Endocytobiosis & Cell Res. 14, 33-44 (2001)

CIRCADIAN GENE EXPRESSION IN ANGIOSPERMS AND GYMNOSPERMS

BIRGIT PIECHULLA*, MONIKA BRINKER, KATJA JÄSCHKE[1], JAN W. KELLMANN, KIRSTEN WISSEL
University of Rostock, Department of Molecular Physiology and Biotechnology, Gertrudenstr. 11a, 18051 Rostock, FRG
[1] von Haller Institute of Plant Sciences, Untere Karspüle 2, 37073 Göttingen, FRG
* Author for correspondence: e-mail: birgit.piechulla@biologie.uni-rostock.de

Key words: Pinopsida, ginkgoopsida, cycadopsida, gnetopsida, circadian gene expression

INTRODUCTION

1985 appeared the first publication that plant genes are under the control of a circadian clock (Kloppstech 1985). This novel finding was documented for three light-induced genes encoding 1) the light harvesting complex proteins *(Lhc),* 2) the small subunit of the ribulose bisphosphate carboxylase *(rbcS)* and 3) the early light induced protein *(elip).* The phenomenon that mRNAs accumulate to different levels at different time points during 24 hours of observation as well as that these oscillations persisted under constant conditions (continuous darkness, continuous illumination, constant temperature) was evidence enough to hypothesize that an endogenous mechanism exists that controls the expression day time dependent. Furthermore, at least for some cases it was shown that the oscillation of mRNA levels is due to day time-dependent or gated transcription (Guiliano et al. 1988, Wehmeyer et al. 1991, Meyer 1993), however the influence of post-transcriptional processes can presently not be estimated. The daily time point to which transcription is gated varies for the different genes and therefore the time points when transcript levels reach their maxima depends very much on the gene, e.g. *Lhc* mRNAs reach their maximum around noon (Piechulla 1999), a catalase gene reaches its maximum late in the afternoon around dawn (Redinbaugh et al. 1990) and nitrate reductase mRNAs accumulate to maximum levels early in the morning significantly before sun rise (Galangau et al. 1988, Deng et al. 1990).

The existence of such a novel regulatory mechanism was manifested in the last 15 years, it is not only present in many different plant species but as well a number of different genes have been registered by now. There are at least 50 plant genes known to be under the control of a circadian clock (summarized in Table 1; Cremer et al. 1990 and 1991). The table documents that not only photosynthesis-

Table 1: Gene expression in angiosperms and gymnosperms

protein	gene	angiosperms	gymnosperms
1-aminocyclopropane-1-carboxylic acid oxidase	*acc* ox	circadian *(Stellaria)* (Kathiresan et al. 1996)	
aminolevulinic acid dehydratase	*ala*D(*hem*B)	diurnal *(Chlamydomonas)* (Matters and Beale 1995) diurnal *(Nicotiana)* (Papenbrock et al. 1999)	constant *(Pinus, Larix, Ginkgo)* (Piechulla et al. unpublished)
ATPase	*atp*A	circadian *(Chlamydomonas)*	
	*atp*B	circadian *(Chlamydomonas)* (Salvador et al. 1993)	
	atp C, D, G	(Oelmüller et al. 1995, Beator and Kloppstech 1994)	
biotin binding protein	bbp	circadian *(Lycopersicon)* (Giuliano et al. 1988)	
carbonic anhydrase	*cah* 1	circadian *(Chlamydomonas)* (Fujiwara et al. 1996)	
catalase	*cat*2	circadian *(Arabidopsis)* (Zhong et al. 1994, 1997)	
	*cat*3	circadian *(Zea)* (Redinbaugh & Scandalios 1990, Boldt and Scandalios 1995)	
circadian clock associated	cca1	circadian *(Arabidopsis)* (Wang & Tobin 1998)	
chalcone synthase	chs	diurnal *(Avena)* (Peter et al. 1991)	
coproporphyrinogen oxidase	*cpo*	diurnal *(Nicotiana)* (Papenbrock et al. 99)	
cysteine proteinase	*cyp*	circadian *(Nicotiana)* (Linthorst et al. 1993)	
early light induced protein	*elip*	circadian *(Pisum)* (Kloppstech 1985)	
elongation factor EF-Tu	*tuf*A	circadian *(Chlamydomonas)* (Salvador et al. 1993)	
ferredoxin	*pet* F	diurnal *(Spinacea)* (Beator 1994) circadian *(Lycopersicon)* (Bringloe et al. 1995)	
ferrochelatase	Fch	diurnal *(Nicotiana)* (Papenbrock et al. 1999)	
germin-like protein	*glp*	circadian *(Sinapis)* (Heintzen et al. 1994)	
glutamine synthetase	*gs*-2	diurnal *(Nicotiana)* (Becker et al. 1992)	
glutamyl tRNA reductase	*hem*A	circadian *(Hordeum)* (Bougri & Grimm 1996, Kruse et al. 1997) diurnal *(Nicotiana)* (Papenbrock et al 1999)	constant *(Pinus, Larix, Ginkgo)* (Piechulla et al. unpublished)
glutamyl semialdehyde aminotransferase		circadian *(Hordeum)* (Kruse et al. 1997) diurnal *(Nicotiana)* (Papenbrock et al 1999)	constant *(Pinus, Larix, Ginkgo)* (Piechulla et al. unpublished)
glycin rich protein	*grp*(*ccr*2)	circadian *(Arabidopsis)* (Heintzen et al 1997, Kreps and Simon 1997)	
high mobility group	HMG1	circadian *(Pharbitis)* (O'Neill & Zheng 1998)	
histone H1	H1c12	diurnal *(Nicotiana)* (Szekeres et al. 1995) circadian *(Lycopersicon)* (Corlett et al. 1998)	
late elongated hypocotyl	lhy	circadian *(Arabidopsis)* (Schaffer et al. 1998)	
leucin zipper protein	PNZIP	circadian *(Pharbitis)* (Zheng et al. 1998)	
light harvesting complex proteins	*Lhc*	circadian (many species) (summarized Piechulla 1999)	constant (several species)
Mg chelatase	*chl* I (ch42))	constant *(Nicotiana)* (Papenbrock et al. 1999)	constant *(Pinus, Larix, Ginkgo)* (Piechulla et al. unpublished)
	chl H, *chl* D	diurnal *(Nicotiana)* (Papenbrock et al. 1999)	
nitrate reductase	*nr*	circadian *(Nicotiana)* (Galangau et al. 1988, Deng et al. 1990, Pilgrimet al. 1993) diurnal *(Lycopersicon)* (Becker et al. 1992)	
nitrite reductase	*nir*	diurnal *(Lycopersicon)* (Becker et al. 1992)	

Table 1 continued

protein	gene	angiosperms	gymnosperms
oxygen evolving enzyme	*oee*	circadian (*Lycopersicon*) (Giuliano et al. 1988)	
phosphoenolpyruvate carboxylase	*pep*C	diurnal (*Sorghum, Zea*) (Thomas et al 1990)	
		constant (*Zea*) (Taylor et al. 1989)	
photosystem	*psa*D	circadian (*Lycopersicon*) (Guiliano et al. 1988)	
	*psa*F,E,D,G,H *pet*C, E, F, *psb* P,Q,R,S,O	diurnal (*Spinacea*) (Oelmüller et al. 1995, Beator and Kloppstech 1994)	
	*psb*D	circadian (*Triticum*) (Nakahira et al. 1998)	
plastocyanin		circadian (*Hordeum*) (Beator et al. 1994)	
protochlorophyllide oxidoreductase	*por* A, B	diurnal (*Hordeum*) (Holtorf and Apel 1996)	
rubisco	*rbc*S	circadian (*Pisum*) (Kloppstech 1985)	
		- (*Lycopersicon*) (Giuliano et al. 1988)	
		- (*Sorghum*) Childs et al. 1995)	
		diurnal (*Zea*) (Taylor et al. 1989)	
rubisco activase	*rca*	circadian (*Arabidopsis*) (Pilgrim and McClung 1993, Liu et al. 1996)	constant (*Gnetum*) (Piechulla et al. unpublished)
		diurnal (*Malus*) (Watillon et al. 1993)	
S-adenosylmethionine decarboxylase	*sam*DC	circadian (*Pharbitis*) (Yoshida et al. 1999)	
sigma factor	*sig*A	circadian (*Triticum*) (Morikawa et al. 1999)	
uroporphyrinogen	*uro*D	diurnal (*Nicotiana, Hordeum*) (Mock et al. 1995, Papenbrock et al. 1999)	
unkown function:			
	PN1	circadian (*Pharbitis*) (O'Neill et al. 1994)	
	PnC401	circadian (*Pharbitis*) (Sage-Ono et al. 1998)	
	clr and *ccr*	circadian (*Citrus*) (Abied and Holland 1994)	
	lir 1	circadian (*Oryza*) (Reimmann and Dudler 1993)	

related proteins but genes that encode proteins with a variety of different functions (e.g. ATP synthesis, chlorophyll biosynthesis, translation, DNA binding proteins, nitrate assimilation) exhibit this typical expression pattern.

DIFFERENT REGULATION OF ORCADIAN GENE EXPRESSION IN VASCULAR PLANTS

To learn more about the underlying mechanism a few genes were characterized in more detail, e.g. *Lhc* genes, *cat* genes, glycin rich protein gene *(grp)*. Most data have been accumulated for the prominently expressed *Lhc* genes (summarized in Piechulla 1999). 48 out of 49 *Lhc* genes from angiosperm species exhibit this typical circadian expression pattern, including the 19 individual members of the tomato gene family. Only one *Arabidopsis Lhc* gene shows constant mRNA levels throughout the day (Millar and Kay 1991). The characteristic rhythmic pattern was also observed in several algae, moss species and fern species (Oberschmidt et al. 1995) suggesting that this is an universal control process present in plant species throughout the plant kingdom, additionally suggesting that it is an evolutionary old process. In contrast to this apparently consistent theme, only three out of ten tested gymnosperm plant species exhibit diurnal or circadian changes of mRNA levels *(Dioon spinulosum, Gnetum gnemon, Pseudotsuga menziesii)* (Alosi et al. 1990; Oberschmidt et al 1995, Piechulla et al. unpublished). At present for seven gymnosperm species belonging to the subgroups Pinopsida, Gingkoopsida and Gnetopsida constant mRNA levels were determined.

Beside the importance of this different regulation at the level of gene expression it is interesting to ask whether this correlates with the specific physiology, morphology or habitat of these vascular plants. Many gymnosperms exhibit an evergreen phenotype. This is reflected in the differences in the anatomy of the leaves which are constructed to sustain several seasons, even under extreme growth conditions. It is possible that this persitance is also documented in the prolonged life span of thylakoid membranes and respective proteins. However, so far no differences in structure and component composition of chloroplasts and thylakoid membranes have been documented (Lewandowska and Öquist, 1980, Shinohara et al. 1992). Furthermore, there is not an unbroken correlation between the evergreen phenotype and the non-circadian expression since no mRNA oscillations are also found in gymnosperms with deciduous leaves (e.g. *Larix, Ginkgo)* or vice versa evergreen angiosperms (e.g. *Hedera helix, Rhododendron sp.)* which exhibit circadian mRNA oscillations (Table 2). Interestingly, it was recently shown that differences at the level of chlorophyll synthesis exist. While the last step in the chlorophyll biosynthesis pathway, the reduction of protochlorophyllide to chlorophyllide is a strictly light-dependent process in angiosperms, it was shown that gymnosperms turn green in darkness (light independent process) (Oku et al. 1974, Bogdanovic 1974, Mariani 1990). Therefore, etiolation is possible in angiosperms while gymnosperm seedlings grown under equivalent conditions are usually green. But again exceptions to the rule are known, e.g. *Ginkgo* and *Welwitschia.* However, the following scenario may possibly be used as a rule of thumb: Plants that are able to synthesize chlorophyll in darkness as well as during illumination do not need a day time-dependent expression *of Lhc* genes because chlorophyll is present all day long, while a strict light-dependent chlorophyll synthesis needs to be correlated with especially timely gated *Lhc* mRNA and protein synthesis.

The apparent differences in gene regulation present in different groups of higher plants do not only apply for the *Lhc* genes but this holds also true for other

Table 2: Comparison of features in gymnosperms versus angiosperms

	circadian *Lhc* expression (*diurnal)	etiolation	evergreen
gymnospermae			
Pinopsida			
Picea	-	-	+
Pinus	-	-	+
Abies	-	-	+
Larix	-	-/+	-
Taxus	-	-	+
Ginkgoopsida			
Ginkgo	-	+	-
Cycadopsida			
Encephalartos	?	+	+
Dioon	+*	?	+
Gnetopsida			
Gnetum	+*	?	+
Ephedra	-	-	+
Welwitschia	-	+	+
angiospermae			
Lycopersicon	+	+	-
Hedera	+	+	+
Rhododendron	+	+	+

genes (Table 1). So far six genes either related to photosynthesis or to the chlorophyll biosynthesis pathway were shown to express constant mRNA levels in *Pinus, Ginkgo, Larix* or *Gnetum* while respective genes in angiosperm species exhibit the typical circadian pattern. Therefore it seems likely that a general difference at the level of transcription and post-transcription exists between these two groups of vascular plants. To analyse this possibility in more detail, we started to investigate the promoters of *Lhc* genes.

Computer alignment and search for the presence of cis-regulatory elements was extensively performed for the promoters of the tomato *Lhc* genes (Piechulla et al. 1991). The following conclusions can be drawn. Known cis-regulatory motifs, such as the G-box (ACGT), the I-box (GATA), the LRE (CCTTATCAT) sequence, associated in the literature with specific functions, are present in several but not all nineteen tomato *Lhc* promoters. For example the LRE was suggested to be responsible for mediating light responsiveness (Grob and Stüber, 1987), and the GATA motif was suggested to be involved in circadian regulation (Borello et al. 1993). Since not all tomato *Lhc* promoters bear the LRE- or GATA-motif, but they are all light inducible and exhibit circadian expression (Kellmann et al. 1993) we

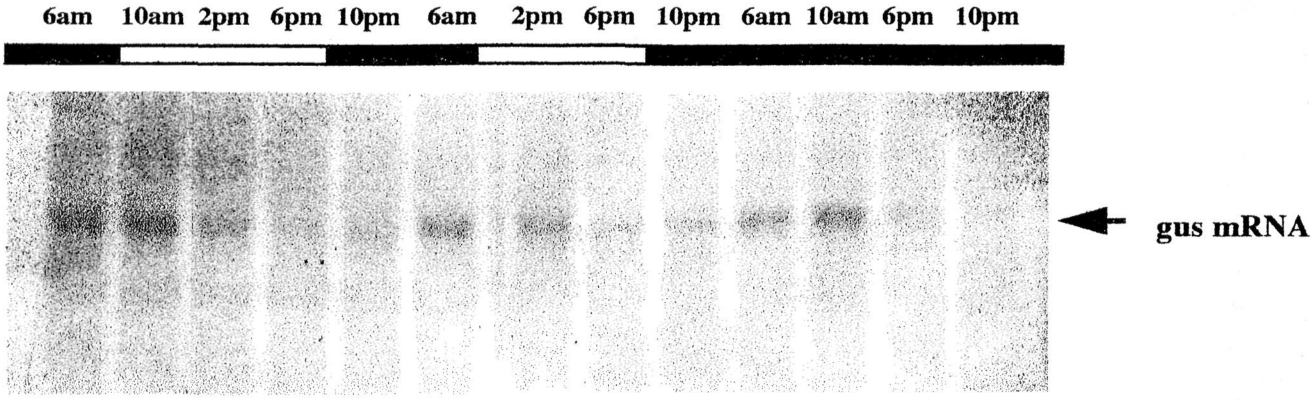

Fig. 1: Determination of gus reporter gene mRNA levels in transgenic tobacco plants. The gus gene is under the control *of the Pinus Lhc* promoter (1.2 kb). Open and dark bars indicate the light and dark phases. Timepoints of leaf harvest are indicated.

have to conclude that these motifs are not the only elements but additional sequences/components are necessary. Promoter deletion analysis of four tomato *Lhc* genes allowed to define short promoter regions that are necessary for circadian expression in transgenic plants (Piechulla et al. 1998). A conserved DNA binding motif 'CAA(N)$_{3\text{-}6}$ ATC' was found to be present in more than 80% of all published *Lhc* promoters. Furthermore a DNA binding factor 'CCA1' was shown to bind to this sequence of the *Arabidopsis Lhc* gene and it was also demonstrated that this CCA1 factor is as well under circadian control (Wang and Tobin, 1998).

Since the *Lhc* transcript levels in many gymnosperms exhibit no oscillations it would be interesting to find out whether cis- and/or trans-regulatory elements found in angiosperms to be related to the circadian control mechanism are also present in gymnosperms. A derivative of the 'CAA(N)ATC' motif is present in the *Pinus contorta* gymnosperm *Lhc* promoter, however the number of variable nucleotides is ten. To answer the question whether the *P. contorta* promoter, bearing the altered consensus sequence, is also able to direct day time-dependent transcription has ultimately to be answered by performing in vitro run off experiments. However, two sets of experiments can be taken as circumstantial evidence that the *Pinus* promoter is not the bottleneck being responsible for the non-circadian transcript accumulation pattern found in so many gymnosperms including *Pinus.* First: The 1.2 kb *P. contorta Lhc* promoter (Barrett et al. 1994) was fused to the gus-reporter system and then transferred into tobacco. The expression pattern was analysed in the transgenic tobacco line, one example is shown in Fig. 1. The results clearly document that the mRNA levels oscillate under LD as well as under DD conditions. Therefore, the *Pinus* promoter is able to drive circadian expression in the angiosperm *Nicotiana tabacum.* Second: We determined the mRNA accumu-

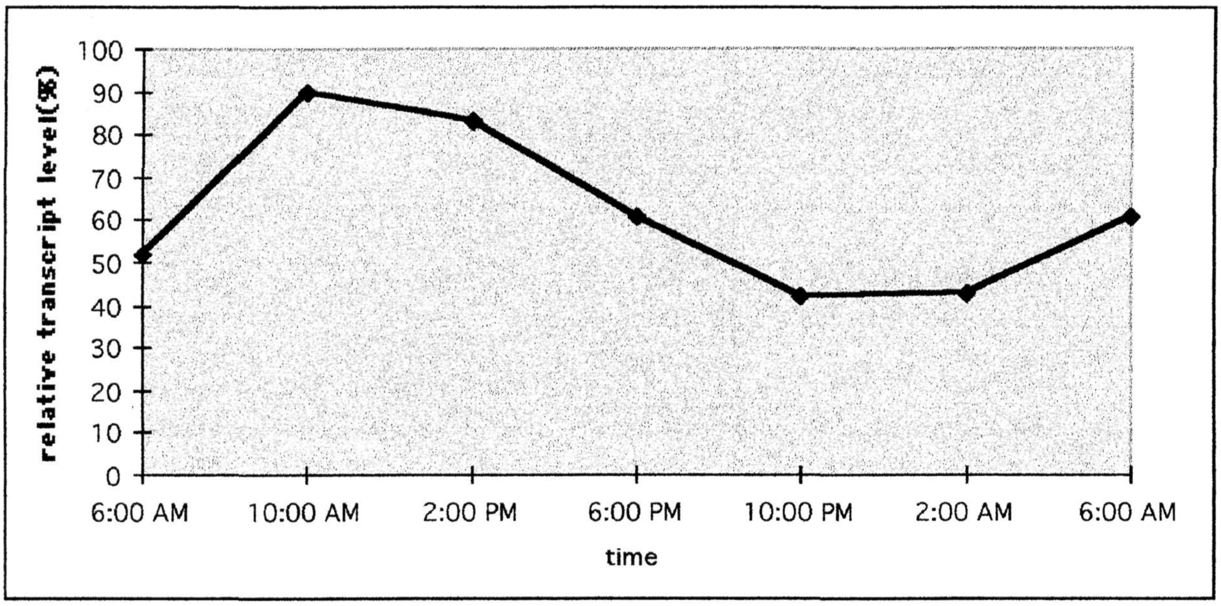

Fig. 2: Determination of relative transcript levels of *Lhc* genes in *Pinus sylvestris* seedlings (8 weeks old) at the fourth day in continuous darkness. Calculations are based on three hybridizations, RNA was standardized to ribosomal RNA

lation pattern in *Pinus sylvestris* seedlings at the forth day in constant darkness.

The relative mRNA levels are depicted in Fig. 2. Even after three days in DD relative high mRNA levels as well as an oscillation with a small amplitude could be detected in *Pinus sylvestris* seedlings. The minimum level with approximately 40% was reached around midnight and the maximum level was reached approximately at 10 am. The amplitude is only twofold (50% increase), compared to an almost 100% increase in angiosperms, but the time points of maximum and minimum are identical to what has been observed in angiosperms. Therefore, these data support the notion that an oscillating *Lhc* mRNA pattern might be present in *Pinus* seedlings.

Although the *Pinus* promoter directs circadian expression in transgenic tobacco and the process of transcription - as can be assumed - is under the control of a circadian clock it remains puzzling that *Lhc* mRNA oscillations are only detectable with a small amplitude on the fourth day in DD, while in contrast pronounced oscillations are easily detectable in tomato. What could be the reason for this difference? A first hint to answer this question is found in the latter experiment. It is interesting to note that fairly high Lhc mRNA levels can still be detected in Pinus seedlings after three days in complete darkness, while less then 10 percent of the mRNA levels can be detected in tomato after the same time in darkness. This observation suggests that the *Lhc* mRNA is much more stable in *Pinus.* We there fore further investigated and compared the mRNA levels in continuous dark condi-

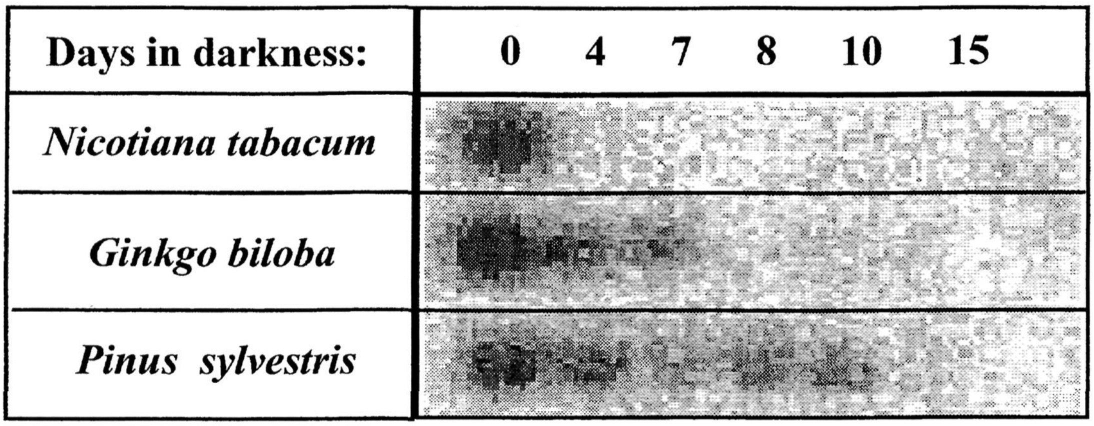

Fig. 3: Determination of *Lhc* RNA levels in *Ginkgo biloba*, *Pinus sylvestris* and *Nicotiana tabacum* kept in complete darkness for 15 days. Time points of harvest were at noon at indicated days.

ditions in tobacco, *Ginkgo biloba* and *Pinus sylvestris* in parallel. Young plants or seedlings were transferred into darkness for 15 days, and mRNA levels were determined at indicated time points (Fig. 3). In *Nicotiana* only at the beginning of the experiment (day 0) *Lhc* mRNA could be detected, while in *Ginkgo* reduced but detectable levels are measured at day 4 and 7. In *Pinus* the decay of *Lhc* mRNA is even slower, since *Lhc* mRNA can be detected at the tenth day in darkness, supporting the above mentioned idea that the *Lhc* mRNA is very stable in darkness or alternatively, *Lhc* mRNA synthesis is present even in dark conditions in this gymnosperm species (independent of light). In contrast, in angiosperms only light-dependent *Lhc* mRNA has been reported so far. Based on the above mentioned results we can conclude that it is very likely that transcription in gymnosperms, similar as in angiosperms, algae, moss and fern species, is under circadian control. However, different in these two groups of vascular plants is the stability of *Lhc* mRNA and/or light-independent *Lhc* gene transcription (Brinker et al. 2001). It remains to be investigated whether RNA stability is also the reason for the constant mRNA levels determined for the other genes (see table 1). At present it is difficult to explain the physiological significance of the presence or necessity of apparently two counteracting processes in gymnosperms i) day time-dependent transcription controlled by a circadian clock with a prerequisite of mRNAs with short half life times and ii) the presence of stable mRNAs (half life time of approximately 16 hrs).

Acknowledgement: The authors would like to acknowledge the contributions to this paper by H.Menzel. We thank Dr. J. Barrett for providing us with the *Pinus Lhc* clone. Financial support was given by the DFG and FCI to B.P.

Abbreviations

continuous darkness (DD), normal light dark day (LD)

REFERENCES

Abied AM, Holland D, 1994. Two newly isolated genes from citrus exhibit a different pattern of diurnal expression and light response. Plant Mol Biol 26: 165-173.

Alosi MC, Neale DB, Kinlaw CS, 1990. Expression of *cab* genes in douglas-fir is not strongly regulated by light. Plant Physiol 93: 829-832.

Barrett JW, Beech RN, Dancik BP, Strobeck C, 1994. A genomic clone of a type I *cab* gene encoding a light harvesting chlorophyll a/b binding protein of photosystem II identified from lodgepole pine. Genome 37: 166-172.

Beator J, Kloppstech K, 1994. Circadian rhythmicity in the expression of genes in higher plants. Mol Biol 13: 203-219.

Becker TW, Caboche M, Carrayol E, Hirel B, 1992. Nucleotide sequence of a tobacco cDNA encoding plastidic glutamine synthetase and light inducibility, organ specificity and diurnal rhythmicity in the expression of the corresponding genes of tobacco and tomato. Plant Mol Biol 19: 367-379.

Becker TW, Foyer C, Caboche M, 1992. Light-regulated expression of the nitrate-reductase and nitrite-reductase genes in tomato and in the phytochrome-deficient aurea mutant of tomato. Planta 188: 39-47.

Bogdanovic M, 1973. Chlorophyll formation in the dark. I. Chlorophyll in pine seedlings. Physiol Plant 29: 17-18.

Boldt R, Scandalios JG, 1995. Circadian regulation of the *Cat3* catalase gene in maize *(Zea mays* L.): entrainment of the circadian rhythm of *Cat3* by different light treatments. Plant J 7(6): 989-999.

Borello U, Ceccarelli E, Giuliano G, 1993. Constitutive, light-responsive and circadian clock-responsive factors compete for the different I box elements in plant light-regulated promoters. Plant J 4: 611-619.

Bougri O, Grimm B, 1996. Members of a low-copy number gene family encoding glutamyl-tRNA reductase are differentially expressed in barley. Plant J 9: 867-878.

Bringloe DH, Dyer TA, Gray JC, 1995. Developmental, circadian and light regulation of wheat ferredoxin gene expression. Plant Mol Biol 27: 293-306.

Brinker M, Klaff P, Wissel K, Kellmann JW, Piechulla B, 2001. Distinct *Lhc* mRNA stabilities in several vascular plant species. J Plant Physiol (in press).

Childs KL, Lu JL, Mullet JE, Morgan PW, 1995. Genetic regulation of development in *Sorghum bicolor.* X. Greatly attenuated photoperiod sensitivity in a phytochrome-deficient *Sorghum* possessing a biological clock but lacking a red light-high irradiance response. Plant Physiol 108: 345-351.

Corlett JE, Wilkinson S, Thompson AJ, 1998. Diurnal control of the drought-inducible putative histone H1 gene in tomato *(Lycopersicum esculentum* Mill. L.). J Exp Bot 49(323): 945-952.

Cremer F, Dommes J, van de Wale C, Bernier G, 1990. Diurnal rhythmicity in the pattern of mRNAs in the leaves of *Sinapis alba.* Plant Physiol 94: 1590-1597.

Cremer F, van de Walle C, Bernier G, 1991. Changes in mRNA level rhythmicity in the leaves of *Sinapis alba* during a lengthening of the photoperiod which induces flowering. Plant Mol Biol 17: 465-473.

Deng MD, Moureaux T, Leydecker MT, Caboche M, 1990. Nitrate-reductase expression is under the control of a circadian rhythm and is light inducible in *Nicotiana tabacum* leaves. Planta 180: 257-261.

Fujita Y, 1996. Protochlorophyllide reduction: a key step in the greening of plants. Plant Cell Physiol 37: 411-421.

Fujiwara S, Ishida N, Tsuzuki M, 1996. Circadian expression of the carbonic anhydrase gene, *Cah*1, in *Chlamydomonas reinhardtii.* Plant Mol Biol 32: 745-749.

Galangau F, Daniel-Vedele F, Moureaux T, Dorbe MF, Leydecker MT, Caboche M, 1988. Expression of leaf nitrate reductase genes from tomato and tobacco in relation to light-dark regimes and nitrate supply. Plant Physiol 88: 383-388.

Giuliano G, Hoffmann NE, Ko K, Scolnik PA, Cashmore AR, 1988. A light-entrained circadian clock controls transcription of several plant genes. EMBO J 7(12): 3635-3642.

Grob U, Stüber K, 1987. Discrimination of phytochrome dependent light inducible from non-light inducible plant genes. Prediction of a common light-responsive element (LRE) in phytochrome dependent light inducible plant genes. Nucleic Acids Res 15: 9957-9973.

Heintzen C, Fischer R, Melzer S, Kappeler S, Apel K, Staiger D, 1994. Circadian oscillations of a transcript encoding a germin-like protein that is associated with cell walls in young leaves of the long-day plant *Sinapis alba* L. Plant Physiol 106: 905-915.

Heintzen C, Nater M, Apel K, Staiger D, 1997. AtGRP7, a nuclear RNA-binding protein as a component of a circadian-regulated negative feedback loop in *Arabidopsis thaliana.* Proc Nat Acad Sci USA 94: 8515-8520.

Holtorf H, Apel K, 1996. The regulation of NADPH-protochlorophyllide oxidoreductases A and B in green barley plants kept under a diurnal light/dark cycle. Planta 199: 289-295.

Kathiresan A, Reid DM, Chinnappa CC, 1996. Light- and temperature-entrained circadian regulation of activity and mRNA accumulation of 1-aminocyclopropane-1-carboxylic acid oxidase in *Stellaria longipes.* Planta 199: 329-335.

Kellmann JW, Merforth N, Wiese M, Pichersky E, Piechulla B, 1993. Concerted circadian oscillations in transcript levels of nineteen *Lha/b (cab)* genes in *Lycopersicon esculentum* (tomato). Mol Gen Genet 237: 439-448.

Kloppstech K, 1985. Diurnal and circadian rhythmicity in the expression of light-induced plant nuclear messenger RNAs Planta 165: 502-506.

Kruse E, Grimm B, Beator J, Kloppstech K, 1997. Developmental and circadian control of the capacity for δ-aminolevulinic acid synthesis in green barley. Planta 202: 235-241.

Kreps JA, Simon AE, 1997. Environmental and genetic effects on circadian clock-regulated gene expression *in Arabidopsis.* Plant Cell 9: 297-304.

Lewandowska M, Öquist G, 1980. Structural and functional relationships in developing *Pinus silvestris* chloroplasts. Physiol Plant 48: 39-46.

Linthorst HJM, van der Does C,Brederode FH, Bol JF, 1993. Circadian expression and induction by wounding of tobacco genes for cysteine proteinase. Plant Mol Biol 21: 685-694.

Liu Z, Taub CC, McClung CR, 1996. Identification of an *Arabidopsis thaliana* ribulose-1,5-bisphosphate carboxylase/oxygenase activase (RCA) minimal promoter regulated by light and the circadian clock. Plant Physiol 112: 43-51.

Matters GL, Beale SI, 1995. Structure and expression of the *Chlamydomonas reinhardtii ala*D gene encoding the chlorophyll biosynthetic enzyme, δ-aminolevulinic acid dehydratase (porpobilinogen synthase). Plant Mol Biol 27: 607-617.

Mariani P, De Carli ME, Rascio N, Baldan B, Casadoro G, Gennari G, Bodner M, Larcher W, 1990. Synthesis of chlorophyll and phytosynthetic competence in etiolated and greening seedlings of *Larix decidua* as compared with *Picea abies.* J Plant Physiol 137: 5-14.

Meyer H, 1993. Untersuchungen zur circadianen Kontrolle der Transkription der *Lhc*a/b-Gene in Tomate. Thesis, University of Göttingen, (Cuvillier Verlag).

Millar A, Kay S, 1991. Circadian control *of cab* gene transcription and mRNA accumulation in *Arabidopsis.* Plant Cell 3: 541-550.

Mock HP, Trainotti L, Kruse E, Grimm B, 1995. Isolation sequencing and expression of cDNA sequences encoding uroporphyrinogen decarboxylase from tobacco and barley. Plant Mol Biol 28: 245-256.

Morikawa K, Ito S, Tsunoyama Y, Nakahira Y, Shiina T, Toyoshima Y, 1999. Circadian-regulated expression of a nuclear encoded plastid sigma factor gene *(sig*A*)* in wheat seedlings. FEBS Letters 451: 275-278.

Nakahira Y, Baba K, Yoneda A, Shiina T, Toyoshima Y, 1998. Circadian-regulated transcription of the *psb*D light-responsive promoter in wheat chloroplasts. Plant Physiol 118: 1079-1088.

Oberschmidt O, Hücking C, Piechulla B, 1995. Diurnal *Lhc* gene expression is present in many but not all species of the plant kingdom. Plant Mol Biol 27: 147-153.

Oelmüller R, Schneiderbauer A, Herrmann RG, Kloppstech K, 1995. The steady-state mRNA levels for thylakoid proteins exhibit coordinate diurnal regulation. Mol Gen Genet 246: 478-484.

Oku T, Sugahara K, Tomita G, 1974. Functional development of photosystem I and II in dark-grown pine seedlings. Plant Cell Physiol 15: 175-178.

O'Neill SD, Zhang XS, Zheng CC, 1994. Dark and circadian regulation of mRNA accumulation in the short-day plant *Pharbitis nil.* Plant Physiol 104: 569-580.

O'Neill SD, Zheng CC, 1998. Abundance of mRNA encoding HMG1/HMG2 class high-mobility-group DNA-binding proteins are differentially regulated in cotyledons of *Pharbitis nil.* Plant Mol Biol 37: 235-241.

Papenbrock J, Mock HP, Kruse E, Grimm B, 1999. Expression studies in tetrapyrrole biosynthesis : Inverse maxima of magnesium chelatase and ferrochelatase activity during cyclic photoperiods. Planta 208: 264-273.

Peter HJ, Krüger-Alef C, Knogge W, Brinkmann K, Weissenböck G, 1991. Diurnal periodicity of chalcone-synthase activity during the development of oat primary leaves. Planta 183: 409415.

Piechulla B, Kellmann JW, Pichersky E, Schwartz E, Förster HH, 1991. Determination of steady-state mRNA levels of individual chlorophyll a/b binding protein genes of the tomato *cab* gene family. Mol Gen Gent 230: 413-422.

Piechulla B, 1999. Circadian expression of the light harvesting complex protein genes in plants. Chronobiology International 16: 115-128

Piechulla B, Merforth N, Rudolph B, 1998. Identification of tomato *Lhc* promoter regions necessary for circadian expression. Plant Mol Biol 38: 655-662

Pilgrim ML, Caspar T, Quail PH, McClung CR, 1993. Circadian and light-regulated expression of nitrate reductase in *Arabidopsis.* Plant Mol Biol 23: 349-364.

Pilgrim ML, McClung CR, 1993. Differential involvement of the circadian clock in the expression of genes required for ribulose-1.5-bisphosphate carboxylase/oxygenase synthesis, assembly, and activation in *Arabidopsis thaliana.* Plant Physiol 103: 553-564.

Redinbaugh MG, Sabre M, Scandalios JG, 1990. Expression of the maize *Cat* 3 catalase gene is under the influence of a circadian rhythm. Proc Natl Acad Sci USA 87: 6853-6857.

Reimmann C, Dudler R, 1993. Circadian rhythmicity in the expression of a novel light-regulated rice gene. Plant Mol Biol 22: 165-170.

Sage-Ono K, Ono M, Harada H, Kamada H ,1998. Accumulation of a clock-regulated transcript during flower-inductive darkness in Pharbitis nil. Plant Physiol 116: 1479-1485.

Salvador ML, Klein U, Bogorad L, 1993. Light-regulated and endogenous fluctuations of chloroplast transcript levels in *Chlamydomonas.* Regulation by transcription and RNA degradation. Plant J 3 (2): 213-219.

Schaffer R, Ramsay N, Samach A, Corden S, Putterill J, Carre IA, Coupland G, 1998. The late elongated hypocotyl mutation of *Arabidopsis* disrupts circadian rhythms and the photoperiodic control of flowering. Cell 93: 1219-1229.

Shinohara K, Murakami A, Fujita Y, 1992. Biochemical characteristics of thylakoid membranes in chloroplasts of dark-grown pine cotyledons. Plant Physiol 98: 39-43.

Szekeres M, Haizel T, Adam E, Nagy F, 1995. Molecular characterization and expression of a tobacco histone H1 cDNA. Plant Mol Biol 27: 597-605.

Taylor WC, 1989. Transcriptional regulation by a circadian rhythm. Plant Cell 1: 259.

Thomas M, Cretin C, Vidal J, Keryer E, Gadal P, Monsinger E, 1990. Light-regulation of phosphoenolpyruvate carboxylase mRNA in leaves of C_4 Plants: Evidence for phytochrome control on transcription during greening and for rhythmicity. Plant Science 69: 65-78.

Wang ZY, Tobin EM, 1998. Constitutive expression of the circadian clock associated 1 (CCA1) gene disrupts circadian rhythms and suppresses its own expression. Cell 93: 1207-1217.

Watillon B, Kettmann R, Boxus P, Burny A, 1993. Developmental and circadian pattern of rubisco activase mRNA accumulation in apple plants. Plant Mol Biol 23: 501-509.

Wehmeyer B, Cashmore AR, Schäfer E, 1990. Photocontrol of the expression of genes encoding chlorophyll a/b binding proteins and small subunit of ribulose-1,5-bisphosphate carboxylase in etiolated seedlings of *Lycopersicum esculentum* (L.) and *Nicotiana tabacum* (L.). Plant Physiol 93: 990-997.

Yoshida I, Yamagata H, Hirasawa E, 1999. Blue- and red-light regulation and circadian control of gene expression of S-adenosylmethionine decarboxylase in *Pharbitis nil.* J Exp Bot 50(332): 319-326.

Zhong HH, Resnick AS, Straume M, McClung CR, 1997. Effects of synergistic signaling by photochrome A and cryptochrome 1 on circadian clock-regulated catalase expression. Plant Cell 9: 947-955.

Zhong HH, Young JC, Pease EA, Hangarter RP, McClung CR, 1994. Interactions between light and the circadian clock in the regulation of CAT2 expression in *Arabidopsis.* Plant Physiol 104: 1-9.