Abstract

Most plants are constructed from repeating units such as phytomers, merophytes and cell packets. Even simple organisms such as the filamentous blue-green alga *Anabaena* show repeating cellular structures, notably with respect to the distribution of their heterocysts. All these are examples of the workings of inherent rhythms of development. Here, these rhythms are discussed from the point of view of L-systems and Petri nets which, although theoretical devices, can bring insights into the possible biological components or processes which establish the rhythms.

11.1 Introduction

More than 100 years ago, Charles Darwin and his son Francis found themselves fascinated by the oscillations of roots, shoots and tendrils, and these they meticulously described in their book ‘The power of movement in plants’ (Darwin and Darwin 1880). Their view was that the growing points of plants as well as their newly produced branches were in a state of continuous rotation, or else they manifested some other form of rhythmic agitation. With the assistance of sophisticated methods of recording and analysing organ growth (e.g. Iwamoto et al. 2006), some of the physical and physiological bases of these oscillations are now becoming better known. Although many of the Darwins’ descriptions related to oscillations of either full-grown or actively growing plant parts, rhythmic and periodic phenomena are now also known to accompany the genesis of new organs at the plant’s meristematic apices. The importance of these organogenetic rhythms is that they lead directly to a repetitious, or modular, type of construction (Notov 2005) which, for higher plants, is vital for their reproduction (sexual and asexual) and their vegetative movements (for example, shoot tropisms involving the repeatedly produced
nodes which comprise the stems of grasses). However, rhythmic formary
activities leading to the development of modular constructions are also found
in ‘lower’ organisms, such as the cyanobacteria (blue-green algae). In this
chapter, we shall describe some examples of rhythmic morphogenesis in both
simple cyanobacteria as well as in more complex higher plants.

Fundamental to analyses of the regulation of growth rhythms in plants is
a representation of the organism as it exists in time. Therefore, it is necessary
to be sure that the interval between observations does not lead to loss of any
information which might shed light on the regulatory factors of development
(Barlow and Powers 2005). Moreover, as will become evident in the present
chapter, we contend that it is desirable to adopt some theoretical framework
which provides a context for the observations made, and which may also, in
time, provide a general model for certain types of organogenetic phenomena
in plants.

11.2 Developmental Theories and Their Application
to Rhythmic Morphogenesis

What are these theoretical frameworks and, importantly, what do they con-
tribute to the study of the rhythms of plant development? In the present case,
we have made use of two methodologies for the exploration of theoretical
pathways of development, which can then be juxtaposed with actual observa-
tions: L-systems (Lindenmayer 1971; Lindenmayer and Jürgensen 1992) and

L-systems handle the transformation of states which, in the present context,
are held to be comprised of a set of biological features which may be
morphological, physiological or structural. The transition between one state
and another occurs during a timestep. When coupled with growth, state trans-
formations comprise the basis of organismic development. If the transitions
are deterministic – that is, if one state is invariably followed by some other
particular state – and if a series of states and their transitions are recurrent,
then a cyclical or oscillating system becomes manifest. The sequence of devel-
opmental changes which emerge is cumulative; the results of former state
transformations are not erased but are added to at each timestep, thereby
bringing about a gradual ‘metamorphosis’ of organic form. The L-systems
discussed in the present chapter are deterministic (D) and interactionless
(0) or with interaction (I), i.e. D0L-systems or DIL-systems, respectively.
The timescale of development is defined by the timesteps which, in turn,
are related to the discreteness of the steps chosen as representative markers
of change.

A Petri net is a set of potential states (represented, in this context, by places
or conditions, but otherwise a ‘state’ is defined as above for L-systems),
events and connecting arcs. A simple net, as opposed to a stochastic net, has