by creating variables which fixed the range of each polynomial (not necessarily the same for each element in the chain) and by using low orders of polynomial so that the shape of segment of the data could be reflected without over-fitting. The second problem was overcome by constraining the elements at their common end points to agree in position and slope. This provided a smooth transition from one polynomial to the next, resulting in a satisfactory overall fit, both mathematically and visually.

Guided by these general requirements, polynomials of varying degree have been splined together; for example, a mixture of straight lines and constants (see Hudson, 1966), several quadratics (Fuller, 1969) or several cubics (Kimball, 1976). In the special application of plant growth studies, where logarithmically-transformed primary data are all but essential, the cubic is the minimum degree of polynomial that can be considered. This is because the first derivative (relative growth rate) must be free to change smoothly with time, that is, there must be continuity also in the second derivative, rate of change of slope. Splines of lower order cannot possess this feature (see, for example, the Fig. 1 of Fuller, 1969).

There are several possible sets of basic functions in terms of which the cubic spline can be expressed. For any set of these there are three main stages in the spline interpolation problem:

(1) the formation of the system of linear equations defining the coefficients of the basic functions;

(2) the solution of this linear system;
(3) the evaluation of the interpolating spline at various values of the argument.

We have chosen to use the so-called *B*-splines, or fundamental splines, as the basic functions because there are good algorithms available for evaluating unconditionally stable *B*-splines (Cox, 1972; de Boor, 1972), even for multiple (coincident) knots. *B*-splines were first studied, in the particular case of equally-spaced knots, by Schoenberg (1946), and then revitalized 20 years later by Curry and Schoenberg (1966). Several authors, including Anselone and Laurent (1968), LaFata and Rosen (1970), Powell (1970), Herriot and Reinsch (1971) and Schumaker (1969), have discussed the use of *B*-splines in interpolation and smoothing.

The principal value of all spline functions lies in their ability to describe lengthy and complicated trends in which 'the particular form of the true function is *not* known; what is known is that the desired function is smooth' (Wahba and Wold, 1975). Splines have far greater flexibility than single regressions (Max and Burkhart, 1976) and provide 'form-free curve fitting' (Du Chateau *et al.* 1972). They can also encompass data which 'exhibit behaviour in one region that may be unrelated to their behaviour in another' (Kimball, 1976). In common with other forms of regression analysis their great strength is in smoothing and interpolation, but not in prediction. Here, the technique of time series analysis (which requires a data set of an extensiveness not often available to students of plant growth) is more appropriate (Hirschfeld, 1970).

This application of spline functions to plant growth analysis is new. Previous workers have used chains of linear segments to describe the progressions of various plant variables on time (Hammond and Kirkham, 1949; Rao and Murty, 1963; Brewster, Bhat and Nye, 1975) while others have used sliding polynomials for the same purpose (Fisher and Milbourn, 1974). Hunt and Parsons (1977) applied the techniques of Hunt and Parsons (1974) (which proceed to a full evaluation of derived quantities such as relative growth rate, leaf area ratio and unit leaf rate) in a manually-operated, piecewise manner. The present method leads to a more thorough realization of this approach by way of the *B*-spline class of cubic regression, using algorithms developed by M. G. Cox from an original set due to Cox (1972) and Cox and Hayes (1973).

GROWTH ANALYSIS PROGRAM

The program executes a sequence of functions, associated with reading data and variables for controlling knots, computing the positions of unspecified knots, fitting splines to the data based on the knot positions, computing the fitted values, and deriving other quantities from those values, with confidence limits.

Input data

Data are presented in the form of data sets in which sequential values for two variates Y and Z are associated with an independent variate in 'time', or some other measure of progress, which we define as X. As data cards can vary widely within this general format, control cards are also required in order to specify which combinations of values, if any, are to make up the Y and Z sets. The user also supplies cards defining the number and position of knots to be used in the spline fit. Here again, the form of the information is flexible, either allowing the user to specify precisely the number and position of knots on the one hand or, on the other, allowing the program to compute both number and position if desired. Alternatively, a combination of specified and unspecified knot information can be offered, with the program deciding on the unspecified.

Number and position of knots

If the user decides that the program should compute the number of knots, then this is calculated as one quarter of the number of separately-identifiable points, or arrays of points, defined by the X variate. If this number is greater than five then the number of knots computed is limited to five, equally spaced over the range of the data. If the number of knots has been fixed, the user then has the option of fixing the positions of none, any, or all of these knots, then letting the program calculate the unknown positions as required.

Computation of the position of knots is based on the positions of the fixed knots, if any. If no knots are fixed then the positions are set initially to the points that equally divide the range of the data between the number of knots. If only some knots are fixed then the initial positions of the remaining knots are set such that they equally divide the sub-ranges in between the fixed knots by the number of estimated knots required for each particular sub-range. Furthermore, the estimated knots are 'migrated' so that the residual sum of squares after fitting splines is reduced. Migrations of the estimated knot positions is continued until the difference between the residual sum of squares in successive iterations varies by less than a quarter of the previous differences. Iteration stops if the residual sum of squares increases.

This migration routine moves estimated knot positions towards the point of inflexion in the fitted splines in the sub-ranges to which the estimated positions apply. At each iteration the lie of the splines changes slightly as the knots move but the iterations always converge because of the limits set on the rate of change of residual sums of squares. At the end of knot migration the penultimate positions of the knots, and their corresponding splines, are used to compute the derived growth-analytical quantities.

Derived quantities

The first step is to compute and print tables of observed and fitted values of Y against X and Z against X, each with upper and lower 95 per cent confidence limits and residual (observed minus fitted) values. These are followed by tables of relative growth rates of Y, given by $(1/Y)(\mathrm{d}Y/\mathrm{d}X)$, and for Z, given by $(1/Z)(\mathrm{d}Z/\mathrm{d}X)$, each with upper and lower 95 per cent confidence limits. The next table is for derived quantities of the form Z/Y, with upper and lower 95 per cent confidence limits and residuals. Finally, derived quantities of the form $(1/Z)(\mathrm{d}Y/\mathrm{d}X)$ are computed from the identity $(1/Y)(\mathrm{d}Y/\mathrm{d}X)/(Z/Y)$, again with upper and lower 95 per cent confidence limits.

Information on the methods adopted for calculating the limits of Z/Y and $(1/Z)(\mathrm{d}Y/\mathrm{d}X)$ is given in the brochure described below.

Availability

We have prepared a brochure of users' instructions (Hunt and Parsons, 1981), copies of which are available on request. This contains, both for the present program and for the 'stepwise' program of Hunt and Parsons (1974), notes on data formating, on controlling the analyses and on the statistical methods adopted, and also facsimile lineprinter listings of the programs (in 1900–ALGOL), of specimen data and of specimen results.

EXAMPLES

Sources of data

The capabilities of this approach to fitting plant growth curves have been tested in two ways: firstly, by a re-analysis of the classical set of data of Kreusler, Prehn and

Hornberger (1879) [also dealt with by Hunt and Parsons (1977), for reasons given by them] and, secondly, by an analysis of two sets of specially-devised artificial data.

Kreusler's data concern maize (*Zea mays* L.) grown under outdoor conditions at Poppelsdorf near Bonn in the 1870s. The variety Badischer Früh grown in 1878 has again been chosen for attention; this forms part of a series including other varieties and years, comparable analyses of which have been performed as a separate operation by Hunt and Evans (1980). Mean dry weight per plant, $\overline{W}$, was measured weekly over the period 20 May to 10 September 1878. Mean values of total leaf area per plant, $\overline{L}_A$, were measured weekly from 11 June. In the analyses all times were expressed as days in the year, taking 1 January as day one. Primary data for $\overline{W}$ and $\overline{L}_A$ appear in Figs 2(a) and (b).

The artificial data were devised to provide stylized but extensive data sets. One [Fig. 3(a)] suggests the growth of an 'annual plant' (from a large propagule, because of the greater analytical difficulty that this presents) over its entire life cycle. The other suggests the growth in a temperate climate of a 'perennial plant' over its first 3 years [Fig. 3(b)]. Alternatively, the latter may be regarded as a series of diurnal progressions in some frequently-measured variate. In each case the degree of variability in the data was appreciable but not excessive. All units in these particular analyses were arbitrary.

The number and position of knots

These are the only matters upon which the intervention of the experimenter is allowed by the program, but correct decisions on the construction of functions approximating to the primary data are essential if realistic trends in the derived data are to be obtained.

For Kreusler's data we set aside the simplest option of all (equidistant knots up to a maximum of $N/4$, where N is the number of abscissal co-ordinates) and decided to try a variety of knot numbers in the first instance, including 'no knots' (an analysis by the methods of Hunt and Parsons, 1974). The analyses were complicated by the fact that while data for $\overline{W}$ form a series of 17, those for $\overline{L}_A$ number only 14.

Table 1 and Fig. 1 provide the evidence upon which the final choices of knot number and position were based. Since adjacent cubic elements agree not only in position but

TABLE 1. *Tests to find the most suitable number and position of knots*

Number of knots	Residual sum of squares	d.f.	Optimal position(s) of knot(s)
None	1·180	13	—
1	0·595	12	196·5
2	0·378	11	161·9
			212·2
3	0·193	10	165·9
			198·8
			212·9
4	0·121	9	162·6
			185·2
			207·8
			230·4
5	0·165	8	158·8
			177·7
			196·5
			215·3
			234·2

A splined regression was fitted to logarithms of the 17 primary data given for total dry weight per plant by Kreusler *et al.* (1879). The original units for dry weight were g; knot positions are days in the year.

also in their first two derivatives, only one degree of freedom is lost with the addition of each knot, despite the fact that this introduces four new parameters into the approximating function. From Table 1 it is evident that as knot numbers increase, residual sums of squares decrease. But this advantage has to be set against the loss of degrees of freedom, moderate though this may be. There will be a point beyond which

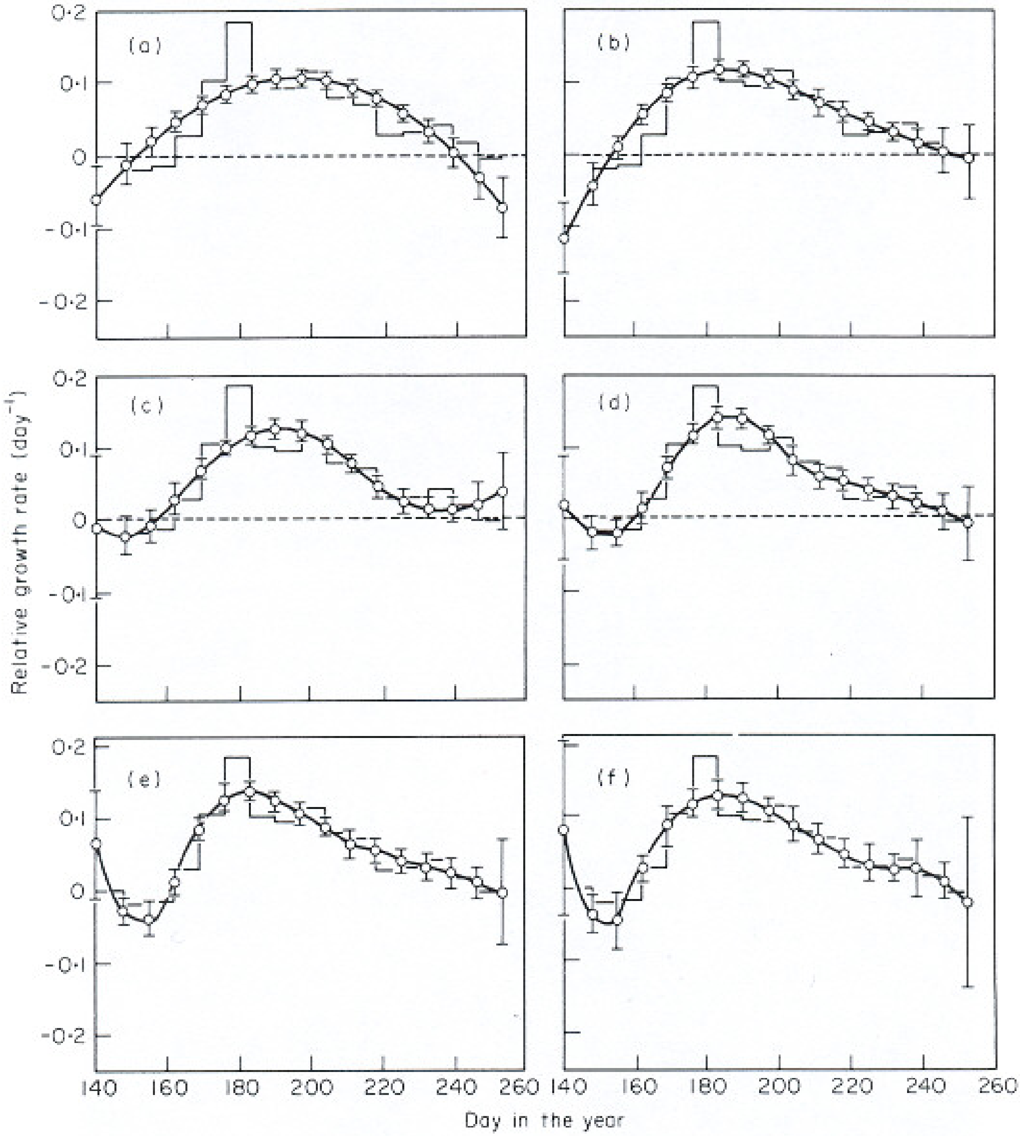

FIG. 1. Relative growth rates in maize calculated from data given for cv. Badischer Früh by Kreusler *et al.* (1879). The splined regressions fitted to the primary data have varying numbers of knots: (a) none (a single cubic polynomial fitted by the methods of Hunt and Parsons, 1974); (b) one; (c) two; (d) three; (e) four; (f) five. Fitted values of instantaneous relative growth rate are plotted, together with 95 per cent confidence limits. In the background to each curve is the progression of mean relative growth rate calculated for the successive harvest intervals. See Table 1 for additional comparisons of varying numbers of knots.

no further increase in knot number is advisable and, depending on individual cases, this may well fall short of the '$N/4$' yardstick. To help to recognize this point, 'observed' and fitted relative growth rates in weight are given in Fig. 1. The 'observed' relative growth rates, $\overline{\mathbf{R}}_W$, are the mean values calculated by the usual method for each period between harvests; the fitted relative growth rates, $\mathbf{R}_W$, are instantaneous values derived from the fitted curves. This provides a far more sensitive indicator of degree of fit than plots of fitted primary data, for on any reasonable scale virtually no differences would be evident amongst fits by splines employing the higher numbers of knots. Figure 1(a) shows that there is pronounced lack of fit in the single cubic polynomial exponential employed by Hughes and Freeman (1967) or chosen ($P < 0{\cdot}05$) by the program of Hunt and Parsons (1974). This part of the figure is a repeat of the Fig. 1(d) of Hunt and Parsons (1977). With one knot in a splined regression [Fig. 1(b)] the 'observed' trend in $\bar{\mathbf{R}}_W$ is followed in a fairly realistic, but heavily-smoothed, fashion (the initial value of $\bar{\mathbf{R}}_W$, near to zero, is missed). In Fig. 1(c) the repeated changes of slope in the primary data are modelled more successfully by the two-knot spline but spurious values of $\mathbf{R}_W$ appear at the end, no doubt due to more important constraints placed upon the splines in other parts of the progression. With three knots [Fig. 1(d)] the approximating function gains sufficiently in flexibility to follow the macroscopic trend in $\bar{\mathbf{R}}_W$ in a wholly realistic way. With four and five knots, small-scale detail begins to be pursued by the function but loss of degrees of freedom leads to widening of confidence limits throughout [Figs 1(e) and (f)].

Arguments such as these can, we suggest, be applied in order to determine the most apposite models even though it is the primary, not the derived, data which are fitted in this approach. In this case we settled for three knots in the fits to $\log_e \bar{W}$ with positions determined by the objective 'migration' process described in the previous section.

When dealing with data for $\log_e \bar{L}_A$ we found two knots sufficient and re-fitted the 14 corresponding values of $\log_e \bar{W}$ with a two-knot curve in order to obtain estimates of leaf area ratio and unit leaf rate. The two-knot curves both for $\log_e \bar{W}$ and for $\log_e \bar{L}_A$ had knots at 192·3 and 222·7 days; in neither case could the 'equidistant' positions be improved on by migration.

For both sets of artificial data we adopted five knots, firstly because the progressions were extensive (33 abscissal co-ordinates) and, secondly, because we wished to demonstrate a high degree of flexibility without over-riding regard for size of confidence limits. Equidistant knot positions were used.

Results of analyses

In the case of the data for maize, Fig. 2 gives progress curves (a) for the logarithms of dry weight and (b) for the logarithms of leaf area; (c) for relative leaf area growth rate, $\mathbf{R}_L$; (d) for leaf area ratio, **F**; and (e) for unit leaf rate, **E**. Fig. 1(d) may be referred to for progress curves in $\mathbf{R}_W$.

Figures 2(a), (b) and (d) show a great number of coincidences between observed and fitted points when plotted on this scale. This is evidence of the close degree of fit which is possible when using spline functions. Values of **E** in the range 6–9 $\mathrm{g\,m^{-2}\,day^{-1}}$ were obtained over the majority of the progression and so $\mathbf{R}_W$ fell largely under the control of **F** which, despite some fairly wide confidence limits (asymmetrical following back-transformation from logarithms), showed a clear maximum in the early part of the series between days 180 and 190. This, in turn, could be traced to a peak in $\mathbf{R}_L$ between days 180 and 190. The progressions in $\mathbf{R}_W$ and $\mathbf{R}_L$ are, over the period which allows direct comparison, very similar in form and magnitude, except that points on the curve for $\mathbf{R}_L$ precede equivalent positions for $\mathbf{R}_W$ by about 10 days. For a fuller discussion of the implications of this difference see Hunt and Evans (1980).

Altogether, the data provide clear evidence that the continuing performance of the whole plant is largely determined by the pattern of deployment of its leaf area and not by ontogenetic variation in the efficiency of its leaves as producers of dry material.

Analyses of the two sets of artificial data appear in Fig. 3. There would again be little advantage in showing spline functions fitted to logarithms of the primary data; instead, successive data points are joined by straight lines, to enable the degree of variability in

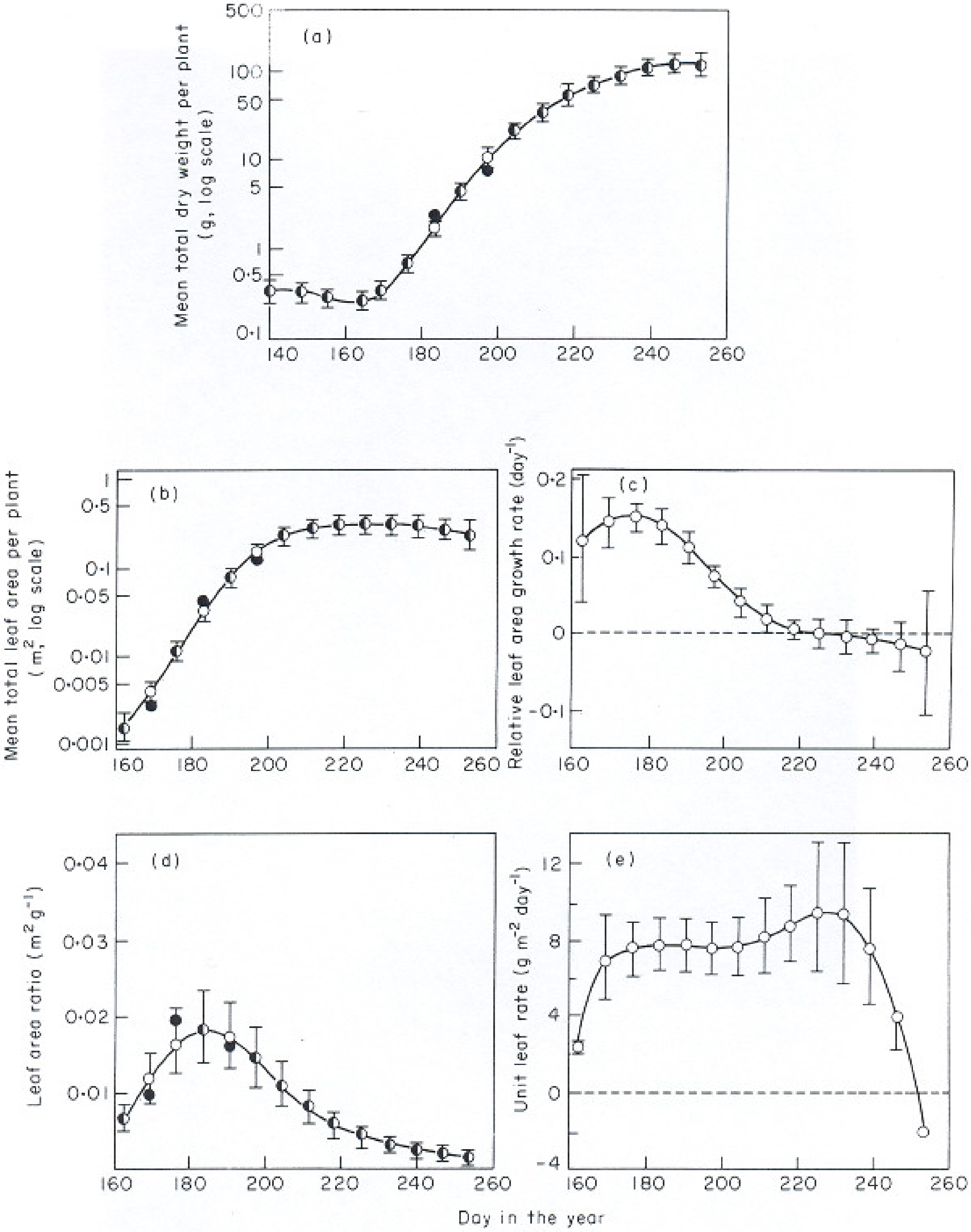

FIG. 2. Primary and derived data on the growth of maize cv. Badischer Früh (Kreusler *et al.*, 1879). (a) Splined cubics fitted to data for $\log_e \overline{W}$ from days 140 to 253 inclusive (three knots); (b) a two-knot fit to $\log_e \overline{L}_A$ from days 162 to 253 inclusive; (c) instantaneous relative leaf area growth rates derived from (b) [for a plot of instantaneous relative growth rate derived from (a) see Fig. 1(d)]; (d) leaf area ratio; (e) unit leaf rate, values of limits not plotted at 246 days are 69·4 and at 253 days −41·9 and 35·6. Throughout, closed symbols represent observed data, open symbols represent fitted data and half-closed symbols represent coincident points. Fitted data bear 95 per cent confidence limits.

the data to be visualized more clearly. But the fit provided by the splines is so close that even at the maxima in these long series of logarithmically-transformed data the observed values of the *untransformed* primary data, to take Fig. 3(a) as an example, lie no further than 18 per cent away from the fitted values. Values of $\mathbf{R}_W$, derived from the fitted splines, are also shown in Fig. 3, with 95 per cent confidence limits.

The artificial primary data given in Fig. 3(a) for an 'annual plant' possess many of the features of previous sets of data for maize, except that (1) the loss of weight following establishment is even more marked, (2) a long, declining plateau in $\log_e W$ is sustained during the plant's maturity, and (3) dry weight finally falls away completely. The progression of $\mathbf{R}_W$ has no difficulty in establishing negative growth in the period 1 to 5 time units and the shallowly-declining plateau between 21 and 27 time units is also significantly negative in slope ($P < 0{\cdot}05$). Despite rapid changes in dry weight after 27 time units, values of $\mathbf{R}_W$ remain stable and coherent (the final two values, which would unduly bias the scale of the diagram were they to be included, are $-2{\cdot}31 \pm 0{\cdot}19$ and $-2{\cdot}66 \pm 0{\cdot}73$ time^{-1}).

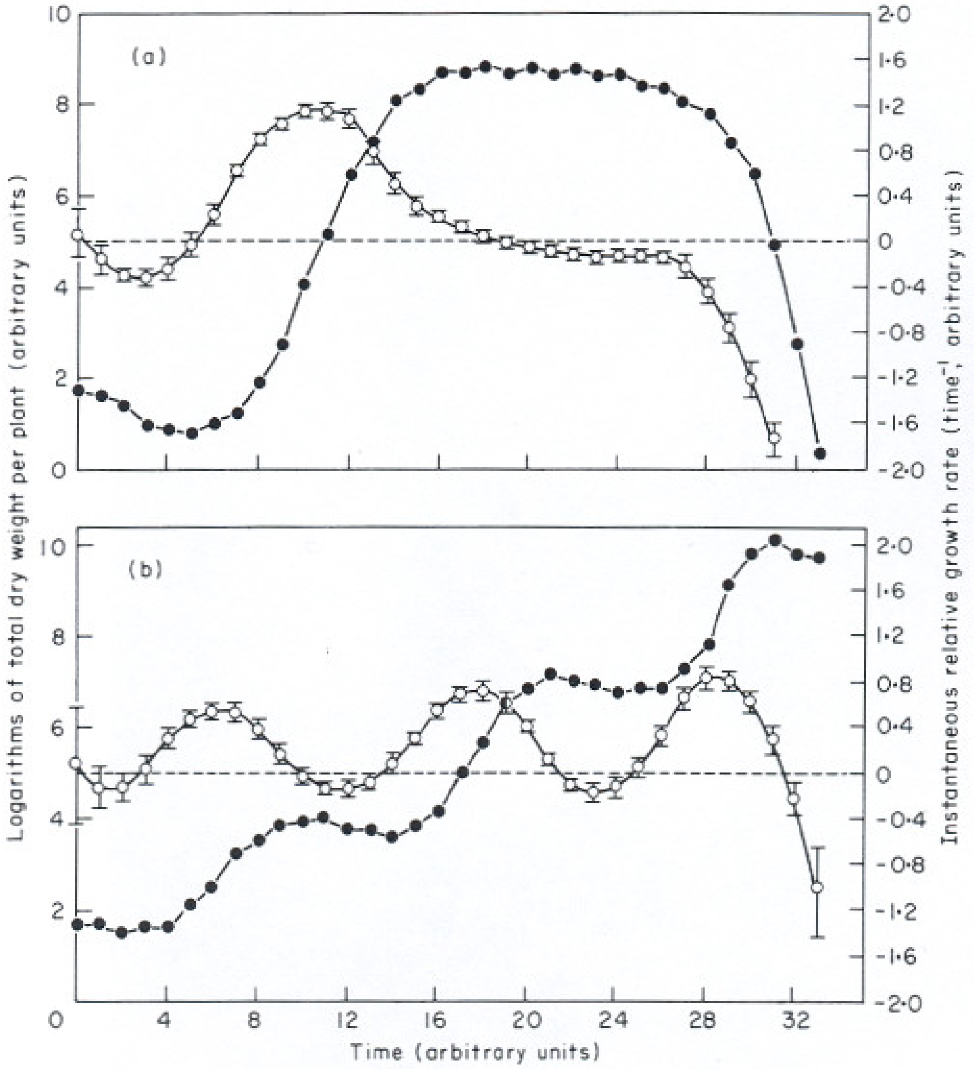

FIG. 3. Specimen analyses of artificial data. Solid symbols represent logarithms of primary values of W; open symbols represent relative growth rates, with 95 per cent confidence limits, derived from five-knot splines fitted to the logarithm of W. The primary data are stylized representations of the growth of (a) an annual plant over its whole life-cycle, (b) a perennial plant over its first 3 years. All units are arbitrary.

The artificial 'perennial plant' (or series of diurnal progressions) exemplified in Fig. 3(b) has repeated changes in the sign of $\mathbf{R}_W$. The shallow troughs in the progression of $\log_e W$ on time contain significantly negative growth ($P < 0{\cdot}05$) and there are even significant differences in the heights of the 'annual' peaks in $\mathbf{R}_W$. The very last value of $\mathbf{R}_W$ in the series reflects more the lack of subsequent information at this point than a spurious trend. For a discussion of real data of this type, involving 60 hourly harvests for total dry weight per plant, see Hunt (1980).

DISCUSSION

It is clear that the methods given here provide entirely satisfactory ways of representing continuous data sets which for reasons of length or complexity lie beyond the reach of the methods of Hughes and Freeman (1967) or of Hunt and Parsons (1974). Examples have been given of the successful analysis of single data sets ranging in complexity from moderate [Fig. 2(b)] to high [Fig. 3(b)]. Yet again we see how an improved quality of fit is much less evident in the primary than in the derived data (see Hunt and Parsons's, 1974, figs 1 and 2; Hunt and Parsons's, 1977, figs 1(c) and (e); Venus and Causton's, 1979, table 1 and the present Fig. 1).

On the number and positioning of knots, our experience of the use of spline functions in plant growth analysis has so far led us to support Wold's four main rules of thumb (1974): (1) have as few knots as possible; (2) have not more than one maximum or minimum and one inflexion per interval (constraints imposed by the cubic elements themselves); (3) have maxima or minima centred in the intervals; (4) have knots close to inflexions.

The method has, for the first time, extended the considerable advantages of the functional approach to plant growth analysis (Hunt, 1979) into areas where extensive data sets prevail. We see no realistic uppermost limit to the length or complexity of data which can be approached in this way since there is no maximum to the number of knots allowed by the present program.

In relation to the other functional approaches to plant growth analysis mentioned in the Introduction, the consideration which chiefly puts the present methods into perspective is the number of available observations (abscissal co-ordinates). We believe that the lowest order possible of polynomial exponential should be used for series of up to about six observations (methods of Hunt and Parsons, 1974), which include as a special case the approach of Hughes and Freeman, 1967). The strength of the Richards function (Venus and Causton, 1979) necessarily lies in series of upwards of about five or six observations. This function also has the special property of being asymptotic: this is indispensible if needed, for example when dealing with individual organs of the plant (Causton and Venus, 1980), but harmful if not. The present splines will become increasingly useful upwards of about 12 observations, with no real upper limit as indicated above. For approaches other than splines, these upper limits may be raised if trends, although lengthy, are unusually simple in form.

Finally, it should be noted that the examples given in this paper have deliberately been chosen to illustrate only the most fundamental properties of the method. They have neglected to illustrate how the program might be used to satisfy the frequent requirement of making comparisons among a family of related data sets. Here, the publication by Hunt and Evans (1980) forms an important adjunct since it demonstrates that splined regressions can overcome a notable difficulty: that of providing biologically-realistic families of related curves while retaining sufficient flexibility to ensure a high degree of statistical exactitude in the fits to individual progressions.

With the addition of the splined regression the field has gained a powerful and flexible new technique and it is possible that, although great refinements will be needed to make the various approaches more homogeneous, this has bridged the last area of major difficulty.

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