# Preface

The purpose of this book is to review our current knowledge of endogenous rhythms in plants. In preparing this book we have focused almost exclusively on circadian rhythms, which are the most thoroughly characterised and widespread of these. Circadian rhythms are biological rhythms that repeat once a day, persist in constant conditions, are entrained to local time and maintain a constant periodicity over a broad range of physiological temperatures. The value of a correctly adjusted circadian oscillator should be easily appreciated by anyone who has travelled between several time zones and suffered from jet-lag, the result of a rapid desychronisation between the internal clock and the surrounding environment.

Plants have played an important role historically in the study of circadian rhythms. As early as 1727, an astronomer De Mairan observed experimentally that rhythms in leaf movement continued in the absence of daily cues. In 1835 similar experiments using *Mimosa pudica* were performed by Candolle. He confirmed the results from a century earlier and went on to demonstrate that these rhythms did not re-occur with a periodicity of exactly 24 hours (and therefore were not a direct response to day and night) but instead had a periodicity that was shorter by one to one and half hours.

In the later part of the nineteenth century Charles Darwin also became interested in the phenomenon, culminating in the publishing of his book 'The Power of Movement in Plants' in 1881. In the early part of the twentieth century Erwin Bünning lead the field of circadian biology hypothesising that circadian rhythms have an adaptive value for organisms and that the rhythms are driven by an endogenous clock. In the mid-twentieth century two researchers Pittendrigh and Aschoff drove the emerging field of chronobiology. The end of the twentieth century has seen the identification of components of molecular oscillators in the model plant *Arabidiopsis* as well as *Drosophila*, Cyanobacteria, mice and *Neurospora*. Intriguingly while the molecular mechanism appears similar across a variety of groups of organisms, there is little conservation of the components used, with only the molecular components of the *Drosophila* and mice clock sharing homology.

Much of our understanding of the mechanism of the circadian clock in plants has come from the development of *Arabidopsis thaliana* as a model circadian organism. Critical to this has been the development of robust high-through put assays for measuring circadian rhythms in this plant. Among these, the development by Millar and Kay of promoter luciferase fusions, which allow measurement of rhythmic changes in promoter activity, have provided the greatest stride forward in understanding the interaction of components of the circadian system. The ability to assay the clock in *Arabidopsis* has allowed the exploitation of a huge number of international resources developed for the dissection of the biology of this model species. Over the past five years the field has made huge advances, identifying photoreceptors involved in entrainment and key components likely to play a pivotal role in the central oscillator. Furthermore, through the pioneering use of micro-array technology, which has identified the coupling of nearly 10% of the transcriptome to the circadian clock, we now have an idea about the extent of the clock's function in regulating the biology of the plant; finally, we have also identified at the molecular level the function of the clock in the control of photoperiodism. Together this new understanding very much supports the hypothesis of Bünning, that circadian rhythms, driven by an endogenous oscillator, have an adaptive value for organisms.

This book not only describes where the field currently stands, it brings together and summarises decades of research. Moreover, all the authors are key figures at the cutting edge of plant circadian research today. The book also provides clear and thought provoking insights into the direction of future plant circadian research.

At its simplest level the circadian system can be visualised as a three component pathway. In this model, the circadian system is divided into three parts: a photoreceptor or photoreceptors, the central oscillator, and the output pathways which culminate in the overt rhythm under examination, the actual 'hands' of the circadian clock. The central oscillator generates the rhythm. This has a period length of usually a little more or less than twenty-four hours. In the absence of an appropriate *zeitgeber* ('time-giver'), such as day and night, the oscillator free-runs to reveal the endogenous period length of the circadian system; however it responds to environmental information received as input from the photoreceptors. The entrained oscillator then interacts with downstream pathways to control the many overt rhythms of the organism, such as leaf movement, activation of the photosynthesis machinery or starch mobilisation.

We have taken this simplistic model as the basis for the layout of this book. Each chapter has been contributed by authors who are actively contributing to this dynamic and fast moving area of plant science. The first three chapters focus on the central oscillator. Chapter 1 outlines the current view of the molecular mechanism of the clock, focusing on a central feedback loop made up of three proteins CCA1, LHY and TOC1. Chapter 2 discusses the roles of other members of the *TOC1/PRR* family on modulating the circadian system and its outputs; this five member gene family contains the central clock component *TOC1* but also four other closely related genes, each of which affects multiple circadian outputs. Chapter 3 considers additional oscillators downstream of and controlled by the central clockwork, in particular the so-called 'slave oscillators', circadian feedback loops resembling those of the clock but whose rhythms are set by the central clockwork.

Chapters 4 and 5 consider photoperception and the mechanisms of light signal transduction (input) to the oscillator are described. In chapter 4, evidence for a role for phytochromes and crytochrome, together with a novel set of blue light photoreceptors in entrainment of the clock, is summarised. This chapter goes on to describe how the clock itself can regulate or "gate" light input blurring the boundary between input, oscillator and output. Finally, it describes our current understanding of thermal entrainment, including recent research identifying a role for *APRR7* and *APRR9*. Chapter 5 gives an in-depth overview of the huge field of plant photoperception, describing the structure and function of each class of photoreceptor and our current understanding of the mechanisms of signal transduction.

The set of chapters discuss the control of processes (outputs) by the circadian clock. In chapter 6, circadian regulation of the transcriptome is described, highlighting the broad range of biological processes regulated by the plant clock. This chapter summarises recent metabolic data and tries to reconcile discrepancies between the transcription regulation by the clock and rhythms in metabolism. Chapter 7 describes the role of the clock in the photoperiodic regulation of flowering. In chapter 8 the role of $Ca^{2+}$ in the architecture of the mammalian clock is described, contrasting this with our current understanding of the function of $Ca^{2+}$ in the plant circadian system. It is not yet clear where $Ca^{2+}$ fits in the plant circadian system; however the authors consider possible functions in transducing light signals, the core oscillator function and conferring rhythmicity on physiological processes. Chapter 9 summarises our current understanding of the clock in a class of plants capable of crassulacean acid metabolism (CAM), focusing on how CAM metabolism itself is regulated by the clock. Finally, chapter 10 discusses how and why the circadian clock has evolved, considering the evidence that possession of a clock enhances fitness in an organism.

We hope this book will provide an exciting and stimulating insight into this rapidly developing field of plant circadian biology. Our book is designed to appeal to the circadian researchers, primarily those based in plant sciences, but we expect it to be of interest and value to the wider circadian field as this is a discipline where research in one model system frequently informs work on another. It is becoming apparent that the circadian clock is having a broad influence on the biology of the plant and as such we hope this book will be of interest to the wider plant science research and teaching communities. It will also be of use to undergraduates and graduate students taking courses in areas of plant signalling, development and environmental responses.