

Contents

Contributors	xiii
Preface	xvii
1 The plant circadian clock: review of a clockwork <i>Arabidopsis</i>	1
FRANK G. HARMON, TAKATO IMAIZUMI AND STEVE A. KAY	
1.1 Introduction	1
1.2 How plant circadian biology got to where it is today	1
1.2.1 Forward genetics	1
1.2.1.1 Direct circadian screens – TOC1, ZTL, TEJ, TIC, LUX	1
1.2.1.2 Non-circadian forward genetic screens – LHY, ELF3, ELF4	4
1.2.2 Reverse genetics – CCA1, PRR3-PRR9	5
1.3 How the components were placed in the plant clock?	6
1.3.1 CCA1, LHY, and TOC1 contribute to a feedback loop at the core of the oscillator	7
1.3.2 The interplay between TOC1 and ZTL sets circadian period	9
1.3.3 PRR7 and PRR9 form a feedback loop that affects CCA1 and LHY expression	9
1.4 Current framework for understanding the <i>Arabidopsis</i> clock	10
1.5 What may pave the way to greater understanding of the clock	12
1.5.1 Forward genetics	12
1.5.2 Genomics and functional genomics	14
1.5.3 Transient functional assays	16
1.5.4 Characterizing protein modification	17
1.6 Conclusion	18
References	18
2 Pseudo-response regulator genes ‘tell’ the time of day: multiple feedbacks in the circadian system of higher plants	25
SHIGERU HANANO AND SETH J. DAVIS	
2.1 Introduction	25
2.2 History of the circadian system	25
2.2.1 The CCA1/LHY- TOC1 model for the <i>Arabidopsis</i> clock	27
2.3 An overview of the phosphorelay two-component system in <i>Arabidopsis</i>	28
2.3.1 AHK and AHP genes involved in the phosphorelay system of <i>Arabidopsis</i>	28
2.3.2 <i>Arabidopsis</i> response regulators	30
2.4 Pseudo-response regulators	31

2.5	Circadian regulation of TOC1/PRR family: CCA1/LHY-TOC1 feedback model and circadian wave form of the TOC1/PRR family	32
2.5.1	Regulation of TOC1 expression	33
2.5.2	Interactions between TOC1 and other PRR family members	34
2.5.3	The role of the evening element in PRR9 regulation	35
2.5.4	Interactions between PRRs and clock components	35
2.6	A detailed description of signal convergence in the <i>PRR</i> genes	36
2.6.1	TOC1/PRR1, At5g61380	36
2.6.1.1	Toc1-2 and TOC1 mini-gene mutants	36
2.6.1.2	TOC1 and phytochrome	38
2.6.1.3	TOC1 and flowering time	38
2.6.2	PRR9, At2g46790	38
2.6.3	PRR7, At5g02810	40
2.6.4	PRR5, At5g24470	41
2.6.5	PRR3, At5g60100	42
2.7	Phylogenetic and epistatic relations between the PRRs	42
2.8	Partners of PRR proteins	44
2.8.1	PIF3-like family	44
2.8.2	ZTL family	44
2.8.3	Other interactions	45
2.9	A brief overview of PRRs in other plants	45
2.10	Perspective	46
2.10.1	Limitations of the current model	48
	Acknowledgements	50
	References	50

3 Multiple and slave oscillators 57

DOROTHEE STAIGER, CORINNA STREITNER, FABIAN
RUDOLF AND XI HUANG

3.1	Introduction	57
3.2	Central and peripheral oscillators in the mammalian timing	58
3.3	Organization of the timing system in plants	60
3.3.1	Are clocks localized in different parts of the plant?	61
3.3.2	Does the same type of clock control rhythms in distinct parts of the plant?	62
3.3.3	Do individual clocks interact with each other?	64
3.3.4	Do chloroplasts retain remnants of a clock of an endosymbiotic ancestor?	65
3.4	Molecular organization of the clock within a plant cell	66
3.5	Linking gene expression to the clockwork – how output genes are regulated	66
3.5.1	Transcriptional control of output genes	66
3.5.2	Identification of cycling transcription factors mediating rhythmic output	67
3.5.3	Post-transcriptional control	68
3.5.3.1	RNA stability	70
3.5.3.2	Polyadenylation	70

3.5.3.3 Splicing	71
3.5.3.4 Translational control mediated by a new class of RNA-binding proteins	71
3.5.4 RNA-based regulation: The role of an antisense RNA	72
3.5.5 Control by second messengers: do Ca^{2+} ions mediate rhythmic output?	72
3.6 Slave oscillators	73
3.6.1 The clock-regulated RNA-binding protein ATGRP7 in <i>Arabidopsis thaliana</i>	73
3.6.2 Transcriptional feedback loop as slave oscillator: EPR1	75
3.7 Summary	76
References	78
4 Entrainment of the circadian clock	85
DAVE SOMERS	
4.1 Introduction	85
4.2 Light perception and entrainment	86
4.2.1 Phytochromes	86
4.2.2 Cryptochromes	88
4.2.3 A novel family of blue light photoreceptors?	90
4.3 Signal transduction and interaction	92
4.3.1 ZTL and phototransduction: phy and cry photoreceptors	92
4.3.2 ZTL and phototransduction: ELF3	92
4.3.3 Other potential photoentrainment intermediates	95
4.4 Coupling to the central oscillator	96
4.5 Circadian gating of photic input	97
4.6 Thermal entrainment	99
4.7 Conclusion	100
References	101
5 Photoreceptors and light signaling pathways in plants	107
VICTORIA S. LARNER, KEARA A. FRANKLIN AND GARRY C. WHITELAM	
5.1 Introduction	107
5.2 Photoreceptor structures	108
5.2.1 Phototropin structure	108
5.2.2 Cryptochrome structure	109
5.2.3 Phytochrome structure	110
5.3 Photoreceptor functions	111
5.3.1 Phototropin functions	111
5.3.2 Cryptochrome functions	112
5.3.3 Phytochrome functions	113
5.4 Cellular and sub-cellular localization of photoreceptors	115
5.4.1 Phototropin localization	115
5.4.2 Cryptochrome localization	115
5.4.3 Phytochrome localization	115

5.5	Photoreceptor signaling	117
5.5.1	Post-translational Phosphorylation	117
5.5.2	Cytosolic signaling mechanisms	118
5.5.3	Regulation of protein degradation	119
5.5.4	Photoreceptor interacting proteins	120
5.6	Crosstalk in photoreceptor signaling	123
5.6.1	Integration of environmental signals	123
5.6.2	Integration of light and endogenous signals	123
5.7	Conclusions	124
	References	125
6	Circadian regulation of global gene expression and metabolism	133
	STACEY L. HARMER, MICHAEL F. COVINGTON, OLIVER BLÄSING AND MARK STITT	
6.1	Circadian rhythms in transcription	133
6.1.1	Monitoring rhythms of transcription	133
6.1.2	Circadian regulation of the transcriptome	135
6.2	Post-transcriptional circadian regulation	136
6.2.1	Proteomics	137
6.2.2	Metabolomics	137
6.3	Circadian regulation of transcription – what kinds of genes, and why?	138
6.3.1	Clock-associated genes	138
6.3.2	Slave oscillators	139
6.3.3	Genes encoding other regulatory proteins	139
6.4	Regulation of plant metabolism	139
6.4.1	Photosynthesis	140
6.4.2	Partitioning of fixed carbon	140
6.4.3	Nitrogen assimilation	141
6.4.4	Secondary metabolic pathways	142
6.5	Circadian regulation of plant growth and development	144
6.5.1	Plant growth	144
6.5.2	Hormone regulation	144
6.5.3	Control of flowering time	146
6.6	How is clock-regulation of gene expression achieved?	146
6.6.1	The evening element (EE)	146
6.6.2	Other circadian associated motifs	147
6.7	Cross-species comparisons	148
6.7.1	Are similar genes clock regulated in all organisms?	148
6.7.2	Rhythmic gene expression in photosynthetic species	149
6.8	Comparing gene expression in constant and diurnal conditions	151
6.8.1	Circadian rhythms vs. diurnal responses	151
6.8.2	Interactions between sugar and circadian regulation	153
6.9	Why have a clock rather than relying on driven rhythms?	155
6.9.1	Might anticipation be key?	155
6.9.2	Do transcript levels correlate with protein levels?	156

6.9.3	Why are the transcripts of stable proteins under circadian regulation?	156
6.10	Future prospects	157
	Acknowledgements	157
	References	158
7	Photoperiodic responses and the regulation of flowering	167
	ISABELLE CARRÉ, GEORGE COUPLAND AND JOANNA PUTTERILL	
7.1	Introduction to photoperiodism	167
7.2	Models for the measurement of day length	168
7.2.1	The hourglass timer	168
7.2.2	The circadian clock	168
7.3	Internal and external coincidence models	170
7.4	Arabidopsis molecular genetics identifies a regulatory pathway that controls flowering in long photoperiods	170
7.4.1	The GI-CO-FT regulatory hierarchy	171
7.4.2	Role of CO and FT in long-distance day-length signaling	174
7.5	Regulation of the Arabidopsis photoperiod pathway: molecular evidence in favor of the coincidence model	175
7.5.1	CO: a major link between photoperiod and the circadian clock	175
7.5.2	How does light coincidence with CO mRNA expression result in the induction of FT transcription?	177
7.5.3	Summary of the evidence in support of the external coincidence model of the photoperiodic regulation of flowering and a role for CO	178
7.6	Interaction between photoperiod pathway and other flowering-time pathways in Arabidopsis	178
7.6.1	Convergence of the photoperiod and vernalization pathways	178
7.6.2	Other pathways converging with the photoperiod pathway?	180
7.7	Comparative analysis of photoperiod regulation in rice and Arabidopsis	180
7.8	Perspectives	183
	References	185
8	Circadian regulation of Ca^{2+} signaling	191
	MICHAEL J. GARDNER, ANTONY N. DODD, CARLOS T. HOTTA, DALE SANDERS, AND ALEX A. R. WEBB	
8.1	Introduction	191
8.2	Ca^{2+} signaling is ubiquitous and versatile	191
8.2.1	Transduction of extracellular signals	191
8.2.2	Spatio-temporal dynamics of $[\text{Ca}^{2+}]_{\text{cyt}}$ increases	191
8.2.3	Circadian oscillations of cytosolic free calcium	193
8.3	The cellular basis of circadian oscillations of plant $[\text{Ca}^{2+}]_{\text{cyt}}$	195
8.3.1	Mechanisms controlling $[\text{Ca}^{2+}]_{\text{cyt}}$ influx	195
8.3.2	So how does the clock control Ca^{2+} influx?	195

8.4	The cellular basis of circadian oscillations of $[Ca^{2+}]_{cyt}$ in mammals	196
8.4.1	The mammalian circadian clock	196
8.4.2	A role for glutamate and cADPR-sensitive ryanodine receptor induced Ca^{2+} release in the entrainment of the mammalian clock	196
8.4.3	The source of $[Ca^{2+}]_{cyt}$ influx	198
8.5	A comparison of the circadian regulation of Ca^{2+} homeostasis in both SCN and plant cells	198
8.5.1	cADPR is a key player in mammalian circadian behaviour	199
8.5.2	A role for nitric oxide in plant clock	199
8.6	Molecular regulation of circadian Ca^{2+} signaling	200
8.6.1	Circadian influx of Ca^{2+} to the cytosol	200
8.6.2	Circadian efflux of Ca^{2+} from the cytosol	202
8.6.3	Ca^{2+} sensor proteins	202
8.7	Physiological targets for circadian oscillations of $[Ca^{2+}]_{cyt}$	203
8.7.1	Difficulties in assigning of physiological function to oscillations in $[Ca^{2+}]_{cyt}$	203
8.7.2	A role for Ca^{2+} in the photoperiodic control of flowering	204
8.8	Conclusions and future prospects	205
	Acknowledgements	205
	References	205
9	The circadian clock in CAM plants	211
	JAMES HARTWELL	
9.1	Introduction	211
9.2	The daily cycle of metabolism in CAM plants	211
9.2.1	Discovery of a circadian rhythm of CO_2 fixation in CAM species	212
9.2.2	CAM CO_2 output rhythms in constant darkness, CO_2 -free air, $15^\circ C$	213
9.2.3	CAM CO_2 -assimilation rhythms in constant light and normal air	214
9.3	Phase responses of CAM CO_2 rhythms	215
9.3.1	Light induced phase shifts	215
9.3.2	Temperature induced phase shifts	216
9.4	The biochemical basis for the circadian rhythm of CO_2 fixation	217
9.4.1	PEPc phosphorylation rhythms	217
9.4.2	Regulation of PEPc phosphorylation	218
9.4.3	Regulation of PEPc kinase activity	218
9.4.4	The contribution of PEPc and Rubisco to CAM CO_2 fixation rhythms	219
9.4.5	The influence of temperature on rhythms of PEPc activity	220
9.4.6	Cloning the PEPc kinase gene from CAM plants	221
9.4.7	Regulation of PPCK	222
9.5	Multiple points of clock control within the CAM pathway?	223
9.6	The molecular identity of the central oscillator in CAM species?	224
9.6.1	The tonoplast-as-oscillator?	225
9.6.2	Is the CCA1/LHY-TOC1 oscillator controlling CAM rhythmicity?	226
9.7	Future perspectives and unanswered questions	229
9.7.1	Starch synthesis rhythms in CAM plants	230
9.7.2	Stomatal rhythms in CAM plants	231

9.7.3	Multiple origins of CAM	232
9.7.4	Insights from CAM plants	233
	Acknowledgements	234
	References	234
10	Clock evolution and adaptation: whence and whither?	237
	CARL HIRSCHIE JOHNSON AND CHARALAMBOS P. KYRIACOU	
10.1	Introductory quotation	237
10.2	Setting the stage: the appearance of circadian clocks	237
10.3	Putative selective pressures	238
10.3.1	Temporal separation of metabolic events	239
10.3.2	'Escape from light'	239
10.4	Cyanobacteria and the first clock genes	241
10.5	The appearance of clocks in photosynthetic eukaryotes	242
10.5.1	Absence of clock gene homologues across taxa	243
10.5.2	Regulatory homologues do exist across taxa	244
10.6	Clocks are widespread in plants: mosses, gymnosperms and angiosperms	244
10.6.1	Clocks in 'primitive' plants	245
10.7	Rhythms controlled by the 'Clockwork Green'	245
10.7.1	Photoperiodic time measurement	246
10.8	Why not an hourglass timer?	247
10.8.1	Advantages of a self-sustained oscillator	247
10.9	The clock as an adaptation: past and present	248
10.10	The circadian clock as an adaptation	249
10.11	Experimental tests of adaptive significance before 1980	249
10.12	Laboratory studies of circadian clocks and reproductive fitness since 1980	251
10.12.1	Advantages of cycles that resonate with the environment	251
10.12.2	Testing clock conferred advantages in other species	253
10.13	Evidence that the clock is still adaptive from studies of organisms in natural environments	254
10.13.1	Environmental gradients	254
10.13.2	Quantitative trait locus analysis	255
10.14	Clocks: Where did they come from? What are they doing now?	255
	Acknowledgements	256
	References	256
	Index	261