

Plant Growth Analysis: The Rationale Behind the Use of the Fitted Mathematical Function

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In plant growth analysis much attention has lately been paid to the use of fitted mathematical functions in describing growth. Experimenters who are, or who find themselves, concerned with the performance of whole plants often wish to derive the conventional indices of growth, such as relative growth rate, leaf area ratio, unit leaf rate ('net assimilation rate' of some authors), leaf area index and crop growth rate. The option now exists of employing either of what Causton (1967, 1970) contrasted as the 'classical' or the 'functional' approaches. In the former approach, mean values of the required quantities are derived over the period intervening between two harvests. In the latter, instantaneous values and their errors are derived from equations fitted to observational data. These equations are normally of the general form $\text{size} = f(\text{time})$. Reviews which cover both approaches, with varying emphasis, have been provided by Radford (1967), Květ *et al.* (1970), Evans (1972) and Hunt (1978).

In the functional approach, which alone concerns this paper, a considerable methodological corpus has evolved (Richards, 1959; Nelder *et al.*, 1960; Vernon and Allison, 1963; Hammerton and Stone, 1966; Causton, 1967; Hughes and Freeman, 1967; Sváb, Mándy and Bócsa, 1968; Richards, 1969; Causton, 1970; Květ *et al.*, 1971; Dudney, 1973; Hunt, 1973; Nicholls and Calder, 1973; Buttery and Buzzell, 1974; Hunt and Parsons, 1974; Khasawneh, 1975; Elias and Causton, 1976; Hunt and Parsons, 1977; Hurd 1977; Sivakumar and Shaw, 1978; Venus, 1978; Venus and Causton, in press). The varying techniques have been used widely; many of the applications then available were listed by Hunt and Parsons (1974) and a review of a more recent selection is in preparation. But, nowhere has much space been taken to discuss the rationale which underlies the use of the fitted function in dealing with time series of observational data on plant growth. Thornley (1976, p. 297) distinguishes between the mechanistic model which is 'couched in terms of mechanisms or how the parts of the system work together, as in a machine' and the empirical model which 'simply redescribes the data, and does not give rise to any information that is not contained in the data'. The present application is clearly one facies of the empirical model.

In the twenties and thirties of this century an extensive literature developed around attempts to construct simple mechanistic models of the growth of (mainly) whole plants. The methods employed then had much in common with those used by the modern empirical modeller, except that biological significance was sought of parameter values. While acknowledging that from time to time simple mechanistic models 'are capable of reproducing the course of growth curves with tolerable accuracy, and sometimes very closely' Richards (1969) concluded that in search for realistic equations of growth 'the outcome has been disappointing'. Williams (1964) stated that 'it has never been possible

to show that any one of them fits the facts so exactly that the others can be excluded' and the same author, with D. Bouma in 1970, suggested that 'the fitting of continuous functions to extensive growth data [in an attempt to achieve a mechanistic model of growth] is rarely justified, for it is unreasonable to expect growth to be governed by a single set of parameters throughout its course, even in a controlled environment'. Unreasonable indeed, and one is led to conclude that whole plants rarely behave as simple machines (except perhaps over short periods of time) and that simple, comprehensive mechanistic models of this type do not exist. Considerably greater elaboration of the models is needed for them to approach reality with any conviction. The chances of the models doing so are further increased if the scope of the exercise is confined to certain sets of conditions, or to the growth of less than the whole plant.

However, even when this pursuit of mechanistic insight into plant growth is consciously abandoned by the curve fitter, what remains may be substantial. This statement conflicts with a common viewpoint, for example that of Waddington (1956, as quoted by Williams, 1964): 'If we can use these formulae "merely as convenient means of summarizing the empirical observations", the theoretical gain has not been great.' In many ways this is untrue in the particular example of plant growth studies where empirical models can bring unique benefits.

In moving from mechanistic to empirical models of plant growth 'the particular mathematical form of the function used is now regarded as of no special physiological significance, but accuracy in the fit achieved becomes the primary aim. The resulting equation for the curve summarizes the growth data in a convenient way; moreover, the original data, disturbed by irregular errors, are replaced by a smoother continuous function' (Richards, 1969).

Thus, the purpose of this empirical modelling is to describe reality in a convenient way. Now, the view of reality adopted here is that of the working scientist: a complex abstraction, formed in the mind of the experimenter from the integration of both direct and indirect observation. What may lie behind this abstraction is, fortunately, not important because in the words of Wigglesworth (1967), 'science is concerned with "verifiability" it is not concerned with ultimate "truth"'. Evans's (1972, p. 6) 'inaccessible plant', when allied to the well-known problems of natural and experimentally induced variability in material, leads students of plant growth (particularly if sequential destructive harvesting is involved) to, at the very best, a set of observational measurements randomly scattered about reality. The rationale behind the use of the fitted function is then simple: if attempts to assess the reality of growth result in a time series of observations scattered randomly about that reality, then a suitable mathematical function fitted to those observations may be expected to regain much of the clarity with which reality is perceived by the experimenter. In a sense, the course of the flow of understanding is reversed and the fitted function reflects back – not perfectly, of course, but at least in the right direction – towards that reality of which the observational data are an imperfect estimate. Paradoxically, the fitted function can be of more value to the experimenter than the data from which it was derived.

Naturally, if the fitting of the function is handled clumsily, then the experimenter's perception of reality will flow still further along its corrupted course. For example, if fitting errors are systematic then a serious distortion of the truth is introduced (Hunt and Parsons, 1977).

Any of the following secondary advantages may also be gained.

- (1) The model provides a convenient summary of a process which is too complex to understand in detail, or does not need to be understood, but which is of practical significance as a whole.
- (2) Much may be said with great economy of expression; a very large body of observational data may be condensed into a few parameter values.

- (3) Comparisons between bodies of data different in origin but similarly treated are made more straightforward (Heath, 1932).
- (4) Many of the assumptions involved in the calculation of mean values of quantities such as unit leaf rate (Coombe, 1960; Evans and Hughes, 1962; Whitehead and Myerscough, 1962; Evans 1972, p. 268) and leaf area ratio (Ondok, 1971) are evaded, the only necessary assumption being that the fitted growth functions adequately describe the primary data.
- (5) Information from all sampling occasions is used in determining each value of the derived quantities.
- (6) The difficulties involved in the pairing of plants prior to applying the classical formulae are avoided [but see Venus and Causton (in press) for an alternative approach].
- (7) The procedure does not depend upon large harvests and the amount of information at risk at each harvest is minimal.
- (8) Provided that plants in different experimental treatments are grown simultaneously, the harvesting of these treatments need not be synchronous: interpolated comparisons are feasible.
- (9) Replication at different points in time need not be equal.
- (10) Small deviations from the overall trend may be smoothed to gain an impression of growth which is free from random fluctuations (fluctuations believed not to be random in origin may be given separate treatment, see Hunt and Parsons, 1977).
- (11) Statistical analyses may be integrated into the same analytical procedure as the calculation of the derived quantities.
- (12) The approach provides the clearest possible perception of time-dependent phenomena such as ontogenetic drift.

Some of these secondary advantages have also been discussed by Vernon and Allison (1963), Hammerton and Stone (1966), Hughes and Freeman (1967), Radford (1967), Květ *et al.* (1971), Evans (1972), Hunt (1973), Hunt and Parsons (1974) and Hunt (1978).

So, in strictly objective terms, if 'accuracy in the fit achieved becomes the primary aim' then the identity of the empirical model is itself of no importance, so long as it represents the primary data as closely as possible. While it may not be possible to argue with this viewpoint on theoretical grounds, to adopt it as the only *modus operandi* will risk practical difficulties from two sources.

Firstly, it is inescapable that the more complicated the mathematical function (that is, the more parameters it contains) the more closely it will fit any given series of experimental observations (that is, the smaller will be the deviations between the fitted function and the original data). But there are objections to such rapacious models on five grounds. (1) For extensive series of data the computation is laborious. (2) Little or no smoothing of the data is done – every small inflection is reproduced (this may or may not be a disadvantage, but it is uncommon for the empirical modeller to require no smoothing at all). (3) The estimation of derived quantities such as first-order differentials is more laborious than in the case of simpler models. (4) The statistical estimation of errors in complicated models, and in their derivatives, becomes extremely difficult (although an important advance in this direction has been made by Venus and Causton, in press). (5) Interpolation may be unstable. For these reasons the simplest model possible should be preferred, to be consistent both with the degree of smoothing required and any mechanistic insights that may exist concerning the process that is being modelled.

A second reason why empirical models which approach perfection statistically may yet be unsuitable representations of the data, is that they may abuse these aforementioned insights. To take a simple example, if growth, such as that of frond area in a young population of *Lemna* spp. L. (duckweed) under non-limiting conditions, is understood on theoretical grounds to be exponential, then the exponential model (first-order polynomial

exponential*) is the only possibility. The experimenter may quite justifiably take the view that any small deviations from exponentiality in his data are of no real importance and deserve to be smoothed out – despite the fact that if such deviations were to be respected some other model would be a better fit on purely statistical grounds.

As plants grow the proportion of purely structural material that they contain normally increases. For this reason relative growth rate cannot remain constant for long and eventually must show a decline as more and more of the plant's material becomes incapable of directly providing further increases in dry weight. Some experimenters thus prefer models which not only allow the possibility of this decline in relative growth rate with time but, by their nature, expect it. Such is the second-order polynomial exponential recommended by Hurd (1977). Similar arguments in advocacy of the third-order polynomial exponential used by Hughes and Freeman (1967) have also been given (A. P. Hughes, personal communication, 1971). But, just as rigid adherence to statistical exactitude may be unjustified, so may its converse: mechanistic requirements are often quite unsupported by the data themselves. Ten cases of this out of 16 were seen in Hurd's (1977) body of data. Evans's (1972, p. 4) 'Procrustean bed' was exemplified.

Thus, choice is determined by two requirements which often conflict: statistical exactitude and what Hurd (1977) called the experimenter's 'biological expectation'. The former may suggest models either more or less complicated than the latter and if the experimenter can justify either of these as being of overriding importance then the other can be ignored. But in the more usual case where both are given some credence, the experimenter himself can be the only arbiter. In a dilemma, prefer simplicity (Nicholls and Calder, 1973; Hunt and Parsons, 1974). Parameter values in the simpler models are also more likely to achieve some biological relevance, if not to attain a precise mechanistic role.

Because of these difficulties of choice the would-be empirical modeller of plant growth may well ask: Is curve fitting of any sort necessary? 'There is a fascination about curve fitting to growth and population data which can all too easily become an addiction' (Williams, 1975, p. 17) and there are certainly situations in which curve fitting may bring no benefit whatever. The experimenter's requirements are either satisfied by the list of advantages given above or they are not. Objectives must be examined carefully.

However, in plant growth studies where it can be established that such advantages are within reach, then the approximating function which replaces observational data as the working description of reality may be considered. After all, *omnes observationes nostrae propter instrumentorum sensuumque imperfectionem non sint nisi approximationes ad veritatem* (all our observations, because of the imperfection of instruments and of the senses, are nothing more than approximations to the truth) (Gauss, 1809).

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* In the terminology of Causton (1967, 1970) a polynomial exponential is the polynomial function in relation to time of the natural logarithm of a growth attribute.

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