



Contents lists available at ScienceDirect

# Plant Science

journal homepage: [www.elsevier.com/locate/plantsci](http://www.elsevier.com/locate/plantsci)



## Review

## Iron around the clock

1  
2  
3 **Qi** Nicolas Tissot, Jonathan Przybyla-Toscano<sup>1</sup>, Guilhem Reyt, Baptiste Castel, Céline Duc<sup>2</sup>,  
4 Jossia Boucherez, Frédéric Gaymard, Jean-François Briat\*, Christian Dubos\*

5 *Laboratoire de Biochimie et Physiologie Moléculaire des Plantes (INRA, CNRS, Montpellier SupAgro, Université Montpellier 2), 34060 Montpellier Cedex 2,*  
6 *France*

### ARTICLE INFO

82  
83  
84  
85  
86  
87  
88  
89  
90  
91  
92  
93  
94  
95  
96  
97  
98  
99  
100  
101  
102  
103  
104  
105  
106  
107  
108  
109  
110  
111  
112  
113  
114  
115  
116  
117  
118  
119  
120  
121  
122  
123  
124  
125  
126  
127  
128  
129  
130  
131  
132  
133  
134  
135  
136  
137  
138  
139  
140  
141  
142  
143  
144  
145  
146  
147  
148  
149  
150  
151  
152  
153  
154  
155  
156  
157  
158  
159  
160  
161  
162  
163  
164  
165  
166  
167  
168  
169  
170  
171  
172  
173  
174  
175  
176  
177  
178  
179  
180  
181  
182  
183  
184  
185  
186  
187  
188  
189  
190  
191  
192  
193  
194  
195  
196  
197  
198  
199  
200  
201  
202  
203  
204  
205  
206  
207  
208  
209  
210  
211  
212  
213  
214  
215  
216  
217  
218  
219  
220  
221  
222  
223  
224  
225  
226  
227  
228  
229  
230  
231  
232  
233  
234  
235  
236  
237  
238  
239  
240  
241  
242  
243  
244  
245  
246  
247  
248  
249  
250  
251  
252  
253  
254  
255  
256  
257  
258  
259  
260  
261  
262  
263  
264  
265  
266  
267  
268  
269  
270  
271  
272  
273  
274  
275  
276  
277  
278  
279  
280  
281  
282  
283  
284  
285  
286  
287  
288  
289  
290  
291  
292  
293  
294  
295  
296  
297  
298  
299  
300  
301  
302  
303  
304  
305  
306  
307  
308  
309  
310  
311  
312  
313  
314  
315  
316  
317  
318  
319  
320  
321  
322  
323  
324  
325  
326  
327  
328  
329  
330  
331  
332  
333  
334  
335  
336  
337  
338  
339  
340  
341  
342  
343  
344  
345  
346  
347  
348  
349  
350  
351  
352  
353  
354  
355  
356  
357  
358  
359  
360  
361  
362  
363  
364  
365  
366  
367  
368  
369  
370  
371  
372  
373  
374  
375  
376  
377  
378  
379  
380  
381  
382  
383  
384  
385  
386  
387  
388  
389  
390  
391  
392  
393  
394  
395  
396  
397  
398  
399  
400  
401  
402  
403  
404  
405  
406  
407  
408  
409  
410  
411  
412  
413  
414  
415  
416  
417  
418  
419  
420  
421  
422  
423  
424  
425  
426  
427  
428  
429  
430  
431  
432  
433  
434  
435  
436  
437  
438  
439  
440  
441  
442  
443  
444  
445  
446  
447  
448  
449  
450  
451  
452  
453  
454  
455  
456  
457  
458  
459  
460  
461  
462  
463  
464  
465  
466  
467  
468  
469  
470  
471  
472  
473  
474  
475  
476  
477  
478  
479  
480  
481  
482  
483  
484  
485  
486  
487  
488  
489  
490  
491  
492  
493  
494  
495  
496  
497  
498  
499  
500

### Keywords:

Iron homeostasis  
Circadian clock  
Chloroplast  
Retrograde signalling  
*Arabidopsis thaliana*

### ABSTRACT

Carbon assimilation, a key determinant of plant biomass production, is under circadian regulation. Light and temperature are major inputs of the plant clock that control various daily rhythms. Such rhythms confer adaptive advantages to the organisms by adjusting their metabolism in anticipation of environmental fluctuations. The relationship between the circadian clock and nutrition extends far beyond the regulation of carbon assimilation as mineral nutrition, and specially iron homeostasis, is regulated through this mechanism. Conversely, iron status was identified as a new and important input regulating the central oscillator, raising the question of the nature of the Fe-dependent signal that modulates the period of the circadian clock. Several lines of evidence strongly suggest that fully developed and functional chloroplasts as well as early light signalling events, involving phytochromes, are essential to couple the clock to Fe responses. Nevertheless, the exact nature of the signal, which most probably involves unknown or not yet fully characterized elements of the chloroplast-to-nucleus retrograde signalling pathway, remains to be identified. Finally, this regulation may also involves epigenetic components.

© 2014 Published by Elsevier Ireland Ltd.

### Contents

Introduction .....	00
Clock regulation of Fe homeostasis .....	00
Fe as an input regulating the clock .....	00
Towards the identification of the signal coupling Fe homeostasis to the circadian clock.....	00
Epigenetic effectors.....	00
Conclusion .....	00
Acknowledgements .....	00
References .....	00

### Introduction

Circadian clocks control various daily rhythms in organisms, providing them with a competitive advantage [1]. Input signals

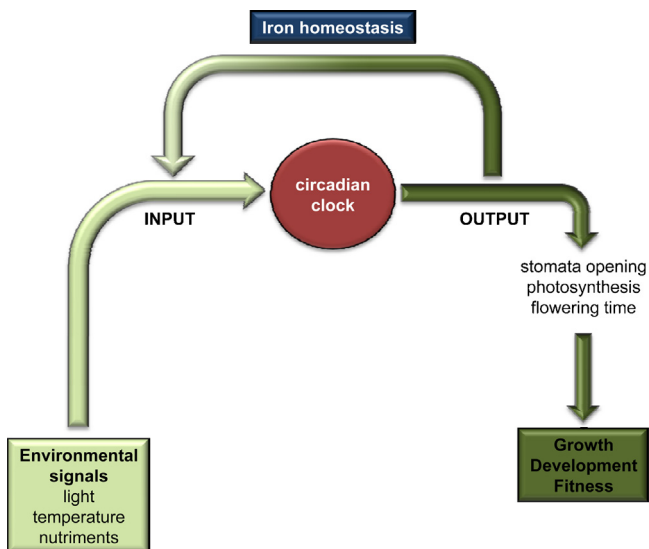
adapt the phase of rhythms in plants to local environmental changes through the central oscillator. The central oscillator is a complex network of interlocked feedback loops involving numerous transcriptional regulators. Central to this network is a feedback loop that connects the morning and evening part of the circadian clock regulatory circuit. This loop is composed of two morning-expressed R1/2-MYB transcription factors [2] CIRCADIAN CLOCK ASSOCIATED 1 (CCA1) and LATE ELONGATED HYPOCOTYL (LHY), and of the evening-phase transcriptional repressor TIMING OF CAB EXPRESSION 1/PSEUDO-RESPONSE REGULATOR 1 (TOC1/PRR1) [3]. Although most of the regulations of the clock occur at the transcriptional level, post-transcriptional and post-translational regulations are also concerned. For example, the evening loop component ZEITLUPE (ZTL) is a F-box protein that targets the highly

\* Corresponding authors at: Bat 7, Campus INRA/SupAgro, Place Viala, 34060 Montpellier Cedex 1, France. Tel.: +33 04 99 61 26 13/29 32.

E-mail addresses: [briat@supagro.inra.fr](mailto:briat@supagro.inra.fr) (J.-F. Briat), [christian.dubos@supagro.inra.fr](mailto:christian.dubos@supagro.inra.fr), [christian.dubos@versailles.inra.fr](mailto:christian.dubos@versailles.inra.fr) (C. Dubos).

<sup>1</sup> Present address: Université de Lorraine, Interactions Arbres – Microorganismes, UMR1136, F-54500 Vandoeuvre-lès-Nancy, France.

<sup>2</sup> Present address: Génétique, Reproduction et Développement, CNRS UMR6293, Clermont Université, INSERM U1103, 24 avenue des Landais, 63171 Cedex Aubière, France.



**Fig. 1.** Schematic representation of the reciprocal interaction existing between iron homeostasis and the circadian clock. The regulation of plant iron homeostasis is under circadian regulation, controlling optimal distribution of iron pools at the cellular and sub-cellular levels throughout plants. Iron status of the plant is modified depending on iron availability in the soil solution, which in turn alter circadian clock periodicity that adapt plant physiology to its new environment.

phosphorylated forms of TOC1 for ubiquitylation and subsequent degradation by the proteasome [4]. Conversely, the interaction of TOC1 with PRR3 prevents its ZTL-mediated degradation [4].

Light and temperature are the major inputs of the clock [5]. Many biological processes including stomatal opening [6], photosynthesis [1], and flowering [7] are outputs of the circadian clock, through the re-programming of expression of various gene sets [8]. More recently, nitrogen, copper, magnesium [9–11] as well as iron [12,13] mineral nutrition has been shown to be regulated by the clock. They constitute another important input acting on the expression of central oscillator genes (Fig. 1) [12–14].

Photosynthesis efficiency is also dependent upon mineral nutrition in addition to light, temperature and the circadian clock. Fe, among metals, has a major role in this process because of its redox properties within proteins of the electron transport chain. Altered Fe homeostasis in *Arabidopsis thaliana* mutants lacking the iron storage protein ferritin in their leaves had impaired carbon assimilation, resulting in a decrease in biomass production [15]. Because Fe homeostasis and photosynthesis are interdependent and both are regulated by the circadian clock ([16]; Fig. 1), it is a major issue to understand how these various determinants of biomass production are integrated into the physiology of plants. In addition to its major role in the photosynthesis process, Fe is also required for respiration, DNA synthesis, nitrogen and sulphur assimilation, and hormone synthesis. Furthermore, Fe being highly reactive with oxygen, it can produce reactive oxygen species (ROS), which are potentially toxic for cell structures [15]. As a consequence Fe content, speciation and distribution in plants need to be finely tuned through the control of Fe homeostasis.

This paper highlights recent new developments that put forward a link between Fe homeostasis and the circadian clock. The principal aim is to propose a critical review of our understanding of the control of Fe homeostasis by the clock, and the impact of Fe nutrition on the expression of clock components. To what extent clock and Fe regulatory circuits can be integrated into a comprehensive scheme will contribute to improve our understanding of the mechanisms by which plants adapt to their fluctuating environment.

## Clock regulation of Fe homeostasis

Fe homeostasis in plants results from the action of integrated regulatory pathways controlling the expression of genes at the transcriptional and post-transcriptional levels. The activation or repression of these genes depends on Fe availability, namely Fe scarcity or Fe excess [17]. These genes encode proteins that are required for Fe uptake by the roots, Fe distribution throughout the whole plant body, and intracellular compartmentation and storage [18,19].

Gramineous plants (cereals) use a chelation strategy to acquire Fe from the soil. Their roots secrete methionine derivatives from the mugineic acid family of phytosiderophores (MAs), which chelate and solubilize Fe(III) in the rhizosphere. The resulting Fe(III)–MAs complexes are taken up by root cells. This MA secretion by roots fluctuates throughout the day in a diurnal manner [20]. For example, MAs secretion from barley roots occurs within 2–3 h after sunrise under Fe-deficient conditions. This rhythmic secretion of phytosiderophores in cereals is mainly mediated by changes in light rather than temperature [21]. Furthermore, large-scale expression analysis of Fe-deficiency stressed barley roots revealed that among the genes whose mRNA steady state level was increased, 25% exhibited different abundance levels in Fe-deficient roots at noon and at night [22]. However, these studies do not address whether these regulations are driven by light independently of the circadian clock. In addition, among the genes highlighted by this transcriptomic approach, no Arabidopsis orthologous genes encoding clock components (e.g. *CCA1*, *LHY*, etc.) have been identified.

The first molecular evidence that Fe homeostasis was connected to the clock came from a genetic screen designed to search for regulators of the expression of the Arabidopsis *AtFer1* ferritin gene, encoding a Fe storage protein located in the plastids [23]. *TIME FOR COFFEE* (*TIC*), a previously described regulator of the circadian clock [24,25], repressed *AtFer1* expression. This finding prompted determining whether *AtFer1* was a cycling gene (i.e. whose expression is rhythmically regulated by the circadian clock). Indeed *AtFer1* cycles with peak expression at dawn. Cycling is abolished in genetic backgrounds mutated for genes of the central oscillator such as *cca1-11* or *lhy-21*. Regulation of ferritin genes (*AtFer1*, *AtFer3* and *AtFer4*) expression by the clock was confirmed by showing that they are direct transcriptional targets of PRR7, a central clock component [26]; PRR7 being involved in the adaptation to iron excess. Furthermore, the promoter activities of *AtFer1* and two other genes involved in the Fe deficiency response (namely *IRT1*, for *IRON-REGULATED TRANSPORTER 1*, the major Fe<sup>2+</sup> transporter in roots, and *bHLH39*, a key transcription factor involved in this process) are under circadian control [27].

## Fe as an input regulating the clock

Three independent studies have recently demonstrated that the period length of the circadian clock is directly modulated by the iron status of Arabidopsis plants. The period is longer under Fe-deficient conditions and shorter under Fe-excess conditions [12–14].

The impact of iron status on the periodicity of the expression of key central oscillator genes was evaluated through the analysis of their promoter activity using the luciferase reporter gene (Tables 1 and 2). This analysis demonstrated that the period length of all the studied circadian clock genes was affected in a Fe-dependent manner, with a greater effect on *CCA1* and *TOC1* promoter activities [12–14]. These variations in the period length are quantitative and directly dependent on the amount of Fe actually available for the plant. This finding was also observed at the mRNA steady state levels [12]. However, the periodicity of the circadian oscillations is also regulated at the post-translational level

Download English Version:

<https://daneshyari.com/en/article/8358270>

Download Persian Version:

<https://daneshyari.com/article/8358270>

[Daneshyari.com](https://daneshyari.com)