

# Plant Growth Analysis: Second Derivatives and Compounded Second Derivatives of Splined Plant Growth Curves

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## ABSTRACT

Recent work employing splined cubic polynomial exponentials as fitted plant growth curves has been extended to include the second derivatives of the splines and their variances. For variates  $Y$  and  $Z$  plotted against time,  $T$ , three new quantities have been derived: (1) the RGR-rate, or the acceleration of  $\ln Y$  in  $T$ ,  $d\{[(1/Y)(dY/dT)]/dT$ , and similarly for  $Z$ ; (2) the relative acceleration rate,  $(1/Y)(d^2Y/dT^2)$ , and similarly for  $Z$ ; and (3) the unit acceleration rate,  $(1/Z)(d^2Y/dT^2)$ . A computer program which derives these quantities, and their errors, from splines fitted to experimental data is described and offered for circulation, and the biological relevance of the new quantities is exemplified by means of analyses of both classical and new data.

Key words: growth curves, approximating functions, empirical models, second derivatives, regression analysis, growth analysis.

## INTRODUCTION

Plant growth analysis, *sensu lato*, involves the quantitative study of the performance of plants or plant components, integrated both throughout the system under study and across ecologically or agronomically-meaningful intervals of time. Ratios, rates, compounded rates and integral durations are its stock-in-trade and many studies in this field now employ fitted 'growth curves' (Hunt, 1979; Causton and Venus, 1981; Hunt, 1982*a*).

One recent methodological contribution to the analysis of lengthy and/or complicated series of data was provided by Parsons and Hunt (1981). They exploited the highly-advantageous properties of splined cubic polynomial exponentials (chains of third-order polynomials fitted to logarithmically-transformed data, with adjacent polynomials agreeing in position, slope and rate of change of slope; Wold, 1974). Examples of practical applications of this method have been provided by Hunt (1980) and Hunt and Evans (1980).

The present work developed from that of Parsons and Hunt (1981) and involves the second derivative, or rate of change of slope, of the cubic splines. Though double-differentiation of fitted growth curves is not new mathematics, it is new plant growth analysis since hardly any of the mathematical functions hitherto used in this context have been able to support the burden of double-differentiation without a substantial, or complete, erosion of form. Cubic splines can, on the whole, withstand this treatment and yet remain useful comparative tools. So they make accessible the advantages that the study of acceleration, as opposed to that of velocity, brings to the comparative description and interpretation of plant growth (see, for example, the preliminary work performed in this field by Heath, 1937 and Idris and Milthorpe, 1966).

The basis of this work was a contract put out by UCPE to Dr M. G. Cox of the Division of Numerical Analysis and Computer Science at NPL, Teddington, for the provision of the second derivatives of fitted cubic splines and their variances. This paper describes

the uses to which these newly-available quantities have been put, both alone and in combination with existing derivatives, and by means of both new and classical examples examines the biological utility of second derivatives and compounded second derivatives as comparative tools in plant growth analysis.

## THEORY

### *Algebraic relationships*

(a) *Between existing derivatives.* Two plant variates,  $Y$  and  $Z$ , are sampled sequentially in time,  $T$ . Classically, these variates are total dry weight per plant and total leaf area per plant. However, in view of the fact that this type of analysis is nowadays often extended far beyond this original context, it is better to regard these variates as having general, rather than particular, identities.

Progressions in the two variates may be analysed either in a logarithmically-transformed form or not, and either in the context of plants grown as spaced individuals or of plants grown as a continuously intermingling population, as in a crop. The combination dealt with here is that of logarithmically-transformed data arising from plants grown as spaced individuals. Hunt (1982*a*) included a complementary explanation of the 'functional' approach to the analysis of traditional quantities in the other three contingencies, from which an analysis along the present lines may also be extended if required.

For both variates, an appropriate approximating function is constructed statistically. In the present work this is a splined cubic polynomial, though the following material is general:

$$\ln Y = y(T) \quad (1)$$

and  $\ln Z = z(T) \quad (2)$

The slope, or velocity of  $\ln Y$  in  $T$  is then obtained to provide the relative (or specific) growth rate of  $Y$ ,  $R_Y$ .

$$R_Y = y'(T) = \frac{d(\ln Y)}{dT} = \frac{1}{Y} \cdot \frac{dY}{dT} \quad (3)$$

and a similar derivative exists in  $R_Z$ , the RGR of  $Z$  (this notation follows the unified scheme devised by Evans, 1972). A sub-division is then performed, in which

$$R_Y = \frac{1}{Y} \cdot \frac{dY}{dT} = \frac{Z}{Y} \times \frac{1}{Z} \cdot \frac{dY}{dT} \quad (4)$$

In practice, the quantity  $Z/Y$  is obtained thus for particular values of  $T$ :

$$\frac{Z}{Y} = \exp [z(T) - y(T)], \quad (5)$$

and is often given the symbol  $F$ . Then, employing Eqn (4),

$$\frac{1}{Z} \cdot \frac{dY}{dT} = \frac{y'(T)}{\exp [z(T) - y(T)]} \quad (6)$$

This quantity is often given the symbol  $E$ .

(b) *Between new derivatives.* New work on cubic splines mentioned in the Introduction, has now made available the second derivatives,  $y''(T)$  and  $z''(T)$ . For  $Y$  we can write

$$R'_Y = \frac{dR_Y}{dT} = y''(T) = \frac{d^2(\ln Y)}{dT^2} = \frac{d\left[\frac{1}{Y} \cdot \frac{dY}{dT}\right]}{dT} \quad (7)$$

The new derivate,  $R'_Y$ , is the *acceleration* of  $\ln Y$  in  $T$ , or the velocity of  $R_Y$  in  $T$ . It may be called the RGR-rate for  $Y$ .

Taking the last term in Eqn (7), and employing the rule for the differentiation of a product,

$$\begin{aligned} R'_Y &= \frac{dY}{dT} \cdot \frac{d\left[\frac{1}{Y}\right]}{dT} + \frac{1}{Y} \cdot \frac{d\left[\frac{dY}{dT}\right]}{dT} \\ &= \frac{dY}{dT} \cdot \frac{-\left[\frac{dY}{dT}\right]}{Y^2} + \frac{1}{Y} \cdot \frac{d^2Y}{dT^2} \\ &= -\left[\frac{1}{Y} \cdot \frac{dY}{dT}\right]^2 + \frac{1}{Y} \cdot \frac{d^2Y}{dT^2}. \end{aligned} \tag{8}$$

The first term in the last line of Eqn (8) is, of course, minus the square of  $R_Y$ ; the second is the acceleration of  $Y$  in  $T$ , expressed per unit of  $Y$ . This latter may be called the relative (or specific) acceleration rate for  $Y$ , or RAR, and be given the symbol  $V_Y$ . From Eqn (8) we may thus write

$$V_Y = \frac{1}{Y} \cdot \frac{d^2Y}{dT^2} = R'_Y + R_Y^2. \tag{9}$$

Then, by using  $Z$  in place of  $Y$ , Eqns (7)–(9) may also be employed to derive a  $V_Z$ .

Using arguments analogous to those implicit in Eqn (4), we may next write

$$\frac{1}{Y} \cdot \frac{d^2Y}{dT^2} = \frac{Z}{Y} \times \frac{1}{Z} \cdot \frac{d^2Y}{dT^2}. \tag{10}$$

Here, the last term is the acceleration of  $Y$  in  $T$ , expressed per unit of  $Z$ . This may be called the unit acceleration rate, or UAR, and be given the symbol  $W$ .

It would be inappropriate to derive the complementary quantity  $(1/Y)(d^2Z/dT^2)$  since, in plant growth analysis, quantities  $Y$  and  $Z$  are conventionally chosen so that  $Z$  is (at least partially) responsible for the production of  $Y$ , but not vice versa.

Finally, for practical methods of evaluating  $V$  and  $W$  we may return to the original approximating functions and, employing Eqn (9), write

$$V_Y = y''(T) + [y'(T)]^2, \tag{11}$$

$$V_Z = z''(T) + [z'(T)]^2 \tag{12}$$

and, employing Eqns (5) and (10),

$$W = \frac{y''(T) + [y'(T)]^2}{\exp [z(T) - y(T)]}. \tag{13}$$

In summary, then, there exist two central relationships: the classical one,

$$R_Y = F \times E; \tag{14}$$

and the newly-derived one, involving second derivatives and compounded second derivatives,

$$R'_Y + R_Y^2 = V_Y = F \times W. \tag{15}$$

A synopsis of these quantities and their units is given in an Appendix.

### Statistical relationships

From former work we have, for each particular  $T$ , the estimated variances of  $R_Y$ ,  $R_Z$ ,  $F$  and  $E$  (Hunt and Parsons, 1981), while from new developments we now have

comparably-estimated variances for  $R'_Y$  and  $R'_Z$ . We also have the mean values  $\bar{R}_Y$ ,  $\bar{R}_Z$ ,  $(\bar{R}_Y^2)$  and  $(\bar{R}_Z^2)$ , calculated across all values of  $T$ . Employing Eqn (9) and standard expressions for the variances of sums and of squares we can proceed, for each particular  $T$ , to the estimated variance

$$\text{var}(V_Y) = \text{var}(R'_Y) + \text{var}(R_Y^2) \quad (16)$$

by way of 
$$\text{var}(R_Y^2) = 4 \text{var}(R_Y) \cdot (\bar{R}_Y^2) / \bar{R}_Y^2 \quad (17)$$

and also do likewise for  $\text{var}(V_Z)$ .

Then, employing Eqn (10) and a standard expression for the variance of a ratio we can obtain, again for each particular  $T$ , the estimated variance

$$\text{var}(W) = W^2 \left[ \frac{\text{var}(V_Y)}{V_Y^2} + \frac{\text{var}(F)}{F^2} \right]. \quad (18)$$

Expressions involving covariance terms, and more complicated than approximations (16) and (18), could alternatively be used. However, preliminary tests have proved these frequently to be unstable, leading to negative variances. It is more expedient to use simpler and more robust estimators, for even though the primary derivatives are not statistically independent, neither are their values linked in any definite way. Covariances can be derived separately as a standing check on the validity of this course of action.

Hence, all of the quantities involved in Eqns (14) and (15) can be provided with values and statistical limits from information on position, slope and rate of change of slope ultimately supplied by functions (1) and (2).

#### COMPUTER PROGRAM

A program for executing all of the foregoing series of calculations has been developed as an extension of one described by Parsons and Hunt (1981) and Hunt and Parsons (1981). The input data are presented in the same way, and the same decisions on the number and position of the 'knots' (junctures of adjoining cubic polynomials) are also required of the experimenter (examples of latter have been fully discussed by Hunt and Evans, 1980; Parsons and Hunt, 1981).

After obtaining the appropriate approximating splines, the program computes and prints tables of observed and fitted values of  $Y$  and  $Z$  for every  $T$ , each with upper and lower 95 per cent confidence limits and a residual (the observed minus fitted value). These are followed by tables of instantaneous values of: RGRs for  $Y$  ( $R_Y$ ),  $(1/Y) (dY/dT)$ ; RGRs for  $Z$  ( $R_Z$ ),  $(1/Z) (dZ/dT)$ ; RGR-rates for  $Y$  ( $R'_Y$ ),  $dR_Y/dT$ ; RGR-rates for  $Z$  ( $R'_Z$ ),  $dR_Z/dT$ ; RARs for  $Y$  ( $V_Y$ ),  $(1/Y) (d^2Y/dT^2)$ ; and RARs for  $Z$  ( $V_Z$ ),  $(1/Z) (d^2Z/dT^2)$ ; all of these values are given for every  $T$  and are accompanied by 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  $(1/Z) (dY/dT)$  are computed from the identity  $(1/Y) (dY/dT)/(Z/Y)$ , and UARs for  $Y$  in terms of  $Z$  ( $W$ ),  $(1/Z) (d^2Y/dT^2)$ , are computed from the identity  $(1/Y) (d^2Y/dT^2)/(Z/Y)$ ; again, both bear 95 per cent limits.

Information on the methods adopted for calculating the limits of  $Z/Y$  and  $(1/Z) (dY/dT)$  is given in a brochure by Hunt and Parsons (1981), which may be read in conjunction with the Statistical Relationships outlined above. This brochure includes users' information for the spline program of Parsons and Hunt (1981), (and also for the 'stepwise' program of Hunt and Parsons, 1974) and it has now been followed by a second brochure giving facsimile lineprinter listings of the new program which includes second derivatives and compounded second derivatives, and of specimen results. All of the programs are written in 1900-ALGOL. Copies of the second brochure (Hunt, 1982*b*), and of its predecessor (which will be found an essential adjunct) are available on request.

## EXAMPLES

*Sources of data*

The potential of this analytical scheme has been assessed in two ways: firstly, by a re-analysis of the classical set of data of Kreuzler, Prehn and Hornberger (1879) (also dealt with by Hunt and Parsons, 1977 and Parsons and Hunt, 1981, for reasons given by the former) and secondly, by an analysis of two sets of newly obtained data.

Kreuzler's data concern maize (*Zea mays* L.) grown under outdoor conditions at Poppelsdorf in 1878. These form part of a series including several varieties and years, comparable analyses of which (though excluding any treatment of second derivatives or compounded second derivatives) have been performed by Hunt and Evans (1980). Mean total dry weight per plant,  $\bar{W}$ , and mean total leaf area per plant,  $\bar{L}_A$ , were measured weekly. All times were expressed as days in the year, taking 1 January as day 1. Primary data appear in Figs 1(a) and (b).

The new data were obtained from seedlings of local natural populations of wavy hair-grass [*Deschampsia flexuosa* (L.) Trin.] and annual poa (or annual meadow-grass, *Poa annua* L.) which were raised from seed on alkathene beads floated on solution culture (Hewitt, 1966, pp. 431–2) in a productive, controlled environment (full nutrient solution, 40 W m<sup>-2</sup> visible radiation, 16 h daylength (08.00–24.00 h), 20 °C day, 15 °C night, 70 per cent r.h.). This environment was maintained in a double-shell plant growth room (Rorison, 1964). Time zero was taken as the day of emergence of the coleoptile and for 35 days five or six plants were harvested daily at random from monospecific populations of spaced seedlings for the determination of replicated values of  $W$  and of leaf dry weight per plant,  $L_w$ . These primary data appear in Figs 2(a) and (d).

*Computation*

Two-knot splines were fitted to both of Kreuzler's series of 14 primary data, with knots positioned at days 192 and 223 in an exact repeat of the procedure described by Parsons and Hunt (1981). Single-knot splines were found to be sufficient for each of the more populous, but nevertheless simpler, sets of new data; optimal knot positions were found at day 10 for *D. flexuosa*, and at day 8 for *P. annua*.

*Results—in general*

Complete series of splined fits and derived quantities appear in the following Figures, which for Kreuzler's maize facilitate comparisons of the behaviour of  $\bar{W}$  and of  $\bar{L}_A$  and for the two native grasses place emphasis on interspecific comparisons.

*Results—for Kreuzler's maize*

The progressions for  $\ln \bar{W}$ ,  $\ln \bar{L}_A$ ,  $R_w$ ,  $R_L$ ,  $F$  and  $E$  [Fig. 1(a), (b), (c), (f) and (g) respectively] have been discussed fully by Hunt and Evans (1980) and by Parsons and Hunt (1981). They appear again here only for the sake of background and continuity. Of the three new quantities, in  $R'$  [the RGR-rate, Fig. 1(d)] the lack of continuity of slope between the successive elements in the acceleration makes the knot positions immediately evident to the eye. Initially, acceleration in both  $\ln \bar{W}$  and  $\ln \bar{L}_A$  is positive, though it declines to zero at day 172 in the case of  $R'_L$  and at day 182 in  $R'_w$ . Thereafter, both quantities remain negative, but in the late renaissance of growth suggested by both  $R_w$  and  $R_L$  at around day 222 [Fig. 1(c)]  $R'$  does rise significantly, both in  $\bar{W}$  and in  $\bar{L}_A$ . Neither rise is sufficient to bring the pattern of growth back into positive acceleration, but deceleration is eased significantly, and the more so in  $\ln \bar{L}_A$ . This information is new.

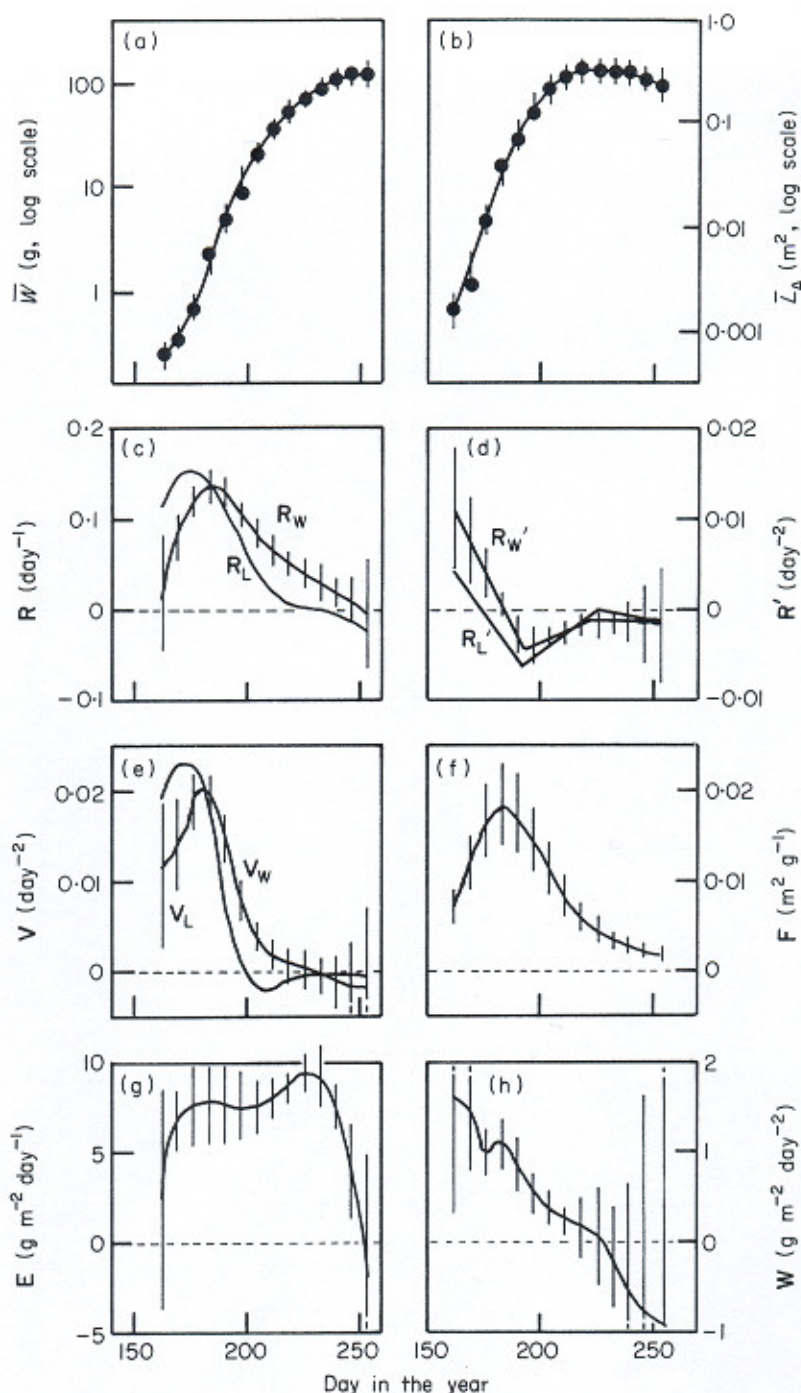


FIG. 1. Observed means and fitted progress curves for (a) total dry weight per plant,  $W$ ; (b) total leaf area per plant,  $\bar{L}_A$ ; and progress curves for instantaneously-derived values of (c) relative growth rate,  $R$ ; (d) RGR-rate,  $R'$ ; (e) relative acceleration rate,  $V$ ; (f) leaf area ratio,  $F$ ; (g) unit leaf rate,  $E$ ; and (h) unit acceleration rate,  $W$ . All fitted and derived data bear 95 per cent confidence limits. Primary data of Kreuzler *et al.* (1879).

Relative acceleration rates [Fig. 1(e)] retreat from the somewhat mechanical behaviour exhibited by  $R'$  because, in addition to incorporating the trend in that derivative, they depend also upon  $R^2$  [see Eqn (9)]. Hence, when either  $R'$  or  $R$  is close to zero,  $V$  is dominated by the other. When  $V$  is positive the variate under consideration is accelerating in either direction; when negative, it is decelerating. The maxima in  $V_W$  and in  $V_L$  each lie a few days earlier than the corresponding maxima in  $R_W$  and in  $R_L$ ,

indicating clearly that the place of these progressions where unit quantities of the primary variates are accelerating most swiftly is not necessarily the place where their logarithms are *changing* most swiftly (later); neither is it where these are *accelerating* most swiftly (earlier, in fact at the very beginning).

The unit acceleration rate [ $\mathbf{W}$ , Fig. 1(h)] has a remarkable progression. Despite wide limits at each end (the inevitable accompaniment to such a highly-derived quantity) it is clear that the most likely overall shape of the progression is that of a uniform decline: the straight line joining the first and last fitted values of  $\mathbf{W}$  passes within the bounds of all of the intervening confidence limits and has a slope of  $-0.028 \text{ g m}^{-2} \text{ day}^{-2}$ . This might perhaps be called the UAR-rate and given the symbol  $\mathbf{W}'$ , a single value encapsulating all of the data displayed in Figs 1(a) and (b). These data encompass a 490-fold change in  $\bar{W}$  and a 170-fold change in  $\bar{L}_A$ , and exhibit such fluid and sinuous progressions as until lately evaded satisfactory attempts at curve-fitting of any kind. Moreover, with the omission only of short periods at either end, these span the entire life history of the plant and incorporate great changes in form and function. All of this is subsumed into a constant  $\mathbf{W}'$ , a single index of the progressive decay in the functional efficiency of total leaf area as a producer of total dry weight.

#### Results—for the two native grasses

When comparing these results with those for maize, three important differences should be borne in mind, apart from the obvious one of there now being a far fuller scheme of harvesting. First, in terms of the life history of the plant, data for the native grasses begin and end sooner. Second, the index of the functional size of the above-ground parts of the plant is not  $L_A$  but  $L_W$ . Third, the environment is constant. These differences have been deliberately sought in order to increase the range of these worked examples. Progressions of  $\ln W$  appear in Fig. 2(a). Not until the plants have displayed sufficient green material to counter early respiratory losses does positive dry weight increase commence. The extent of this dip in the early part of the growth curve depends jointly upon the size of the reserves of the endosperm and upon the inherent velocity of vegetative growth. Though Kreuzler's data as used in this paper show very little of this early dip in  $\bar{W}$  [Fig. 1(a)], Parsons and Hunt (1981) included additional data for  $\bar{W}$  alone (which in the original experimentation preceded the first records of  $\bar{L}_A$  made) and demonstrated a dip in the growth curve which was sustained for over 20 days (that is, until the weight of the initial sample was regained). Part of this large dip will have been due to the slowness of the crop's development in the cool, wet May experienced at Poppelsdorf in 1878, and part due to the relatively large seed reserves of maize (Kreuzler reported a mean, gross dry weight of 328 mg per seed). *D. flexuosa* in the present study had a mean dry weight of 0.43 mg per seed with a dip lasting for 6 days, and *P. annua* a weight of 0.26 mg with a dip lasting for 2 days.

A striking contrast between the two species is evident in Fig. 2(b), where the two progressions of  $\mathbf{R}_W$  are broadly similar in kind but greatly different in degree. With Fig. 2(c),  $\mathbf{R}_W$  rises rapidly to a maximum in both species, though far earlier in *P. annua* (where  $\mathbf{R}'_W$  is zero at 7 days) than in *D. flexuosa* (where  $\mathbf{R}'_W$  does not reach zero until 13 days). Both species then show a more or less linear decline in  $\mathbf{R}_W$  ( $\mathbf{R}'_W$  continuing at, or just below, zero for both). The maximum values of  $\mathbf{R}_W$  are  $0.173 \text{ day}^{-1}$  for *D. flexuosa* and  $0.296 \text{ day}^{-1}$  for *P. annua*. To reach its maximum  $\mathbf{R}_W$  so quickly,  $\ln W$  in *P. annua* initially shows great acceleration:  $0.089 \text{ day}^{-2}$ , or eight times the fastest acceleration shown by maize in Fig. 1(d).

The beginnings of the progressions for  $\ln L_W$  [Fig. 2(d)] are quite different from those shown for  $\ln W$ , for increase in  $L_W$  is continuous. Maximum  $\mathbf{R}_L$  is therefore at the beginning [Fig. 2(e)], and markedly so in the case of *P. annua*, which undergoes a rapid

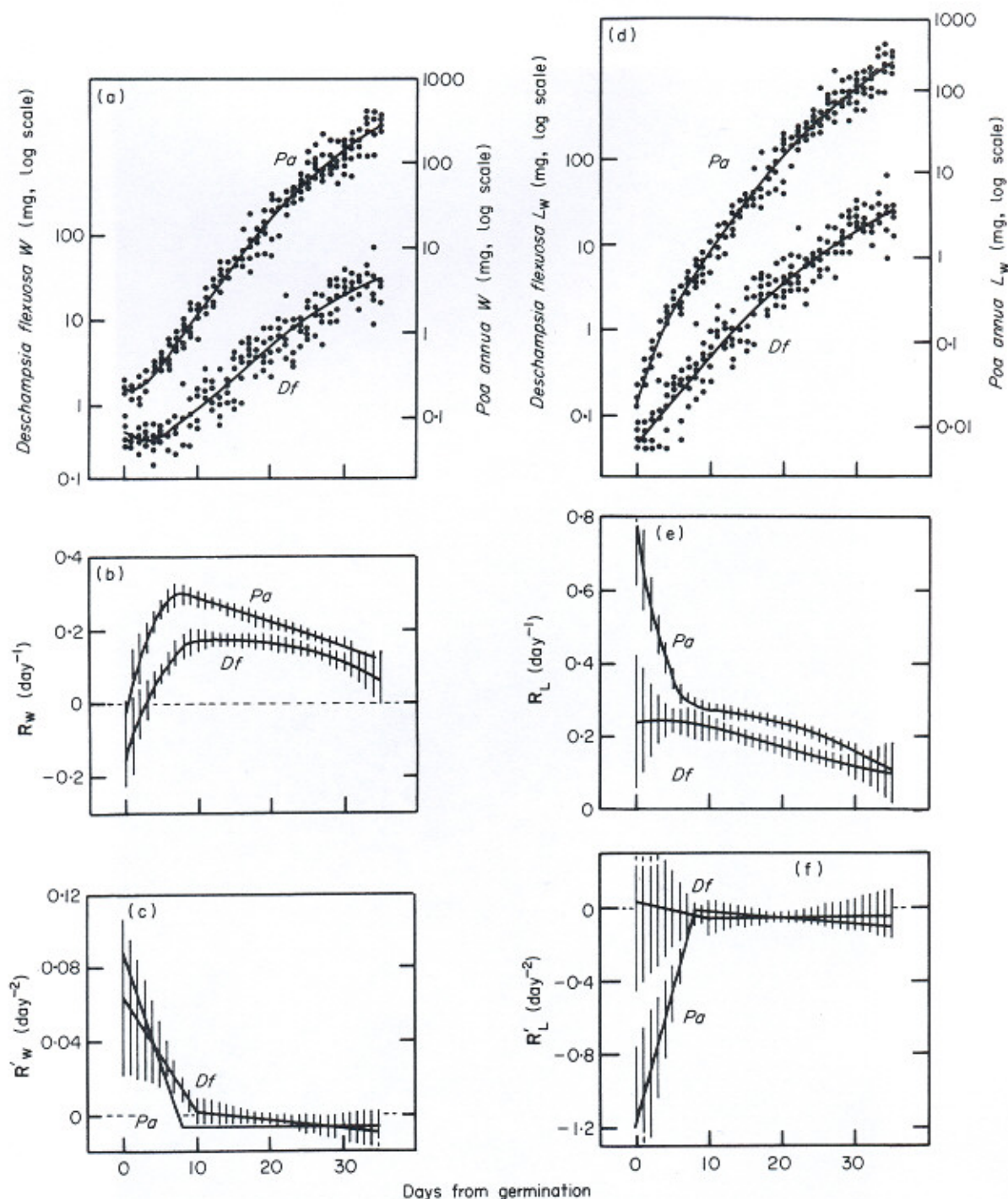


FIG. 2. Progress curves for (a) observed and fitted total dry weights per plant,  $W$ ; for instantaneously-derived values of (b) relative growth rate,  $R_w$ ; and (c) RGR-rate,  $R'_w$ ; for (d) observed and fitted total leaf dry weights per plant,  $L_w$ ; for instantaneously-derived values of (e) relative leaf growth rate,  $R_L$ ; and for (f) RGR-rate for leaf dry weight,  $R'_L$ . All derived data bear 95 per cent confidence limits. New primary data for the grasses *Deschampsia flexuosa* (*Df*) and *Poa annua* (*Pa*).

loss of acceleration over the first few days of growth [Fig. 2(f)]. Thereafter,  $R_L$  declines gently and at 35 days, in both species,  $R_w$  and  $R_L$  are both near to  $0.1 \text{ day}^{-1}$ . Compared with *P. annua*, the performance of *D. flexuosa* in Figs 2(e) and (f) seems remarkably bland.

Interspecific comparisons show that progressions in  $V_w$  and in  $V_L$  are similar in form [Figs 3(a) and (b)]. The efficiency of total dry weight as an accelerator of its own production ( $V_w$ ) declines steadily in both species and is throughout higher in *P. annua*.



Derivate  $V_L$  behaves likewise. Unlike the progressions of  $V$  in the case of maize [Fig. 1(e)], these two show no innate maxima in the constant environment. Absolute levels of  $V_W$  and  $V_L$  are, within either species, comparable throughout, though this would be unlikely to be repeated in plants without such a huge proportion of the above-ground material being productive of further dry weight.

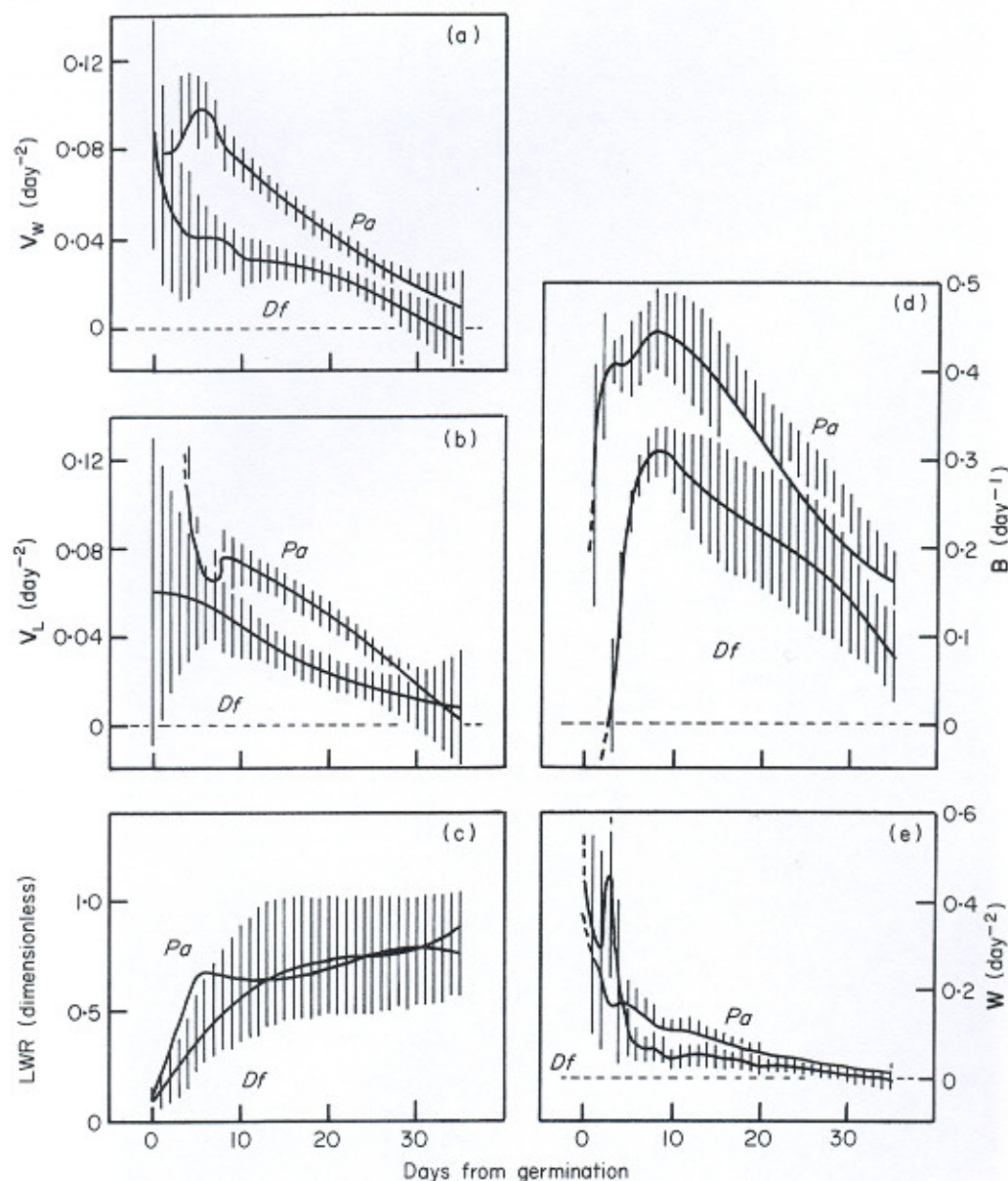


FIG. 3. Progress curves for instantaneously-derived values, with 95 per cent confidence limits, of (a) relative acceleration rate for total dry weight,  $V_W$ ; (b) relative acceleration rate for leaf dry weight,  $V_L$ ; (c) leaf weight ratio, LWR; (d) unit shoot rate,  $B$  (unit leaf rate on the basis of leaf dry weight); and (e) unit acceleration rate,  $W$ . From new primary data for the grasses *Deschampsia flexuosa* (*Df*) and *Poa annua* (*Pa*).

Progressions of LWR [ $L_W/W$ , Fig. 3(c)] show that leafiness rises rapidly at first (particularly in *P. annua*) since  $R_L > R_W$ , then continues to rise, but more steadily (with both species being broadly equal from 10 days onwards). At the end, both species have approximately 80 per cent of their dry weight in leaf material.

Unit leaf rates on the basis of leaf dry weight,  $(1/L_W)(dW/dT)$  (a derivate which has been called unit shoot rate by Hunt and Burnett, 1973, and to which Hunt, 1978, gave

the symbol **B**) appear in Fig. 3(d). In both species, **B** rises rapidly from great negativity to reach a maximum at around 8 days. It then declines uniformly, but in *P. annua* values are throughout approximately half as great again as in *D. flexuosa*, a difference significant at  $P < 0.05$  for much of the progression. Clear ontogenetic decline is demonstrable here, and a clear interspecific difference.

Unit acceleration rates [Fig. 3(e)] do not show the simple downward drift seen in **W** for Kreuzler's maize [Fig. 1(h)]. Rather, the progression for both species forms a reversed J-shaped decline. This behaviour is nevertheless consistent with a linear decline in the ability of total leaf area to accelerate the production of total dry weight when it is remembered that  $L_W$ , not  $L_A$ , is its basis. As grasses undergo vegetative development, a given  $L_A$  comes to represent more and more  $L_W$  (specific leaf area, the ratio  $L_A/L_W$ , commonly falls). Done on the basis of  $L_W$ , a curve for **W** will underestimate the true activity of  $L_A$ , and more and more so as the series proceeds. This will have the effect of making a linear progression appear J-shaped, which is what we see. Despite this, the progression of *P. annua* remains significantly above that for *D. flexuosa* for most of its length, confirming the earlier conclusions that both species are subject to a similar pattern of ontogenetic decline in the productive ability of their leaf material, but operate at inherently different levels of activity.

#### DISCUSSION

What is the significance of the three new derivatives? The foregoing examples have made it clear that **R'**, **V** and **W** have each provided information not available from the traditional growth-analytical device of considering  $R = F \times E$ . The RGR-rate, **R'**, is a straightforward acceleration (though applied to the *logarithms* of primary data). Splined cubic polynomial exponentials are among the first functions to be employed in plant growth analysis which can survive the double differentiation necessary for the derivation of **R'** though even so, as we have seen, their bones are laid bare in the process [Figs 1(d), 2(c), (f)]. Now, if one accepts (what has never been disproved) that the 'true' growth curve of whole, vascular plants over their entire life history is infinitely complex, and therefore supple and form-free, then what one would expect to see as one differentiated-out *this* curve would be a series of smooth progressions (without breaks of slope) that became increasingly featureless as the differential series ascended, but never discontinuous, gradually decaying away to minute ripples *en route* to a flat zero at the infinite derivative. The mathematical facts of life, however, dictate that the second derivative of the cubic spline is a series of linear elements agreeing in position, that the third derivative is a series of horizontal steps (with histogram-type discontinuities), and that the fourth derivative is a horizontal line along zero value. So, these splines are, whatever their advantages over previous methods, still no more than rough-and-ready functions which behave only superficially like the supposedly underlying trend and soon dissolve in form with successive differentiation.

In human biology, seamless second derivatives are occasionally obtained from very high-order polynomial growth curves (see, for example, Joossens and Brems-Heyns, 1975), but these present more limited opportunities for plant growth analysis (Parsons and Hunt, 1981; Hunt, 1982*b*, p. 109) since their workings are not so immediately controlled as those of the present splines. If great play were to be intended for **R'** it might be advisable to move on one step to splined quartic polynomial exponentials (which would give quadratic splines in progressions of **R'**). But this would be at the cost of a great deal of the control which the experimenter may exercise over fits to the primary data themselves when using the cubic degree of spline. This control can, of course, be abused; but not to have it would be a loss.

The relative acceleration rate, **V**, recovers its seamlessness despite involving **R'**. This

asset is substantial and, combined with the fact that it may be defined in terms of the pure variate alone, and not of the variate's logarithms, makes it a valuable addition to the concept of dry weight (or whatever) as procreator of itself, with all of the advantages and disadvantages that this implies. Maxima, zeros and minima in  $V$  assist in defining 'cardinal points' in the life of the plant in each particular environment, hence their value as comparative tools should be substantial. For example, if maximum  $R$  in the seedling phase is to be assessed as a predictor of tolerance of environmental stress (and hence contribute to a scheme in which all vegetation in its established phase is controlled by environmental stress and physical disturbance, Grime, 1974, 1977, 1979), it will be necessary to obtain more refined estimates of this supposedly adaptive feature of the plant's gross physiology than Grime and Hunt (1975) found it possible to obtain in their broad, but preliminary, studies. Several possibilities relating to values, slopes and maxima in  $R$ ,  $R'$  and  $V$  would present themselves for correlation with field distributions if similarly comprehensive studies of the early growth rates of seedlings could be undertaken on a larger scale.

As for the unit acceleration rate, and its slope  $W'$ , their context may be made clear by remembering that relative growth rate was first hoped to be a comparatively stable 'efficiency index' for the particular plant growing in the particular environment (Blackman, 1919). When it was shown, by Briggs, Kidd and West (1920*a*), to be subject to substantial ontogenetic drift, the same hopes were transferred, in large measure, to unit leaf rate (Gregory, 1918; Briggs, Kidd and West, 1920*b*). Though ULRs in Kreuzler's maize (taken as a whole, see Hunt and Evans, 1980) sustain these hopes to some extent, later experimental work (reviewed by Evans, 1972, p. 345) showed that ULR, too, was innately subject to drift. Some of this is evident at the beginnings and ends of the progression shown in Fig. 1(g). Despite the behaviour of UAR in the two native grasses [Fig. 3(e)], which can be explained, it is tempting to think of the slope of this rate of acceleration of the production of dry matter per unit of leaf area as being a further step in the direction of obtaining for comparative use an index of plant performance which is stable for a large part of the plant's life history.

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## APPENDIX

A synopsis of quantities derived from variates  $Y$ ,  $Z$  and  $T$  [see also Eqns (14), (15)].

Name of derived quantity	Instantaneous definition	Symbol	Units
Relative growth rate*	$\frac{1}{Y} \cdot \frac{dY}{dT}$	$R_Y$	$T^{-1}$
Leaf area ratio†	$\frac{Z}{Y}$	$F$	$Z Y^{-1}$
Unit leaf rate†	$\frac{1}{Z} \cdot \frac{dY}{dT}$	$E$	$Y Z^{-1} T^{-1}$
RGR-rate*	$\frac{dR_Y}{dT}$	$R'_Y$	$T^{-2}$
Relative acceleration rate*	$\frac{1}{Y} \cdot \frac{d^2Y}{dT^2}$	$V_Y$	$T^{-2}$
Unit acceleration rate	$\frac{1}{Z} \cdot \frac{d^2Y}{dT^2}$	$W$	$Y Z^{-1} T^{-2}$

\* An analogous quantity also exists for variate  $Z$ .

† This name and symbol applies to the particular case where  $Y$  is total dry weight per plant and  $Z$  is total leaf area per plant. Analogous quantities involving different plant variates may have different names and symbols.