

1 Introductory

‘... if arithmetic, mensuration, and weighing be taken away from any art, that which remains will not be much’.

PLATO, *Philebus* (Jowett’s translation, iv, 104 (1875))

‘... the growth and development of an organism is the result of a number of ontogenetic processes, among which complex interrelations exist. The interpretation of these interrelations, and of the manner in which the processes are integrated to produce the living plant, is the fundamental problem in the study of growth’.

A. H. K. PETRIE (1937)

At the time of his death, Petrie had completed early drafts of two or three chapters of a book which was to have been called ‘The Developmental Physiology of Plants’, and the above quotation from Plato had been placed at the beginning of Chapter 2, ‘The Change in Dry Weight and Leaf Area, and First Steps in the Analysis of Growth Rate’. Unfortunately the book had not reached a stage from which it could have been completed by any of his colleagues, and we had to content ourselves with placing the quotation on the title page of a bound volume of Petrie’s papers in plant physiology for the Library of the Waite Institute, Adelaide.

The second quotation is from one of Petrie’s published papers, and epitomizes his thinking and general approach to the study of growth, though more extended statements along the same lines had in fact appeared a year earlier (Ballard and Petrie, 1936). Although his research output was quite remarkable in quantity and quality, Petrie did not live long enough to bring this kind of thinking to its full fruition, but he did succeed in transmitting some of his enthusiasm and outlook to his rather few research students and those who became his junior colleagues. This book is intended as a very belated tribute from one who was privileged to be associated with him for almost nine years.

Petrie was the son of Dr James M. Petrie, who was for many years Macleay Research Fellow of the Linnean Society of New South Wales. After holding junior academic posts in Sydney and Melbourne he was awarded an 1851 Exhibition Scholarship, and this enabled him to study

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under G. E. Briggs of Cambridge. Petrie actually took his current interest in ionic absorption to Cambridge and, with Briggs, eventually published pioneer studies on the application of the Donnan equilibrium to the ionic relations of plant tissues. He was also strongly influenced by the course of lectures on growth given by Briggs at that time.

Petrie returned to Melbourne in 1929, and in 1931 he was invited to join the staff of the University of Adelaide as plant physiologist of the Waite Agricultural Research Institute. He accepted the challenge, and, although he did not immediately give up his interest in ionic relations, he turned his attention more and more to growth and development. In this he was undoubtedly influenced by A. E. V. Richardson, the then director, with whom, in spite of marked differences in temperament, he shared common objectives. One of these was the raising of agricultural research from the level of pure empiricism to one which could boast a sound body of knowledge and theory. Indeed Petrie was one of the first in Australia to attempt to interpret relevant elements of agricultural practice in terms of plant physiological processes.

Petrie believed that the temporal drifts in size, structure and chemical composition of a plant during its development were the results of drifts in metabolism, and with remarkable singleness of purpose he set himself to study these progressive physiological changes. Petrie's usual approach was to alter the external nutrient supply, to apply temporary periods of drought, or to prevent inflorescence development; all as means to the understanding of growth. He saw the necessity for precise quantitative description, and he knew that a great amount of it would be needed before general principles could emerge and be evaluated. To a degree, Petrie's work was still in the data-collecting stage at his death, but it was far more than an elaborate exercise in classical growth analysis. The second quotation at the head of this chapter amply attests a recognition of the significance of organization at the biological level. In particular, Petrie stressed the importance of competitive demand within the plant for metabolites and nutrients. He and others from the group have contributed substantially to our knowledge of the uptake and redistribution of mineral elements during development, and this contribution has been reviewed in some detail (Williams, 1955).

In sum, I believe it is true to say that Petrie's contribution is a large and continuing one; that a considerable body of research in crop physiology and plant response stems from his influence and insights; and that such studies have become academically respectable because of him. Further evidence, if that be needed, is that his voluminous data on

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the growth of the tobacco plant (collected almost 40 years ago) have recently been made the basis of a simulation study which explores the carbon economy of the tobacco plant (Hackett, 1973).

However, the present book has to do, not so much with the integration of physiological processes as with the prior need for quantitative description. It was this no doubt which prompted Petrie's use of the quotation from the *Philebus*, though, in one sense, this is curiously inappropriate to the main body of biological knowledge. 'Arithmetic, mensuration and weighing' are, of course, tremendously important to genetics, biochemistry and biophysics, but the rest of biology has been, and still is predominantly qualitative in content. Yet one can scarcely say that 'that which remains' – and this includes systematics, morphology, anatomy and the whole corpus of evolutionary theory – 'will not be much'.

Why, then, has so little attention been paid to quantity and time in biology? Some reasons which spring to mind are purely technical. Organisms are variable entities, and measurements, especially growth measurements, are subject to inherent variation which may be many times greater than the experimental errors of actual measurement. This calls for appropriate design of experiments and statistical treatment, and biologists have not always been good at these things. Then, too, many of the critical events in developmental biology take place when the organisms or their parts are exceedingly small. It is easy to look on and record such events with the aid of microscopy, but to record them in terms of quantity and rate is another matter. It adds at least another dimension to the problems of natural variation already referred to.

More potent reasons, perhaps, have been the sheer magnitude of the descriptive task and the limited number of workers. And those that have been attracted to biology have rarely been competent in mathematics or the physical sciences. However, the climate of scientific opinion has also been against the growth of a sound quantitative biology. By that I mean that it has not been fashionable to think of organisms as systems having a hierarchic order which demands investigation at all levels. Weiss (1969) puts the problem very clearly in his chapter in *Beyond Reductionism*. He says, 'There is an age-old controversy in biology between the two opposite extremes of "reductionism" and "holism". The former finds concurrently its most outspoken advocates in the field of so-called "molecular biology". If this term is used to imply no more than a deliberate self-limitation of viewpoint and research to molecular interactions in living systems, it is not only per-

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minent and legitimate, but has to its credit some of the most spectacular advances in modern biology. If on the other hand, flushed by success, it were to assume the attitude of a benevolent absolutism, claiming a monopoly for the explanation of all phenomena in living systems, and indeed were issuing injunctions against the use of other than molecular principles in the description of biological systems, this would obviously show a lack of practical experience with, or disregard of, the evidence of supra-molecular order in living systems.'

This incisive statement is well summed up by the aphorism, 'Thought is abstract: and the intolerant use of abstraction is the major vice of the intellect' (Whitehead, 1933). And abstraction is used intolerantly when that which is abstracted from is regarded as unimportant.

I am not qualified to pursue this controversy in depth, nor is this the place to do so. However, it takes very little practical experience to enable one to agree wholeheartedly with Weiss's further statement that 'the *principle of hierarchic order* in living nature reveals itself as a demonstrable descriptive fact regardless of the philosophical connotations that it may carry'. Those wishing to read further on these matters should consult the much neglected book, *Biological Principles* (Woodger, 1929), and the more recent *Hierarchy Theory* (Pattee, 1973).

The central purpose of this book, then, is to provide precise quantitative descriptions of shoot-apical systems of very diverse types. Except for wheat, for which a description of the developing inflorescence is also provided, these are all for vegetative apices. These descriptions were made possible by a development of the old technique of serial reconstruction, which permits the early growth of leaf primordia and related tissues to be measured as volume.

Wilhelm His (1888) drew attention to the importance of measurement for the understanding of morphogenetic processes, and it is to him that we owe the procedure of serial reconstruction. In one place he says: 'The ways of determining the forms and volumes of germs and embryos are somewhat longer and more tiresome than the simple inspection of stained sections; but the general scientific methods of measuring, of weighing, or of determining volumes cannot be neglected in embryological work, if it is to have a solid foundation of facts, for morphologists have not the privilege of walking in easier or more direct paths than workers in other branches of natural science.'

While serial reconstruction has been used many times for the description of form changes in embryos and embryonic organs in animals and

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plants, it does not seem to have been used in any precise quantitative sense. The procedure is described in the appendix, together with sampling and related procedures which have been found helpful.

Only the studies with wheat (Williams, 1960, 1966a; Williams and Rijven, 1965; Williams and Williams, 1968) and subterranean clover (Williams and Bouma, 1970; Williams and Rijven, 1970) have appeared as research papers; the others are now published for the first time. Indeed, it was the need to have all the studies together for ready comparison which prompted their presentation in book form. This has the further advantage that, since all the studies of Chapter 4 have used the same methods, these could be relegated to the appendix, thus avoiding to some extent the clutter of the standard research paper. Even more important was the need for an appropriate medium for the development of the thesis that plant growth is subject to a variety of constraints which need to be recognized alongside those determinants which are accepted almost without question.

I did not become aware of the possible importance of physical constraint as a determinant of growth until the long period of exponential growth sustained by the clover leaf primordium was recognized as an optimal solution to a developmental problem, a solution which involved the system as a whole, and not only the concurrent intracellular events. This awareness quickly led to the recognition that the curious pattern of primordium growth in wheat was also readily interpreted in terms of physical constraint, and this concept began to enter into my thinking when it came to selecting apices for detailed study.

Now the cause-effect relations with which we are most familiar are ones which relate to systems which can be isolated sufficiently to permit the testing of hypotheses *in vitro*. Increasingly, such hypotheses are being checked by *in-vivo* studies using labelling and other techniques. However, it is suggested that hypotheses relating to the higher levels of organization may be difficult if not impossible to test by experiment. In such cases conviction may have to come, in part inductively, by the comparative study of relevant biological systems, in part deductively, by setting up a general theory which has powers of prediction. Such after all, is the history of the study of evolution and the general theory of natural selection (Huxley, 1954). In what follows, then, I make no apology for drawing attention to the likely operation of physical constraint within the point-by-point descriptions of Chapter 4. To do otherwise would be cumbersome in the extreme. This hypothesis already has experimental backing in that we know that root growth is very sensitive

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to constraining pressures, and that the early growth and emergence of wheat tillers are subject to physical constraint (see Chapter 7). For all that, only comparative study of developmental systems will show us the extent of its operation, and I suspect that a consistent body of observational fact will remain the best support for possible theoretical developments for some time to come.

[A useful review has been supplied by Vidaver (1972) on the effects of pressure on the metabolic processes of plants. The work reviewed relates mainly to effects of variation in hydrostatic pressure, and probably has little relevance to the localized operation of physical constraint.]

It is a sobering thought that a physicist should have supplied what appears to me to be a quite profound statement on the problem of biological hierarchy (Pattee, 1970). In an introductory statement he says, 'if you ask what is the secret of life, you will not impress most physicists by telling them what they already believe – that all the molecules in a cell obey all the laws of physics and chemistry. The real mystery. . . is in the origin of the highly unlikely and somewhat arbitrary constraints which harness these laws to perform specific and reliable functions. This is the problem of hierarchical control'. Later he gives the more succinct statement, 'If there is to be any theory of general biology, it must explain the origin and operation (including the reliability and persistence) of the hierarchical constraints which harness matter to perform coherent functions'. He warns that such a theory is not simply a set of descriptions at each level, but must concern itself with the interfaces between the levels. The natural tendency to concentrate on one level of organization at a time carries with it the likelihood that the technical languages at each level will become incompatible.

This book, then, is an attempt by a practising biologist to work out the implications of this sort of thinking. It is concerned with the relations of organs within well defined biological systems (shoot apices), and considerable effort has gone into their precise quantitative description. At the same time, the genesis of form is kept constantly before the reader by the use of three-dimensional, scale drawings, and with photomicrographs. The drawings, in particular, have helped greatly in identifying events which were seen to be correlated with changes in relative growth rates of various primordia. Whatever may come of the interpretations which have been placed on those events, there will remain a considerable body of new information about shoot-apical systems. Nevertheless, the notion that constraint is an important determinant of growth rate is not new, as is attested by the quotation from

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Richards at the head of Chapter 8. It is also the simplest interpretation of the range of rates set out in Table 2.1 (p. 13).

From time to time and especially in Chapter 8, attention is drawn to the possibility that certain events constitute optimal solutions to specific developmental problems. In particular, this applies to strict exponential growth within systems in which sequences of like members remain in close contact. There are also many problems in morphogenesis, including those of phyllotaxis, to which optimality principles would seem to apply. The reader is referred to Rosen (1967) for an introductory account of the mathematical techniques and some applications.

A secondary theme of the book is that of phyllotaxis. I have attempted to set out and to apply the procedures, which we owe to Richards (1951), for the objective description of shoot-apical systems. To date, these have not been used in any systematic way, and one suspects that most botanists have been daunted by the theoretical detail of the original. Simple geometrical modelling has also been used to study the generation of Fibonacci and other spiral systems from the decussate condition of the dicotyledonous seedling.

Chapter 5, on the dynamics of leaf growth, extends the quantitative description to chemical change in two contrasting leaf types, clover and wheat. To that extent it takes a look at the integration of physiological processes in the growth of the leaf, and it points the way to precise in-vivo study of metabolism in leaf primordia and other embryonic organs during rapid growth. Key concepts here are the relative growth rate R , and G , the rate of production of one metabolite per unit of another based on terminal values for an interval.

The sixth chapter shows that quite complex biological systems, such as inflorescences can be described with precision if the need should arise.

When this book was being planned the intention was to include a critical survey of the concepts of growth analysis, its current status and limitations. The need for this is much reduced as a result of the appearance of *The Quantitative Analysis of Plant Growth* (Evans, 1972), and what little remains to be said would be difficult to place here.

Some other general texts that can be recommended for related reading are, *Apical Meristems* (Clowes, 1961), *Shoot Organization in Vascular Plants* (Dormer, 1972), *The Growth of Leaves* (Milthorpe, 1956), *Growth and Organization in Plants* (Steward, 1968), *The Control of Growth and*

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R. F. Williams

Excerpt

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Differentiation in Plants (Wareing and Phillips, 1970) and ‘Growth as a general process’ (Whaley, 1961). A recent book, *Analysis of Leaf Development* (Maksymowych, 1973) is perhaps closest of all to the subject matter of the present volume. However, it is based largely on one species, *Xanthium*, and the emphasis is upon the phase of leaf expansion, which I have tended to neglect.

2 The quantitative description of growth

‘If the rate of assimilation per unit area of leaf surface and the rate of respiration remain constant, and the size of the leaf system bears a constant relation to the dry weight of the whole plant, then the rate of production of new material, as measured by the dry weight, will be proportional to the size of the plant, i.e. the plant in its increase in dry weight will follow the compound interest law.’

‘The rate of interest, r , may be termed the *efficiency index* of dry weight production.’

‘It is clear. . .that the efficiency of the plant is greatest at first and then falls somewhat, but the fall is only slight until the formation of the inflorescence, when there is a marked diminution in the efficiency index.’

V. H. BLACKMAN (1919)

Although it is commonly acknowledged that we owe to Blackman the first clear statement of the mathematical principles underlying the law of exponential growth, his ‘efficiency index’ has had an extraordinary history of criticism and rejection. The efficiency index is, of course, none other than the relative growth rate – a concept which has always been eminently respectable. No doubt the nature of the analogy – that of compound interest – and reference to it as a physiological constant are the bases of the misunderstandings. His earliest critics were Kidd *et al.* (1920) and they were effectively answered by Blackman (1920) in the same volume of the *New Phytologist*. Of special interest is the contention of Kidd *et al.* that the *only* way in which plants can be compared is by the comparison of the whole series of efficiency indices throughout their life-cycles. This was a valuable suggestion, even though Blackman correctly countered that, in the absence of such detailed information, the comparison of average efficiency for longer periods is of value. It is certainly not the *only* way, but a very large number of growth studies involving treatment and other comparisons over extended portions of life-cycles have demonstrated its importance.

That Blackman is still being misunderstood will be apparent from a perusal of an otherwise excellent chapter on quantitative interpretations of growth by Steward (1968, see pp. 417–8), and Dormer (1972) says in one place, ‘This consideration is sufficient to expose the fundamental

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artificiality of the compound interest scheme; it represents the growth of a body which remains meristematic throughout.' Macdowall (1972), on the other hand, goes too far in his defence of Blackman's 'kinetically proper expression of rate of plant growth', when he asserts that 'the strange and uninterpretable changes that have been reported for relative growth rate, even in the initial phase of growth, have encouraged suggestions of an elusive "internal factor" and have forced continued reliance on the "technique of growth analysis"'. One can agree that classical growth analysis has put so much stress on the components, net assimilation rate and leaf area ratio, that the relative growth rate itself has been divested of much of its significance. One can also approve the assumption that early vegetative growth is near enough to exponential for Macdowall's type of kinetic study, but not his dismissal of time trends on the supposition that they are uninterpretable. Growth analysis itself has provided partial interpretation of such trends, and internal factors are not less real for being imperfectly understood.

Relative growth rate is so well established as a concept that we would do well to retain the name. Macdowall's proposal to replace it by 'growth coefficient' has little to commend it, though his defence of Blackman serves as a reminder that relative growth rate is in fact the fundamental measure of organic growth. Indeed, it is a superbly sensitive yard-stick for growth not only of whole plants, but also of organ assemblages and individual parts. Fig. 2.1 attempts to justify this claim, and is derived from data presented more fully below.

The three curves of absolute weight change at the top of Fig. 2.1 all cover some six logarithmic cycles of size, so it is scarcely surprising that they conceal more than they reveal about early stages of growth. The same data on a logarithmic scale gives equal weight to all stages because growth, after all, is multiplicative rather than additive in character, except in rather exceptional circumstances. There are some obvious differences between the three sets of data, including the positioning of points of inflexion and the existence of strictly linear segments at different stages for clover and wheat.

Before proceeding further it will be as well to define the concept of relative growth rate. For any attribute of size, W which is changing with time, t the relative growth rate, R at any instant is

$$R = \frac{1}{W} \frac{dW}{dt} = \frac{d \ln W}{dt},$$