I. INTRODUCTION

In contemporary studies of morphogenesis in plants, attention is being centred more and more on growth and the genic control of metabolism. It is held that the inception of new organs and the differentiation of tissues result from the localised accumulation of gene-determined substances. If this "substance" view of morphogenesis is accepted, the primary problems are then seen to relate to the nature of the "morphogenetic substances" and the factors which determine their patternised distribution. It is here that the student of morphogenesis has encountered one of his greatest difficulties: it seems improbable that biochemical concepts alone will enable him to give an adequate account either of the inception of pattern or of the progressive organisation during development which characterises the species. That specific substances, e.g. auxin, are of great importance in morphogenesis is now accepted, but thus far no adequate biochemical theory of organisation has been advanced. Such knowledge as we have of metabolic changes in embryonic regions does little to explain the assumption of form, the differentiation of tissues, and the orderly development of the individual species, with all its distinctive features. And although there is evidence that many of these developments are gene-controlled, our knowledge of the actual mechanism involved is both slender and speculative. On analysis, and as a working hypothesis, it seems that this mechanism, in its most fundamental aspect, must be sought in the laws of physical chemistry as applied to the metabolic systems found in embryonic regions. In particular, we have to inquire if anything is known regarding the physical chemistry of organic reaction systems which would account for the inception of some of the characteristic patterns in plants. In a contemporary paper, Turing (1952) has advanced a theory, based on a comprehensive mathematical study of diffusion reaction systems, which goes a considerable way towards providing an explanation of the inception of pattern in living organisms. This theory is considered in its general botanical application in the present paper.

One major result of the comparative morphological studies of the post-Darwinian period, and also of the contemporary period of renewed interest in morphogenesis, has been an appreciation of the fact that similar morphological and anatomical features may be found in organisms of quite distinct taxonomic affinity. These

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Footnote: Although, as Arber (1950) has pointed out, the term form in its full connotation deals comprehensively with the characteristic shape of an organism, or of its parts, the term pattern has also been used extensively in morphological studies in recent years - a use that is not recorded in the Oxford Dictionary. Nevertheless, the term, being virtually self-explanatory, is a convenient one, and, in addition, it carries the implication that, as in an artistic design, a morphological or structural development may be characterised by repetitive features. The term is also useful in specifying particular aspects of the organisation which becomes manifest during development.

homoplastic developments, which have resulted from parallel or convergent evolution, have also been aptly described as constituting homologies of organisation and are of general occurrence in the Plant Kingdom. Indeed, the main formal and structural features in plants can be referred to a comparatively small number of kinds of pattern (see Section II). This being so, the factors which determine these kinds of pattern, or homologies of organisation, should be ascertained and closely investigated - a view already expressed by Lang in 1915.

In each instance where the assumption of form, or the inception of pattern, is being considered, it is essential to have some leading idea, or system of ideas, that will serve as a working basis for investigations. The contemporary explanation of comparable or homogenous developments in related organisms is that there are genes, or groups of genes, which are common to the organisms, and that these control or determine the observed developments.* But where similar features are present in unrelated organisms, the comparable developments cannot be attributed to common groups of genes. In attempting to explain the phenomenon of homology of organisation two possibilities may be entertained: (i) comparable morphological features appear because essentially the same kind of process is operating in each of the non-related organisms; or (ii) that essentially different processes may, nevertheless, yield comparable morphological results. On grounds of probability, the first explanation seems preferable to the second, but, because of the very great diversity of

* Genetical investigations (Harland, 1936; de Beer, 1957) show that the situation may be considerably more complicated).

living organisms the second cannot, and should not, be eliminated out of hand. Whether we are concerned with developments which are considered to be more or less directly gene-controlled, or with homologies of organisation, in which the importance of specific genetic factors has yet to be ascertained, the visible phenomena of morphogenesis have their inception in biochemical and biophysical reaction systems. In view of the prevalence of homology of organisation in the Plant Kingdom, it is cogent to inquire if there are any reaction systems which, because of their nature, are likely to be, or will necessarily be, of general occurrence in living organisms. Or, in other words, is anything known of reaction systems, of the kind likely to occur in plants, which would account for the inception of certain kinds of pattern?

A single example of homology of organisation may be considered by way of indicating the need for a new approach to these problems. In all classes of plants, the root stele as seen in cross-section consists of radiating plates of xylem alternating with bays of phloem. This pattern has its inception at the root apex and is not determined by the presence of lateral members. In small roots the pattern is simple, the xylem typically consisting of one or two to four or five xylem plates: in large roots there may be ten to twenty radiating xylem plates, i.e. pattern, though considerably more complex, is essentially a repetition of that seen in small roots. Now, as a fact, no generally accepted hypothesis relating to the inception of the pattern in root steles has yet been advanced. Familiarity with root structure may perhaps engender the impression that we understand what we see when we examine a cross-section under the microscope; but, in fact, we have, thus far, very little knowledge of the factors which determine the characteristic differentiation of tissues. Broadly speaking, the same is true of all the tissue systems in plants; and the same general observation could be made regarding our knowledge of morphogenesis. Goebel (1922) pointed to the repetitive occurrence of pattern during development and to the relative constancy of scale of the 'units of pattern' at the time of their inception. Thoday (1939) has indicated how this conception could be used to account for the increasing structural complexity in roots of increasing size, i.e. as the stele enlarges more units of pattern can be accommodated. If this be accepted, then the fundamental problem is to discover the factors which determine the unit of pattern.

Every anatomical and morphological development is the result of antecedent physiological processes, and several, or many, steps may be involved. Hence any adequate theory of the inception of pattern (as in the root stele given above) must take account of the nature and properties of embryonic tissue and of the physical chemistry of reacting organic substances - the metabolites involved in growth and differentiation. Furthermore, if we assume, as a working hypothesis, that substance differences are involved in the differentiation of phloem and xylem, then the problem is to account for the characteristic localisation of specific substances, i.e. for the patternised distribution of metabolites that precedes the visible tissue pattern.

As it seems to the botanical author, Turing's diffusion-reaction theory of morphogenesis provides a new approach and contributes materially to our understanding of the mechanism of morphogenesis and histogenesis, particularly in their more general aspects.

In the present paper the theory is briefly outlined and discussed (<u>See</u> Section III). In the following section an indication is given to the various kinds of pattern found in plants to the inception of some of which the theory mey have a special application.