

## A COMPUTER PROGRAM FOR DERIVING GROWTH-FUNCTIONS IN PLANT GROWTH-ANALYSIS

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### INTRODUCTION

In many plant growth-studies it is often useful to compare values of the several well-known growth-functions between species or treatments or at different times during an experiment. For over 50 years it has been customary to derive such functions in the form of mean values over the intervening period of time between two harvests (see Radford (1967) for a review of conventional formulae). More recently, however, various workers have taken advantage of high-speed computing facilities to fit smooth curves to experimental data and thence to derive fitted values for the growth-functions which may be plotted continuously. Vernon & Allison (1963), Hammerton & Stone (1966), Hughes & Freeman (1967), Radford (1967), Ondok & Květ (1971) and Evans (1972) have listed the advantages which this method enjoys. Vernon & Allison (1963), Hammerton & Stone (1966), Ondok & Květ (1971) and Hunt (1973) have made comparisons between the two methods by means of worked examples.

Considerable variety, nevertheless, exists in the methods employed in this later approach to growth-analysis. Normally functions of the type  $1/Y.dY/dX$ ,  $Z/Y$  and  $1/Z.dY/dX$  are desired. Most commonly  $Y$  is whole-plant dry weight,  $Z$  is total leaf-area and  $X$  is time, yielding, respectively, relative growth-rate (RGR), leaf area ratio (LAR) and unit leaf rate (ULR). (The functions may also take many other forms: see Hunt & Burnett (1973) for a recent example of the use of a reasonably full series.)

To derive some of these functions Vernon & Allison (1963), Allison & Watson (1966), Allison (1969), Kirby (1969), Moorby (1970), Monyo & Whittington (1971) and Sobulo (1972) fitted quadratic regressions to  $Y$  and to  $Z$  *v.* time, a method which is of only limited validity (see Hammerton & Stone (1966) and Evans (1972) for critiques). Goodman (1968) and Kornher (1971) used cubic polynomials for a similar purpose and Koller, Nyquist & Chorush (1970) used polynomials of the fifth to seventh degrees. Rees & Chapas (1963) fitted Gompertz curves to  $Y$  and to  $Z$ . Ledig (1969) and Ledig & Perry (1969) have both used logistic, or modified logistic, curves to derive growth-functions. Hammerton & Stone (1966) used modified exponential curves. Other workers have fitted logarithmically transformed raw data by means of various polynomials: linear (Hunt 1970; Scott 1970), quadratic (Buttery 1969; Eagles 1969 (and elsewhere)) and cubic (Goldsworthy 1970). Lupton, Ali & Subramaniam (1967) employed a mixture of regressions including linear, quadratic and log-quadratic in fitting experimental data. Hughes & Freeman (1967) have published details of a general-purpose growth-analysis program in which cubic regressions were fitted to time series of logarithmically transformed values of  $Y$  and  $Z$ . A complete range of fitted values for the logarithms of  $Y$ ,  $Z$

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and for  $1/Y.dY/dT$ ,  $1/Z.dZ/dT$ ,  $Z/Y$  and  $1/Z.dY/dT$ , where  $T$  is time, were printed-out together with their standard errors.

This latter program has been of considerable value in interpreting the results of plant growth-studies and has seen extensive use in fitting long series of experimental data (Hughes & Cockshull 1969; Ojehomon 1970; Bean 1971; Thornley & Hesketh 1972; Hunt & Burnett 1973). Nevertheless, the fitting of these cubic regressions to shorter series of data or to series in which the trends with time are not strongly curvilinear has posed certain interpretational problems (Evans 1972; A. Troughton, personal communication; R. Hunt, unpublished). In such instances it appeared to the present authors to be an advantage to allow the possibility of a lower-order polynomial fit where necessary or desirable. A program has, therefore, been constructed along the lines of that of Hughes & Freeman (1967), in which the aforementioned growth-functions are derived from the most apposite of a stepwise series of fits (up to the third order) to logarithmically transformed raw data.

The immediate application of this program has been in the analysis of standardized data on the growth of native plant species collected as part of a large-scale screening programme conducted by the Nature Conservancy Grassland Research Unit at the University of Sheffield (J. P. Grime & R. Hunt, unpublished). It is hoped that the program might also be convenient for workers who may wish to take advantage of regression techniques of growth-analysis in cases where data from only a few sequential harvests are available or where the trends with time in logarithmically transformed data are linear or simply curvilinear. The program may suit the simpler of the cases in which data from a longer series of 'continuous harvests' are available.

This paper gives a description of the program and an example of its operation. Comparisons are made with the Hughes & Freeman (1967) program and a discussion of possible applications is included.

### THEORY

The data for variates  $Y$  and  $Z$  are transformed to logarithms to render their variability more homogeneous with time ( $X$ ). Polynomials of varying degree are fitted to the transformed data by the least squares method.

The polynomial of best fit is indicated in an analysis of variance table which, for each variate, yields the ratio of the regression mean square for each particular order of fit to its residual mean square. This ratio is tested using Fisher's  $F$ -test starting with the highest-order ratio. If a ratio is not significant at  $P < 0.05$  then the sum of squares corresponding to that degree of fit is pooled with the residual sum of squares and a new residual mean square is calculated. The next lowest order of fit is tested against the new residual mean square and, if this ratio is not significant, the process is repeated until either a fit is found to be significant or the position of 'no fit' is reached. In this event a mean and standard error are calculated.

The orders of polynomial fitted to the variates  $Y$  and  $Z$  on  $X$  may be different, and are, therefore, best represented by general formulae:

$$\log_e Y = \sum_{i=0}^{N_y} a_i X^i \quad (1)$$

where  $N_y$  is the order of polynomial for  $Y$  (such that  $0 \leq N_y \leq 3$ ) and  $a_0$  to  $a_{N_y}$  are the coefficients and

$$\log_e Z = \sum_{i=0}^{N_z} b_i X^i \quad (2)$$

where  $N_z$  is the order of polynomial for  $Z$  (such that  $0 \leq N_z \leq 3$ ) and  $b_0$  to  $b_{N_z}$  are the coefficients. These functions are derived from the three variates in the manner of Hughes & Freeman (1967):

$$\frac{1}{\bar{Y}} \cdot \frac{dY}{dX} \quad \text{and} \quad \frac{1}{\bar{Z}} \cdot \frac{dZ}{dX} \quad (3)$$

$$\frac{Z}{Y} \quad (4)$$

$$\frac{1}{\bar{Z}} \cdot \frac{dY}{dX} \quad (5)$$

Standard errors for expressions (1) to (5) are calculated and confidence limits are obtained by multiplying the standard error by the 5% significance value of Student's  $t$ -distribution (two-tailed), using the residual degrees of freedom from the highest-order significant fit of  $Y$  or  $Z$  on  $X$ .

The derived functions given by (4) and (5) have standard errors containing a term for the covariance of  $Y$  and  $Z$ . This is calculated by applying the formula:

$$\sum_{i=1}^N (\text{observed } \log_e Y_i - \text{fitted } \log_e Y_i) \cdot (\text{observed } \log_e Z_i - \text{fitted } \log_e Z_i) \quad (6)$$

where  $N$  is the number of observations.

The computer program reads and transforms the raw data, carries out an analysis of variance and prints out the analysis of variance table. This is followed by a print of the polynomials used for calculating fitted values. The program then calculates and prints for each value of  $X$  the observed and fitted values for the logarithms of the variates  $Y$  and  $Z$ . The fitted values have standard errors and 95% confidence limits. The derived functions given in (3) are calculated next and printed together with standard errors and 95% confidence limits, followed by observed and fitted values for function (4) also with standard errors and limits attached to the fitted values. Finally, the program calculates and prints values for function (5), again with standard errors and 95% limits.

The program is written in ALGOL W (Wirth & Hoare 1966). A full listing and a statistical specification are available on request.

### EXAMPLE

Selected data from the aforementioned Nature Conservancy screening programme are used here as an example. These data relate to the growth of numerous native plant species under potentially productive, controlled-environment conditions. The experiments covered approximately the first 5 weeks of growth after germination and were chosen here to illustrate the application of this computer program to relatively short series of experimental data. Two grassland species are considered: *Holcus lanatus* L. (Yorkshire fog) and *Nardus stricta* L. (mat-grass). *Holcus* is a 'broad-leaved' grass occurring in the Sheffield region, on soils usually moist and fertile with a surface pH commonly in the range 4.5–6.0. Typical habitats include leached meadows, rough grassland and cattle pasture. *Nardus* is a 'fine-leaved' grass and is restricted to infertile, acidic soils of pH 3.0–4.5. Its typical habitats include hill pastures, rough grassland or wasteland on acidic substrata and moorland. Data from both species have been analysed via both the present program and the Hughes and Freeman program. The variates used were  $X$ , time;  $Y$ , dry weight;  $Z$ , leaf area. The choice of symbols for the variates and functions

involved in these analyses broadly follows the principles of Evans (1972). Symbols are defined as introduced and also listed in an appendix.

### Experimental methods

Seeds from collections local to Sheffield were germinated on moist filter paper in the environment to be used in the experiment. At 3 days after radicle emergence the seedlings were transferred to sand/solution culture and were grown for approximately 5 weeks at a visible radiation level of  $38.0 \text{ W m}^{-2}$  ( $0.0545 \text{ cal cm}^{-2} \text{ min}^{-1}$ ). The temperature regime was  $20 \pm 0.5^\circ \text{ C}$ , day and  $15 \pm 0.5^\circ \text{ C}$ , night (18 h daylength). Relative humidity was always above 60%. At each harvest four or five plants of both species were taken for dry weight and leaf-area estimations: *Holcus* was harvested at 11, 20, 28 and 35 days after planting, *Nardus* was harvested at 14, 20, 27 and 34 days. Leaf-area, in the case of *Nardus*, was taken as the area of a projection of the rolled leaf on to a flat surface. The experiments were performed at Sheffield during the spring and summer of 1968 in growth-rooms described by Rorison (1964).

### Quantitative analysis

The data were transferred to punched cards. Whole plant dry weight,  $W$ , was punched in milligrams and total leaf-area,  $L_A$ , in square centimetres. Regressions were fitted to the natural logarithms of  $W$  and  $L_A$ . In the Hughes and Freeman analysis third-order (cubic) polynomials were fitted throughout. In the stepwise program, for *Holcus*, no fit above the quadratic was found to be significant at  $P < 0.05$ : in *Nardus*, the fits obtained were both linear. In these cases the orders of polynomials fitted to both  $\log_e W$  and  $\log_e L_A$  were the same within each species. Other cases have been found in which the orders of fit for  $\log_e W$  and  $\log_e L_A$  were one, or more, degrees apart (see p. 304).

Table 1. *An analysis of variance for data on the growth of Holcus lanatus and Nardus stricta*

Source	d.f.	(a)		d.f.	(b)	
		Cubic regressions SS( $\log_e W$ )	SS( $\log_e L_A$ )		Stepwise regressions SS( $\log_e W$ )	SS( $\log_e L_A$ )
<i>Holcus lanatus</i>						
Linear	1	84.7597***	52.6083***	1	84.7597***	52.6083***
Quadratic	1	0.6222**	1.2145***	1	0.6222**	1.2145***
Cubic	1	0.0034n.s.	0.0685n.s.	—	—	—
Residual	16	0.8142	0.6047	17	0.8176	0.6732
Total	19	86.1995	54.4960	19	86.1995	54.4960
<i>Nardus stricta</i>						
Linear	1	11.0621***	7.9702***	1	11.0621***	7.9702***
Quadratic	1	0.3828n.s.	0.0659n.s.	—	—	—
Cubic	1	0.0151n.s.	0.0187n.s.	—	—	—
Residual	15	1.6694	1.7952	17	2.0674	1.8797
Total	18	13.1295	9.8499	18	13.1295	9.8499

Part (a) refers to the cubic regressions of the Hughes & Freeman (1967) program, part (b) to the present stepwise regressions.

Significance levels are: \*\*\*,  $P < 0.001$ ; \*\*,  $P < 0.01$ ; n.s.,  $P > 0.05$ .

An inspection of the analysis of variance (Table 1) reveals that, in comparison with the stepwise regressions, variance has been withdrawn from the residual source in the cubic regressions into non-significant cubic, or quadratic and cubic, terms (cf. Table 1(a) and (b) for both species). At this stage both methods make clear the nature of the trends

with time in the raw data, viz. log-quadratic in *Holcus* and log-linear in *Nardus*. It is in the later stages of the analysis that the inclusion of non-significant higher-order terms may cause confusion or uncertainty.

### Results

Fig. 1 gives the raw data and the fitted regressions and growth-functions obtained for both species via the Hughes and Freeman program. The notations used are: relative growth-rate and relative leaf-area growth-rate,  $R$  and  $R_L$ ; leaf area ratio, LAR; unit leaf rate,  $E$ . The values plotted are instantaneous fitted values for each harvest occasion. Ninety-five per cent confidence limits are attached. These are the limits within which the true value would fall in an infinite series of identical experiments on 95% of occasions.

### Discussion

It is evident from an inspection of Fig. 1(a, b) that the cubic regressions are good fits to the logged data, but the forms of the curves for the derived growth-functions and the size of their confidence limits leave several questions unanswered. Are the substantial fitted differences between the two species with respect to  $R$  and  $R_L$  genuine only in the middle of the period studied? Does  $R$  really decline with time in both species? Is the final upward trend in  $R_L$  in *Nardus* authentic? Are the real trends in  $E$  rising in the case of *Holcus* and falling in the case of *Nardus*? Related to the first question is the general phenomenon of relatively large confidence limits at the ends of the fitted curves which, here and elsewhere (Evans 1972), raises uncertainties over the true extent of the fitted changes with time.

When the same data were analysed by means of the present stepwise regression program a clearer picture developed (Fig. 2). Polynomial terms not significant at  $P < 0.05$  were discarded and the analysis proceeded only on the basis of the highest-order polynomial found to be significant at this level. Little difference emerged between the two methods of treating the data with respect to fitted values for  $\log_e W$  and  $\log_e L_A$  (Fig. 2a, b) but in the case of the derived growth-functions considerable differences became apparent. Here, the two plants differed clearly and significantly in  $R$  throughout the period of the observations. The falling trends with time in  $R$  (seen in Fig. 1c) were revealed to be genuine in the case of *Holcus* but not so in the case of *Nardus* ( $P < 0.05$ ). Fitted values for  $R_L$  were clearly separate at the beginning of the observations but converged towards the end, without the final rise in *Nardus* suggested by Fig. 1(d). Because of the forms of the original regressions the trends in  $R$  and in  $R_L$  were found to be linear, or unchanging, with time: the original data do not support a more complex interpretation ( $P < 0.05$ ). LAR decreased significantly with time in *Holcus* but not in *Nardus*—a conclusion which it is also possible to make from Fig. 1. Finally, fitted values of  $E$  did not differ significantly between the two species at any time. The slight rise in  $E$  with time, observed in the case of both plants, is apparently genuine.

From Fig. 2 it is possible to draw the conclusion that the greatly superior yields obtained from *Holcus* after a short period of growth in the seedling phase are due, not to any inherent superiority in the efficiency of its leaf-area as a producer of dry material, but to the much greater leafiness of the plant in the early stages of growth. This, in turn, can be traced to a much higher initial relative leaf-area growth-rate than that observed in *Nardus*. In *Holcus*, however, both  $R_L$  and LAR declined rapidly and by the end of the experiment had almost, or quite, reached the values fitted for *Nardus*. Nevertheless, the initial advantage that high values of  $R_L$  and LAR conferred on *Holcus* resulted in this

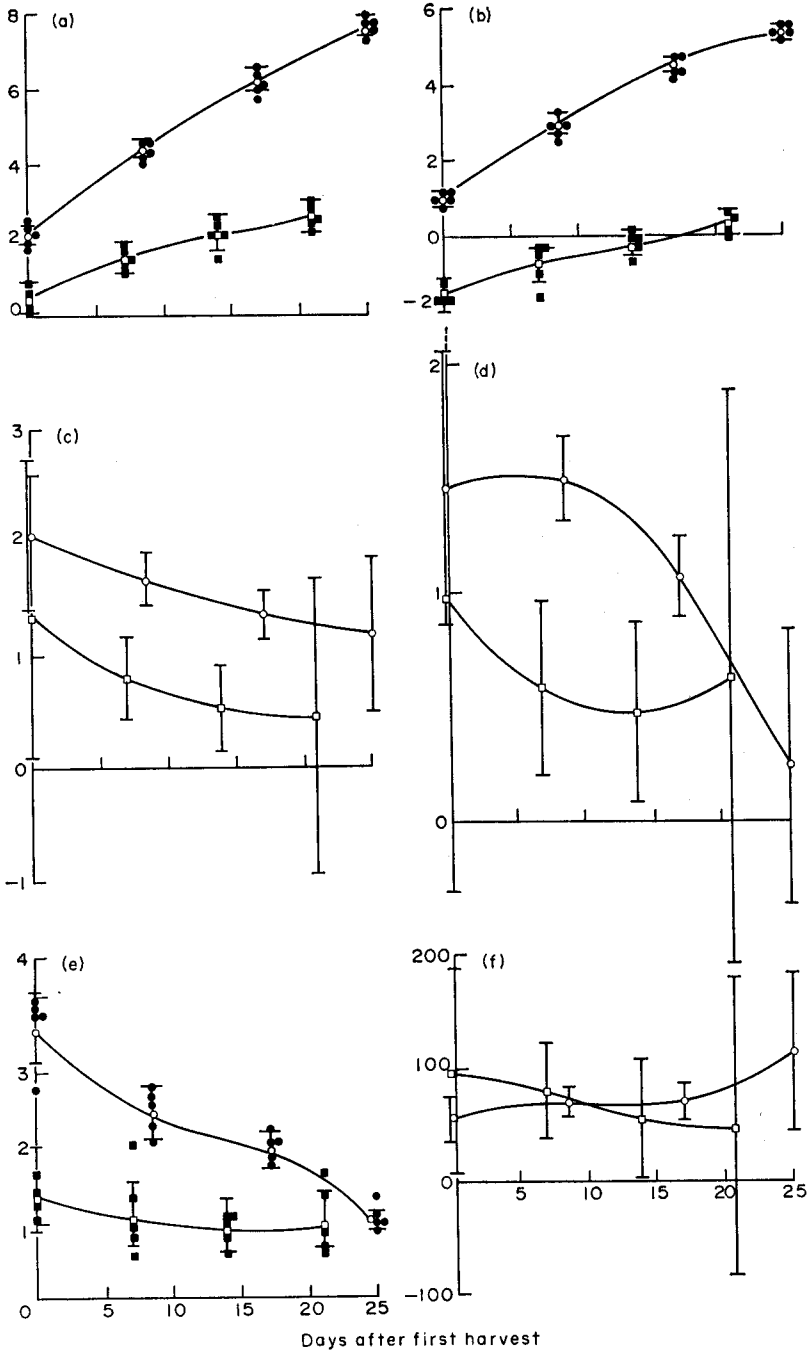


FIG. 1. An analysis of data on the growth of *Holcus lanatus* and *Nardus stricta* by means of the Hughes & Freeman (1967) computer program. (a)  $\text{Log}_e W$  (mg); (b)  $\log_e L_A$  ( $\text{cm}^2$ ); (c)  $R$  ( $\text{week}^{-1}$ ); (d)  $R_L$  ( $\text{week}^{-1}$ ); (e)  $\text{LAR}$  ( $\text{m}^2 \text{g}^{-1} \times 10^2$ ); (f)  $E$  ( $\text{g m}^{-2} \text{week}^{-1}$ ). Solid symbols are observed data, open symbols are fitted values;  $\circ$ , *H. lanatus*,  $\square$ , *N. stricta*. Ninety-five per cent confidence limits are attached to the fitted values.

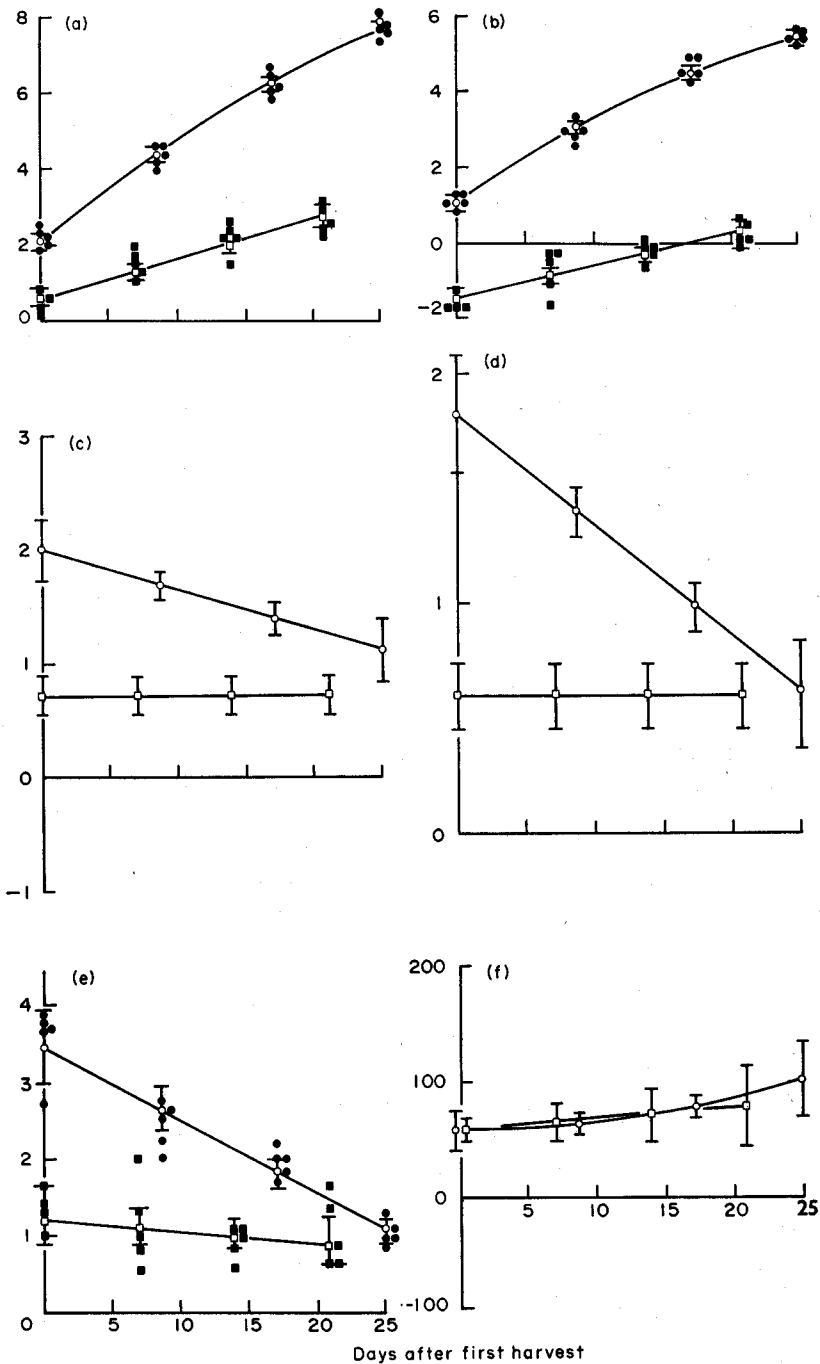


FIG. 2. An analysis of data on the growth of *Holcus lanatus* and *Nardus stricta* by means of the stepwise regression computer program described in the text. (a)  $\log_{10} W$  (mg); (b)  $\log L_A$  (cm<sup>2</sup>); (c)  $R$  (week<sup>-1</sup>); (d)  $R_L$  (week<sup>-1</sup>); (e)  $LAR$  (m<sup>2</sup> g<sup>-1</sup> × 10<sup>2</sup>); (f)  $E$  (g m<sup>-2</sup> week<sup>-1</sup>). Solid symbols are observed data, open symbols are fitted values; ○, *H. lanatus*, □, *N. stricta*. Ninety-five per cent confidence limits are attached to the fitted values.

plant increasing its dry weight differential over *Nardus* from an initial factor of 4.30 to one of 131 after only a slightly longer period of growth.

This is not to say that these conclusions are not possible from Fig. 1. Rather that, in this former figure, one might perhaps be tempted to make more than would be justified of the difference between the two species in the behaviour of  $E$  and to neglect, or to reject as spurious, their initial differences with respect to  $R$  and  $R_L$ .

## DISCUSSION

In the example given the interpretation of the derived functions is made clearer and more straightforward by the introduction of the stepwise regression analysis. In cases where the species or experimental treatments provide less distinct contrasts than in this example it is easy to see that the present method of analysis might make the difference between success and failure in demonstrating dissimilarities between sets of data or derived functions or in establishing significant trends with time.

In particular, the problem of widening confidence limits towards the ends of the fitted curves is eased considerably when non-significant higher-order terms are eliminated from the regressions. Other workers have evaded this problem by discarding the initial and final fitted values (A. P. Hughes, personal communication; Hunt & Burnett 1973) and by making comparisons only from the central parts of the fitted curves. The advantages of the present analysis, in which such a strategy may seldom be necessary, are obvious in cases where data are available for only a few harvest occasions and where the maximum use of data is required.

The analysis of data from the Nature Conservancy screening programme, mentioned in the present introduction, has involved the processing of 192 sets of data similar to those previously discussed: a total of 384 fitted regressions (some with five harvest occasions). Of this total, 210 were linear, 104 were quadratic, sixty-eight were cubic and two were 'no fit', all decided at  $P < 0.05$ . In these 192 sets of data the orders of polynomial fitted to  $\log_e W$  and to  $\log_e L_A$  were the same in 114 cases, were one degree apart in forty-nine cases, two degrees apart in twenty-eight cases and three degrees apart ('no fit'/cubic) in one case. The present program is thus highly flexible in that it can accommodate a wide range of combinations of simple trends in pairs of logged variates. Similar statistics that have appeared in the literature confirm that the cubic term is often only of occasional importance: Bean (1971) analysed three sets of logged data for *Festuca arundinacea* Schreb., each with nine harvest occasions and found that the cubic term was significant in none of them ( $P < 0.05$ ). Hunt & Burnett (1973) performed a total of thirty-six log-cubic regressions for *Lolium perenne* L. using the Hughes & Freeman program and found a significant cubic term only in four cases ( $P < 0.05$ ). Nine harvests were available here, too.

In cases where the logged dependent variates show simple and regular progressions against the independent variate, this program might possibly be used for other applications in which it is desired to compare values for functions of the form  $1/Y.dY/dX$ ,  $Z/Y$  or  $1/Z.dY/dX$ . In the context of plant growth-analysis all situations between a simple experiment of two harvests and a medium-term series of observations with any number of harvests might be served, provided that the trends to be modelled did not include plateaux or sharp inflections. In each case this approach would enjoy a complete freedom in respect of the numbers of plants included at each harvest. For the description of (logged) trends more complex than (a) lines, or (b) simple curves with or without smooth



inflections, one must look to more complex models—but this is not the aim of the present programme. Here, the authors have presented a standardized analysis for a variety of relatively simple situations in which the analysis imposes the minimum of its own pattern on the results and thus seeks to represent the true situation as closely as possible.

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### SUMMARY

A computer program, written in ALGOL W, is described in which classical plant growth-analysis functions of the form

$$1/Y.dY/dX, Z/Y \text{ and } 1/Z.dY/dX$$

are derived from curves fitted to the logarithms of sequential estimates of  $Y$  and  $Z$ . A stepwise regression procedure is incorporated in which polynomial regressions of the first to third order can be fitted independently to  $Y$  and to  $Z$  according to inbuilt statistical tests on trends in the input data. A further facility giving merely a mean and standard error is included for cases where no significant trends exist.

The program is suitable for applications in which workers might wish to take advantage of regression techniques in plant growth-analysis but where data from only a few sequential harvests exist. The simpler of the cases in which data from a longer series of 'continuous harvests' are available might also be served.

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## APPENDIX

### *Symbols and abbreviations used in the text*

<i>a, b</i>	Coefficients	$R_L$	Instantaneous relative leaf-area
d.f.	Degrees of freedom		growth-rate ('relative leaf
<i>E</i>	Instantaneous unit leaf rate		growth-rate' of some
	('net assimilation rate' of		authors)
	some authors)	RGR	Relative growth-rate
<i>F</i>	Variance ratio	SS	Sum of squares
<i>i</i>	Index value, or power	<i>t</i>	'Student's' <i>t</i>
$L_A$	Total leaf-area	<i>T</i>	Time
LAR	Leaf area ratio	ULR	Unit leaf rate ('net assimilation
<i>N</i>	Number of observations		rate' of some authors)
$N_y, N_z$	Orders of polynomial for <i>Y, Z</i>	<i>W</i>	Watt
<i>P</i>	Probability	<i>W</i>	Whole-plant dry weight
<i>R</i>	Instantaneous relative growth-	<i>X</i>	General independent variate
	rate	<i>Y, Z</i>	General dependent variates

## NOTE ADDED IN PROOF

Since this paper went to press Nicholls & Calder (1973) have published a discussion on the use of regression analysis for the study of plant growth. In a worked example on the growth of two species of *Atriplex* they demonstrated that increasing the complexity of the regressions used to describe the changes with time in logged variates increases the standard errors of estimate of fitted growth-functions and may also lead to spurious fitted values for the growth-functions themselves. Nicholls and Calder concluded that '... each set of data has to be considered on its own for the selection of the appropriate regression model. Over fitting is a real trap... '.

## REFERENCE

- Nicholls, A. O. & Calder, D. M. (1973). Comments on the use of regression analysis for the study of plant growth. *New Phytol.* 72, 571-81.