Introduction

This book is heretical for two reasons. Firstly, although it is written by a biologist for the attention of other biologists, its subject matter is strongly mathematical and statistical. Secondly, it advocates an expansion in the use of the empirical model which simply 're-describes' observational data, thus — not rejecting but — forcing back into coexistence the more fashionable mechanistic model with its offers of insights into how living systems work. In making no apology for this standpoint, I suggest only that it is justified because it is what the subject presently needs. Let me elaborate.

The British school of plant growth analysis, which had its origins in the work of F. G. Gregory, V. H. Blackman, G. E. Briggs and co-workers, in their turn drawing some inspiration from nineteenth-century German work, has now been in existence for some sixty years. The method of this school, which amounts to nothing more than a special way of looking at the growth of whole plants, has to varying degrees found a place in the publication of thousands if not tens of thousands of scientific studies. The appeal of the method has always been that useful information may be obtained in amounts out of all proportion to the original outlay in equipment and experimental effort. Though no longer wholly in the van of plant physiological research, the method retains a permanent usefulness in two areas. Firstly, where the frontiers of knowledge about the growth of plants lie closest, as with unexplored experimental subjects or unusual environments and, secondly, where the unique advantages of the method are needed either *per se*, or as preliminaries or adjuncts to other studies of plant growth, be they ecological, genetical, physiological, biochemical or, particularly, agricultural, where the method has quite possibly received its greatest single use.

In the present book I set out the relevance to this field of the so-called 'computer revolution'. There is (almost) no branch of biology into which the advent of high-speed digital computers has not made substantial inroads. As I write, the 'lower end' of this vast field is becoming ever more extensive, with ever more computing power in pocket and desk calculators becoming, in real terms, ever more cheaply available. The purpose of my text is to point out the opportunities that this state of affairs provides, and to review the possibilities for progress in what Causton (1967) has called the 'functional' as opposed to the 'classical' approach to the subject.

2   Introduction

The reader I have in mind is simply the experimenter who grows plants and makes sequential measurements on them. He is the student at college or university who is undertaking a project which involves some form of quantitative comparison between experimental subjects or treatments, or the research student or established worker, maybe not principally in this field at all, who has a similar requirement. The standard of mathematical background needed will in algebra and geometry be less than O-level, and in the differential and integral calculus, only elementary. In statistics, familiarity with one of the cited statistical texts for biologists will suffice, with more advanced reading only being necessary – and then not always – in the field of regression analysis.

I have no doubt that to present this text from the point of view of the working biologist may attract criticism, but I can shelter impudently behind the brave stand made by works such as Kenneth Mather's *Statistical Analysis in Biology* (1964) and J. Maynard Smith's *Mathematical Ideas in Biology* (1968). The organization of this text serves the needs of plant growth analysis only; statistical and mathematical ideas are introduced in illogical sequence and are then often incompletely specified. These cupboards are raided greedily in the interests of the experimenter studying plant growth. Nonetheless, it is my hope that, provided the reader also pursues such first-rate statistical texts as the aforementioned Mather (1964) or Norman T. J. Bailey's *Statistical Methods in Biology* (1964) or Geoffrey M. Clarke's *Statistics and Experimental Design* (1980), and David R. Causton's *A Biologist's Mathematics* (1977) (which is uniquely valuable because of its particular emphasis on the process of growth), he will not go far astray. J. N. R. Jeffers's first two 'Statistical Checklists' (on design, 1978, and on sampling, 1979) will help, and if all else fails there is always Moran's (1974) bibliography of statistical bibliographies to enable lost ways to be re-found.

None of this is to say that specialist advice, particularly from statisticians, is unwelcome. This is a truth so obvious that it can be overlooked, for statisticians as *partners* in biological research are still comparatively rare (Finney, 1978). When P. J. Radford in 1967 wrote about 'Growth analysis formulae – their use and abuse' the statistical content of his paper amounted to no more than crumbs from the table and yet, as a source of information to biologists, this paper has been seized upon eagerly: to June 1981 it has received a total of 152 citations (*Science Citation Index*). Radford's publication is obviously a 'Desert Island Reprint' for the marooned experimenter in whole-plant physiology. When planning this book it was the complete absence of any comprehensive account, based either statistically or biologically, of the use of fitted curves in plant growth analysis that prompted me to proceed.

In mathematics the problem of giving offence is less acute since the issues involved are for the most part either too simple to warrant critical attention, or else beyond solution.

What of my second guilty admission, the advocacy of empiricism? These waters are too deep to sound here; this I risk in Chapter 3. For the moment let me say that I advocate both empiricism and mechanism in modelling plant growth, but in this place empiricism. One only has to look to commerce and industry, to economics and meteorology, for examples of the great and unashamed use of the approximating function for smoothing, interpolation and prediction. These benefits cannot be denied to students of plant growth because they are supposed to be devoid of mechanistic insight. But, having polarized these two approaches to the study of plant growth it is only fair to draw them some way together again by stating that they are in many respects inseparable, being linked by subterranean channels that are often incompletely understood. Many examples of this will be met with in the course of my text.

What, then, is the book about? It would be too sweeping to say that it surveys the use of fitted regression curves in plant science since it includes no coverage of curves used to describe calibrations, photosynthetic responses, temperature optima, fertilizer responses, allometric relationships, quantal responses (all or none), and the like. By the same token, though when fitting plant growth curves I have inevitably come to favour certain statistical instruments, it would be wrong to confine the text to these alone. Such a course would be too narrow and too suggestive of propaganda. The scope, then, has been defined as one of the middle ways between these two: a review of as complete a selection as possible of the literature in which fitted mathematical functions have been used to link some measure of plant size to the independent variable, time, and used, wherever possible, not merely as representations of the data, but also with some statistical or derivational purpose. By introducing plant growth analysis, the role played in it by the fitted curve, and a sizeable sample of the applications of this approach up to and including 1980, I hope to set the aforementioned reader on the right track for the selection, construction and interpretation of plant growth curves appropriate to his particular needs.

How does the book stand in relation to others in the field? Since these are few an appraisal, albeit partisan, is easy. For many, many years, newcomers to plant growth analysis were served only by a heterogeneous collection of review articles. These naturally increased in number, and varied in approach, as time went by, but it was not until 1972 that G. Clifford Evans's *The Quantitative Analysis of Plant Growth* provided a definitive survey of the field for newcomers and established practitioners alike. So great was its depth of coverage, with extensive excursions into related fields such as experimental design and procedure, environmental measurement and control, and respiratory and photosynthetic studies, that for a time it seemed that little remained to be said on the matter. However, two new considerations gradually arose. One was the need for an introductory text, in book form, for use in relatively

4   Introduction

short courses on growth analysis, for which *The Quantitative Analysis of Plant Growth,* though eminently readable, was unsuitable for reasons of length alone. The other was the need for some comparative coverage of the use of fitted curves in plant growth analysis, an activity which, while receiving due mention in *The Quantitative Analysis of Plant Growth*, had in the meantime expanded considerably. To meet both of these needs I offered *Plant Growth Analysis* (1978a). Here, within necessarily compact limits, I tried to survey both plant growth analysis itself and the role played in it by fitted curves. Its readers were referred to *The Quantitative Analysis of Plant Growth* for a more thorough exposition of the 'classical' (non-curve-fitting) approach to the subject and are now referred to the following pages for more information on growth curves. In passing, two (quite unrepresentative) comments from reviews of *Plant Growth Analysis* are answered in Chapter 8. Two related volumes remain and one of these, *The Biometry of Plant Growth* (1981) by David R. Causton and Jill C. Venus, is very close in coverage to the present one. Indeed, when the two works were first mooted it was envisaged that they might proceed as a matched pair, uniform in presentation and notation and with a rigid division of coverage. For various reasons, including timing, this proved to be impracticable and so Causton and Venus's book now stands as an advanced and more specialized adjunct to the more introductory and broader treatment of plant growth curves given here. After some duplication between each's introductory chapters, differences soon become apparent to the reader. *The Biometry of Plant Growth* serves the present volume as an extended and rigorous source of information on regression theory and on the use of the Richards function, and on allometry and the analysis of the growth of plant components. In this last respect it has strong links with R. F. Williams's *The Shoot Apex and Leaf Growth* (1975) which, in turn, presents a wealth of morphogenetic observations unmatched by any of the aforementioned.

1

Overture

1.1 Growth

All living organisms are, at various stages in their life history, capable of 'growth' in the sense of change in size, change in form and change in number, given suitable conditions. These three processes together form an important part of the phenomenon of life itself and among natural systems help to distinguish the living from the non-living. Of course, many of the latter may also be said to 'grow': crystals, river deltas and volcanic cones can change recognizably within human time-scales. But, this apart, even within self-reproducing biological organisms a precise definition of what is meant by 'growth' is not at all easy. Definitions may range from an unequivocal state-ment about change in a specified dimension to a highly abstract state of affairs in which the verb 'to grow' means nothing more than 'to live' or even 'to exist'. Following Hunt (1978a), I advance no firm definition to cover the use of the term in this book other than to say that it will be used to describe irreversible changes with time, mainly in size (however measured), often in form, and occasionally in number.

1.2 Plant growth

From *Biological Abstracts* it is possible to gain the harrowing information that in the last decade alone well over 60 000 separate publications have appeared which may be said to involve, quite specifically, some aspect of 'plant growth'. Clearly, in a work at this level and of this length it is necessary to pare away whole fields of study, from cell division, through growth regula-tion and morphogenesis, to environmental physiology and agronomy, if what remains is to contribute in a worthwhile way towards filling a gap in the literature. Accordingly, none of the aforementioned topics will receive attention in their own right, the special scope of this work being confined to the analysis by means of fitted curves of series of observations on the growth of plant organs, whole individuals, populations and communities.

What form may such observations take? To introduce the reader to some 'hard data' at the earliest opportunity, I quote a selection from a series of classical experiments performed at Poppelsdorf, West Germany in the 1870s.

6   *Overture*

In this series, U. Kreusler and his co-workers demonstrated that the growth of an annual plant under natural conditions followed a course that has since been recognized as typical of many. In Table 1.1 their data are given for the increase with time in mean dry weight and leaf area per plant in *Zea mays* (maize) cv. 'Badischer Früh' grown in 1878 (Kreusler, Prehn and Hornberger, 1879). This set of observations was the culmination of several years' work with different varieties of maize and the measurements were heavily replicated. Save for the conversion of cm^2 to m^2, values are reproduced exactly as given by Kreusler.

Table 1.1   Observations made by Kreusler, Prehn and Hornberger (1879) on the growth of 'Badischer Früh' maize at Poppelsdorf in 1878.

Date of harvesting	Day in the year	Mean total dry weight per plant (g)	Mean total leaf area per plant (m^2)
20 May	140	0.3282	n.a.
28 May	148	0.328	n.a.
4 June	155	0.287	n.a.
11 June	162	0.255	0.00179
18 June	169	0.308	0.00292
25 June	176	0.637	0.01244
2 July	183	2.319	0.04192
9 July	190	4.654	0.07622
16 July	197	9.019	0.1301
23 July	204	20.001	0.2136
30 July	211	34.557	0.2805
6 August	218	57.587	0.3384
13 August	225	70.095	0.3047
20 August	232	85.165	0.3025
27 August	239	111.649	0.2976
3 September	246	124.760	0.2684
10 September	253	121.990	0.2387

These primary data are of high quality and remain relevant, even after the passing of more than a century, to the process of describing and interpreting the growth of whole plants; this, despite the fact that they were collected long before modern methods of experimental design and sampling had evolved. Various sets of data from this series have become a classical quarry for those wishing to test suggested improvements in methods of analysis (for references to previous activity of this type see Hunt and Parsons, 1977, Hunt and Evans, 1980 and Parsons and Hunt, 1981). I propose to continue to use these data as a methodological touchstone and they will run like a thread throughout the book, re-appearing in various places and analysed in different ways. What can be seen on first inspection of them?

This particular set forms a series of seventeen observations made, with one exception, at weekly intervals throughout a whole 'growing season'. We see that both measures of plant 'size' span a substantial range; we see also that it was evidently not feasible to determine total leaf area per plant until the fourth sampling occasion. And there we must leave this section, for any more than these preliminary observations on the structure of this data set would come into the category of . . .

1.3 Plant growth analysis

Obvious though it may seem, the first stage in the analysis of data such as those given in Table 1.1 is to plot them out. When this is done (in Fig. 1.1a) we encounter a first difficulty. Because the changes in dry weight over the whole period are of the order of 370-fold, very little of the first phases of development is revealed in this simple plot of dry weight against time on an arithmetic scale. If these data are transformed to (natural) logarithms we can see more clearly what is happening (Fig. 1.1b). There is no special reason why natural, rather than common, logarithms should be used for this purpose (or indeed, if convenient graphical display is the sole objective, some other trans- formation such as square root), but since these data will be referred to again in contexts that will require this particular transformation, it is convenient to introduce it here.

We see that the plant shows no change in dry weight for the first ten days or so. Then it actually loses weight until about twenty days have passed. Here is an example of another difficulty encountered in defining growth: no increase in weight has occurred but there has been considerable differentiation of leaf tissue in the young seedling (at the expense of total dry weight). From about day 170 the newly-differentiated leaves begin to contribute substan- tially to carbon assimilation and a so-called grand period of growth begins in
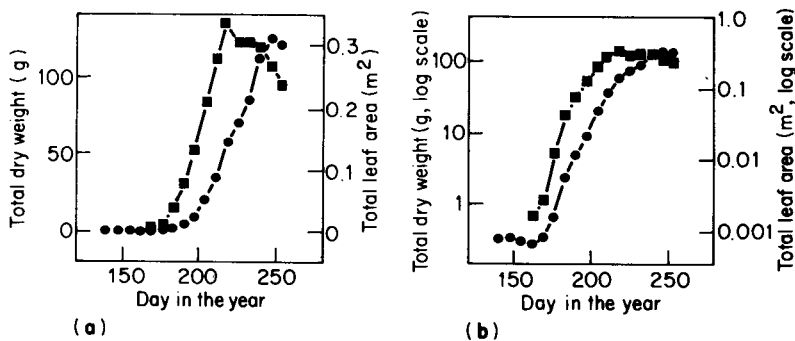

Fig. 1.1   Data from Kreusler *et al.* (1879) on the growth of 'Badischer früh' maize in 1878; (●) mean total dry weight per plant; (■) mean total leaf area per plant. Part (a) is plotted on arithmetic and part (b) on logarithmic scales. For numerical values see Table 1.1.

which the unfolding of new leaves and an increase in total dry weight occur continuously. The plants flower at about day 205 and an increasing proportion of assimilate is now directed into the developing ear or cob with a corresponding tendency for the lower leaves to atrophy. Finally, at about day 246 net dry weight increase ceases although growth in the sense of a continuing partition of dry weight into ears continues.

This pattern of growth, with great variation in the magnitude of the dry weight values, in the symmetry of the curve and in the time scale which it occupies, is general among annual plants grown in a productive environment. In perennial plants the pattern is similar at first but later, at least in a temperate climate, dry weight increase proceeds in a series of annual steps which may be linked by periods of negative growth in between. Naturally, the environmental conditions affect the magnitude of growth at all stages.

Such preliminary synopses of data can take us only so far, so over the last sixty years an additional body of quantitative techniques has been built up which allows the experimenter to derive important comparative information about the undisturbed growth of whole plants under natural, semi-natural or artificial conditions. These techniques require only the simplest of primary data, such as those described above, and have collectively become known by the informal title 'plant growth analysis'. The origins of this activity have been chronicled by Evans (1972, pp. 189–205) and the whole field is reviewed in Chapter 2, where there are also references to all the alternative résumés. For the time being, it need only be noted that these techniques are, above all, powerful comparative tools, since they have been developed so as to negate, as far as possible, the inherent differences in scale between contrasting organisms so that their performances may be compared on an equable basis. Hunt (1978a, Table 1) listed, as an example of the comparative utility of one of the chief concepts of plant growth analysis, the rates of dry weight increase (irreversible growth in size) for a variety of organisms grown under favourable conditions. These ranged from increases of below 10 per cent per day in large trees, through intermediate rates in herbaceous plants, algae, fungi and microorganisms, to rates exceeding 20 000 per cent per day in an anti-*Escherichia coli* phage. Despite much variation within groups, one broad conclusion was clear: the larger and more complex the organism, the lower the rate of dry weight increase possible, when expressed on a percentage basis. This trend is generally held to be due to the increased morphological and anatomical differentiation which is necessary to sustain life in large systems. This differentiation leads to translocatory pathways of increased length between the point of entry of raw materials into the organism and the site of its nucleoprotein replication (Williams, 1975). The point illustrated was that although the differences in organization between these groups could scarcely be greater, calculations made in this way allowed fair quantitative comparisons to be drawn.

1.4 Plant growth analysis in relation to other fields of activity

Even setting aside the great tracts mentioned in section 1.2, 'plant growth analysis' forms only a part of the activity of studying plant growth in relation to time.

On the broadest scale this study involves an assessment of the primary production of vegetation in the field, considered at the ecosystem and community levels of organization. An outline of the techniques involved here has been given for herbaceous communities by Milner and Hughes (1968) and Singh, Lauenroth and Steinhorst (1975). The role of primary production in the energetics of the whole ecosystem has been summarized by Phillipson (1966). In comparison with studies at this level, the growth analysis of communities focuses attention on much less extensive processes, both in time and in space. Its emphasis is on the more specific and on the more detailed. It has both the disadvantage of providing only a limited, short-term view of events and the advantage of enabling a more precise idea of the nature of plant/time/environment interactions to be gained.

At the population level of organization there coexists the complementary field of demography, on which the study of population dynamics is built. Developed mainly around studies on the human population its aim is more to describe and interpret the changes that occur in numbers of individuals rather than their changes in biomass per individual or their rates of functioning expressed on a unit basis. Keyfitz (1968) has written a mathematical introduction to this field and Smith and Keyfitz (1977) have collected together a very broadly-based anthology of leading publications. In biology, animal science has borrowed more heavily from demography, but there are important implications also for plant science in many of the concepts such as birth and death rates, survivorship and life expectancy (Harper and White, 1974). Solomon (1976) gave an excellent introduction to the biological applications of demography, Sarukhán and Harper (1973) provided a specific botanical example of a study involving some of its techniques, and Harper (1977, pp. 515–643) reviewed progress in the field to that date.

At the organ and organismal levels in plant science demography was not represented until Bazzaz and Harper (1977) published an account of the growth of *Linum usitatissimum* (cultivated flax). These authors applied life-table and other demographic analyses to *leaf* birth and death (in contrast to the more usual case where attention is paid to the birth and death of whole individuals). Hunt (1978b) commented on this new role for demography in relation to the existing role played by plant growth analysis at this level and further work by Hunt and Bazzaz (1980) showed that the leaf demographic approach to the growth of plants operated best when there were many, standard, short-lived 'modules' (clearly identifiable leaves or cohorts of leaves). Plant growth analysis, examining the individual rates of development and functioning of the 'modules', depended on these being relatively fewer, slowly changing and persistent.

10   *Overture*

Finally, there are studies of plant photosynthetic production — the 'applied' aspects of photosynthesis research — aiming to investigate the plant/environment relationship at the level of the leaf, leaf segment and chloroplast. The various methods appropriate for studies here have been reviewed by Šesták, Čatský and Jarvis (1971). In comparison, plant growth analysis suffers the disadvantage of providing little information about plants to environmental factors, even though valuable clues if not detailed explanations, may sometimes emerge. On the other hand, the great advantage of many of the quantities involved in plant growth analysis is that they provide accurate measurements of the sum performance of the plant integrated both throughout the whole undisturbed plant and across substantial intervals of time. To predict this from the starting point of purely physiological observations would involve many dangerous assumptions. In plant growth analysis the system is judged more by results than by promises. Nátr and Kousalová (1965) and Ondok (1978) also discuss these problems.

So, from the community through to the organ, and beyond, plant growth analysis shares the field with many related activities. In a way, each of these is more specialized than plant growth analysis but none retains its conceptual unity over so wide a range. It remains for the experimenter to examine the possibilities within the various approaches and to enter this continuum at a level appropriate both to the aims of his investigation and to the facilities that he has at hand. If his approach is to involve plant growth analysis, and in particular the use of fitted growth curves, then information in this book will find its mark.

1.5 The 'classical' and the 'functional' approaches to plant growth analysis

A notable dichotomy between two approaches to the subject evolved, in the main, during the 1960s. The above names were first used by Causton (1967); Radford (1967) used the term 'dynamic' for what we shall call the 'functional' approach, but terminology is relatively unimportant provided it is realized that one approach necessarily involves the use of fitted curves and the other does not. We have:

(i)   the 'classical' approach, in which the course of events is followed through a series of relatively infrequent, large harvests (with much replication of measurements), the literature in the field running to thousands or tens of thousands of publications;

(ii) the 'functional' approach, in which harvests supplying data for curve-fitting are smaller (less replication of measurements) but more frequent, and of which the publications may be numbered in hundreds.

The two approaches are not mutually exclusive if time and space are no object (harvests may be large *and* frequent) but it is not often that such a