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A 273-bp Promoter Region Is Responsible for Circadian Regulation of S-Adenosylmethionine Decarboxylase Gene Expression in Carnation

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S-Adenosylmethionine decarboxylase (SAMDC) activity and mRNA amount increase in a light-dependent manner, and the accumulation of *SAMDC* transcripts might be partially regulated by a circadian clock in tritordeum and *Pharbitis nil*. However, no research has been reported on the circadian regulation of SAMDC activity and corresponding gene expression. Here, we determined that SAMDC activity and its mRNA accumulation changed diurnally in carnation leaves. To identify the promoter region responsible for this rhythmicity, we performed northern blot analysis using a *GUS* cDNA probe in transgenic tobacco plants. The *GUS* gene was under the control of serial deletions of the 5'-flanking region of a genomic clone corresponding to *CSDC9* (*gCSDC9*). The region between -754 and -274, which negatively regulated the accumulation of *GUS* mRNA, had two HD-Zip-2 binding sequences (TAATAATTA) that were found by PLACE analysis of the promoter region. Another region at 273 bp upstream from the transcription initiation site was sufficient for diurnal expression of *GUS*, and contained the putative sites responsible for diurnal expression, i.e., the GT-1 consensus sequence (GGTAAT) and a sequence necessary for this circadian expression (CAACTTCATC).

Keywords: S-adenosylmethionine decarboxylase, carnation, circadian clock, *cis*-element, promoter, transcriptional regulation

S-Adenosylmethionine decarboxylase (EC 4.1.1.50, SAMDC) catalyzes the conversion of S-adenosylmethionine to decarboxylated S-adenosylmethionine, a donor of aminopropyl moiety to putrescine (Put) and spermidine (Spd). The synthesis of Spd and spermine (Spm) is mainly regulated by the level of decarboxylated SAM; activity of SAMDC is a rate-limiting step in the polyamine biosynthetic pathway (Greenburg and Cohen, 1985; Tassoni et al., 2000). In plants, polyamines (PAs) have been linked to a variety of growth and developmental processes, including cell division, vascular differentiation, embryoid formation in tissue culture, root initiation, adventitious shoot formation, flower initiation and development, and the control of fruit ripening and senescence (Evans and Malmberg, 1989).

Molecular, genetic, and transgenic approaches have increased our understanding of how PAs function (Kumar et al., 1996, 1997; Tiburcio et al., 1997; Walden et al., 1997). Genes encoding plant SAMDC have been reported in potato (Mad Arif et al., 1994), spinach (Bolle et al., 1995), *Catharanthus roseus* (Schröder et al., 1995), carnation (Lee et al., 1997), *Ipomoea nil* (Park et al., 2001), and pea (Marco and Carrasco, 2002). SAMDC activity is highly regulated by a variety of physiological, hormonal, and environmental stimuli (Tabor and Tabor, 1984; Evans and Malmberg, 1989; Mariæ et al., 1992). This activity dramatically rises when the leaves of *Pharbitis nil* are illuminated (Hirasawa and Shimada, 1994; Kamachi and Hirasawa, 1995). Such a light-dependent increase is concomitant with changes in the levels of SAMDC mRNA after lights-on (Yoshida and Hirasawa, 1998; Park et al., 2001). Both the blue light photoreceptor- and phytochrome-mediated pathways are involved in light-regulation of the *SAMDC* gene, and calcium homeostasis is involved in both red and blue light-induction of *SAMDC* expression (Yoshida et al., 1999, 2002).

Circadian rhythms have been described for nearly every eukaryotic organism as well as some prokaryotes (Kondo et al., 1993; Lee and Son, 2005). In many higher plants, gene expression controlled by the circadian clock has been reported with several genes for nitrate reductase (Deng et al., 1990; Pilgrim et al., 1993), catalase (Boldt and Scandalios, 1995; Zhong and McClung, 1996), glycine-rich protein (Carpenter et al., 1994; Heintzen et al., 1994), small subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (RBCS) (Pilgrim and McClung, 1993; Hwang and Herrin, 1994), and chlorophyll a-b binding protein (CAB) (Millar and Kay, 1996). Among the genes involved in PA biosynthesis, *SAMDC* expression has been shown to be regulated by a circadian clock at the transcriptional level in tritordeum (Dresselhaus et al., 1996) and *Pharbitis nil* (Yoshida et al., 1999).

Here, we monitored SAMDC activity and mRNA accumulation to identify the putative sequence necessary for circadian expression and consequent rhythmically regulated expression of the *SAMDC* gene.

MATERIALS AND METHODS

Plant Materials and Growing Conditions

Carnation (*Dianthus caryophyllus* L. cv. White sim) was grown under standard greenhouse conditions at 23°C with a 16-h photoperiod. To study the circadian-regulated expression of SAMDC, the plants were transferred to controlled growth chambers under LD (12 h light/12 h dark) conditions for several days. For our continuous-light (LL) and -dark

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(DD) experiments, some of the LD-grown plants were transferred to LL or DD conditions.

SAMDC Activity Assay

SAMDC activity in the carnation leaves was determined as previously described, using 0.1 μCi [carboxy-^{14}C] SAM (60 mCi mmol^{-1}) per reaction as substrate (Lee et al., 1997).

Northern Blot Analysis

To obtain total RNA, carnation leaves were harvested, frozen in liquid nitrogen, and stored at -70°C before extraction. Total RNA was isolated as described previously (Lee et al., 1997). Samples were electrophoretically separated, transferred to membranes (Hybond N$^+$; Amersham, UK), hybridized at 42°C, then washed and exposed to a phospho-image plate. ^{32}P-Radiolabeled specific probes for *CSDC9* and *CSDC16* and a ^{32}P-radiolabeled probe for *GUS* cDNA were made using the Klenow enzyme.

Plasmid Construction

To construct the 5′ deletion mutants of the *gCSDC9* 5′-flanking region, PCR primers were designed to amplify portions of that region, using plasmid 1821+5′-UTR as template. Unique restriction sites were introduced: *Hin*dIII at the 5′ end and *Xba*I at the 3′ end. PCR products were digested with *Hin*dIII/*Xba*I and cloned into a 35S-promoterless pBI121 (Clontech, USA). All the PCR fragments used for constructs were entirely sequenced with a T7 Sequencing kit (Amersham).

Plant Transformation

Binary vectors were introduced into *Agrobacterium tumefaciens* strain LBA4404 by the freezeing-thaw method. Tobacco leaf discs were transformed with *A. tumefaciens* as described by Horsch et al. (1985). Shoots were rooted on a solid MS medium containing 100 mg L^{-1} kanamycin sulfate, then transferred to soil and raised to maturity in growth chambers.

RESULTS

Circadian Regulation of SAMDC Activity

Circadian-regulated gene expression of *SAMDC* at the transcriptional level has been described in tritordeum and *Pharbitis nil* (Dresselhaus et al., 1996; Yoshida et al., 1999). Here, we investigated the previously unreported circadian regulation of SAMDC activity corresponding to gene expression. To identify whether this activity is regulated by a circadian clock, we first assayed leaf SAMDC activity from carnation in growth chambers under long-day (LD) conditions, i.e., 12-h light/dark cycles. SAMDC activity was also measured after LD-treated plants were then transferred to continuous light (LL) or continuous darkness (DD). Under LD, SAMDC activity began to increase late in the 12-h dark period, reaching a maximum level during the first 6 h after the lights were turned back on. Activity then decreased to the end of the light phase, with the lowest amount of activity being detected early in the next dark period (Fig. 1A). This periodicity of activity persisted for another 2 d after the plants were transferred to LL conditions (Fig. 1B). In contrast, when the plants were moved to DD conditions, this

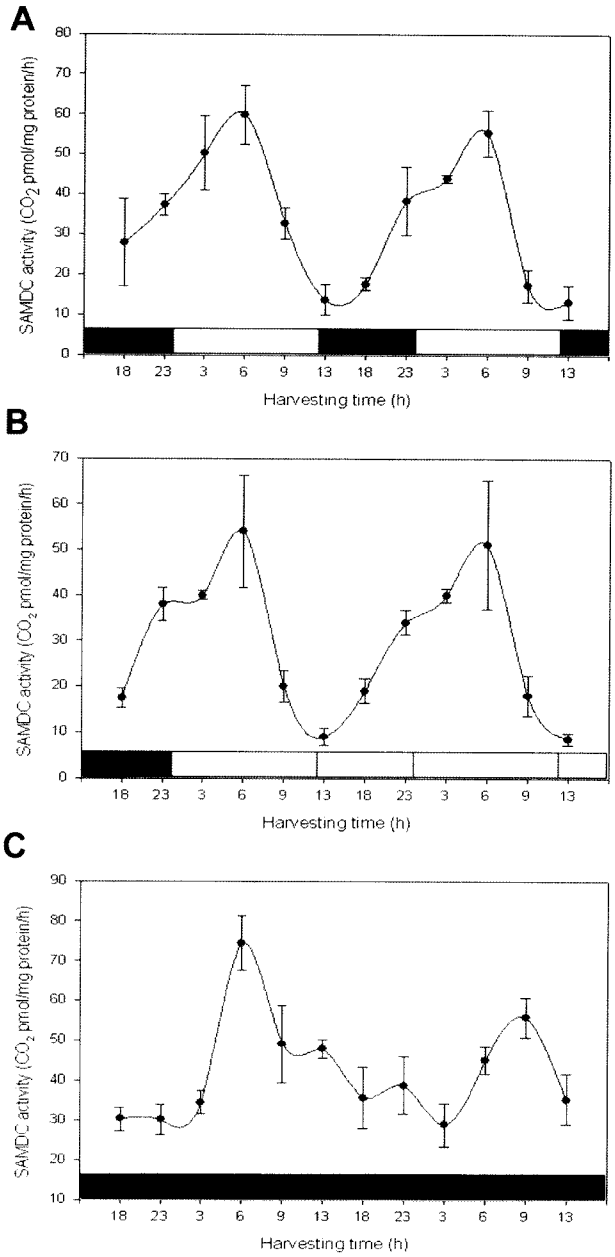

Figure 1. Circadian rhythmicity of SAMDC activities in carnation (*D. caryophyllus*). Assays were performed with soluble proteins extracted from leaves of plants grown under a 12-h light (open bar, 0-12 h) and 12-h dark (solid bar, 13-24 h) cycle (**A**), continuous light period (**B**), or continuous dark period (**C**). Leaves were harvested at times indicated. All experiments were performed three times and SAMDC activity was presented as mean ± SD.

periodicity continued for only 1 d before weakening (Fig. 1C). These results suggest that SAMDC activity may be partially regulated by a circadian clock in plants. Under LD and LL conditions, the highest level of SAMDC activity ranged from 51 to 59.9 pmol CO_2 mg protein^{-1} h^{-1} compared with a maximum activity peak of 74.6 pmol CO_2 mg protein^{-1} h^{-1} under DD (Fig. 1).

Circadian Regulation of the Accumulation of *SAMDC* mRNA

To investigate the possibility that circadian-controlled SAMDC activity may be regulated at the transcriptional

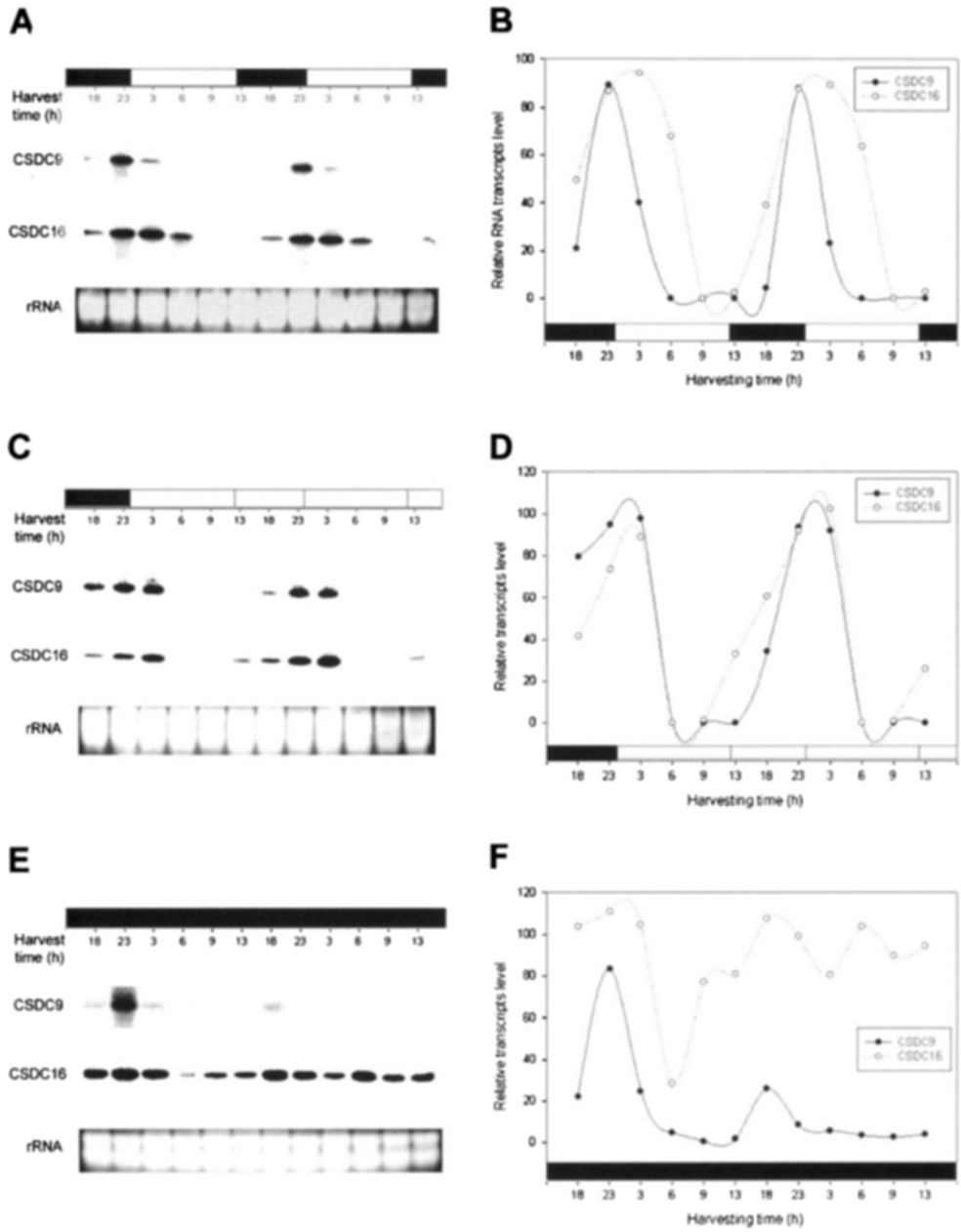

Figure 2. Rhythmic accumulation of two carnation *SAMDC* mRNAs (*CSDC9* and *CSDC16*). Northern blot analysis with *CSDC9*- and *CSDC16*-specific probes (**A, C, E**). Equal amounts of total RNA were loaded on each lane as adjusted by ethidium bromide staining of rRNA bands. Solid and open bars represent dark and light periods, respectively. Results in **A, C,** and **E** are quantitatively presented in **B, D,** and **F**, respectively. Experiment was performed twice with nearly identical results; one representative data set is shown.

level, we performed northern blot analysis using two *SAMDC*-specific probes originated from cDNAs (*CSDC9* and *CSDC16*) cloned from carnation petals. Under LD conditions, the mRNA level of *CSDC9* started increasing in the middle of the dark period, reaching a maximum accumulation just before the illumination phase began. *CSDC9* transcripts then declined rapidly early in the light phase, to a minimum level at the middle of that treatment segment. In contrast to the accumulation pattern for *CSDC9*, the mRNA level of *CSDC16* started to increase late in the 12-h dark period, reaching a maximum during the first 3 h of the light phase. *CSDC16* transcript levels then decreased in the middle of that light segment, to a minimum point at the end of that phase (Fig. 2A, B). Under LL conditions, the mRNA accumulation for *CSDC9* was regulated rhythmically, but started to rise at the end of the dark period, peaking at the time that corresponded to 3 h after illumination began under LD. Although the high level of *CSDC16* transcripts endured longer in the light phase than did those of *CSDC9* in our LD experiment, the expression pattern of the former under LL was similar to that determined for *CSDC9* under LD (Fig. 2C, D). In our DD trial, the periodicity of mRNA accumulation for both genes persisted for 1 d before showing a weakened rhythmicity. The timing of those maximum levels for both *CSDC9* and *CSDC16* corresponded to 1 h before illumination began under LD. From the second day after transferring to DD conditions, the mRNA accumulation of *CSDC9* was maintained at a low level, showing a tran-

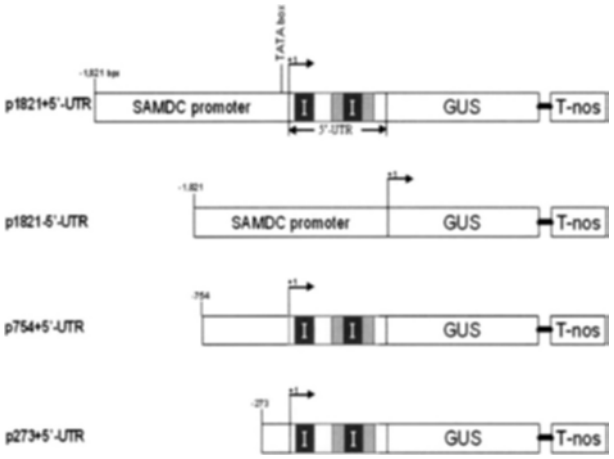

Figure 3. Schematic diagrams of deleted *SAMDC* 5′-flanking regions fused to *GUS* reporter gene. p1821+5′-UTR contains 1821 bp of promoter region and 1179-bp 5′-UTR involving two introns and uORF; p1821-uORF: 1821 bp of promoter region and 5′-UTR without uORF involving an intron; p1821-5′-UTR: 1821 bp of promoter region only; p273+5′-UTR: 273 bp of promoter region and 5′-UTR; p158+5′-UTR: 158 bp of promoter region and 5′-UTR. The first intron (I) intervenes within 5′-UTR (black box), and second intron intervenes within uORF (shaded gray) of *SAMDC* gene. TATA box is located at -32 to -26; transcription start site (+1) is indicated by arrow.

sient, low peak at the time corresponding to 6 h after illumination in LD. In contrast, accumulation of *CSDC16* transcripts arrhythmically oscillated at a high level from the second day after plants were transferred to DD conditions (Fig. 2E, F).

Promoter Region Necessary for Diurnal Expression of *SAMDC*

To investigate the regulatory mechanism for diurnal expression of the *SAMDC* gene, we isolated a genomic clone corresponding to *CSDC9* from carnation leaves and made the deleted constructs (Fig. 3). We focused on identifying the promoter region involved in the rhythmic expression of *CSDC9* under LD conditions because *SAMDC* expression is diurnally regulated, and also partially circadian clock-regulated. mRNA accumulation of *GUS* was periodically regulated under the control of the *SAMDC* promoter containing a 5′-untranslated region (5′-UTR), although the highest level was attained 3 h after illumination began for the transgenic tobacco plants (Fig. 4). That maximum point was delayed for 3 h compared with that determined for *SAMDC* mRNA accumulation (cf. Fig. 2A). The periodicity of *GUS* expression was not altered by the deletion of the 5′-UTR, but expression of that gene was quantitatively affected (Fig. 4B). *GUS* transcript levels were remarkably decreased in plants transformed with the p754+5′-UTR, but were nearly recovered in transgenics with the p273+5′-UTR. A promoter fragment between -754 and -274 b contained two putative binding sites for the *Arabidopsis* homeobox gene (ATHB-2, TAATAATTA) at the positions of -621 and -693; this gene is regulated by light signals that function as a negative autoregulator of its own gene (Ohgishi et al., 2001). Our PLACE analysis identified a promoter region between -273 and -1 b that contained a putative GT-1 consensus sequence (GGTAAT) and a putative sequence necessary for circadian expression (CAACTTCATC) at positions -123 and -96,

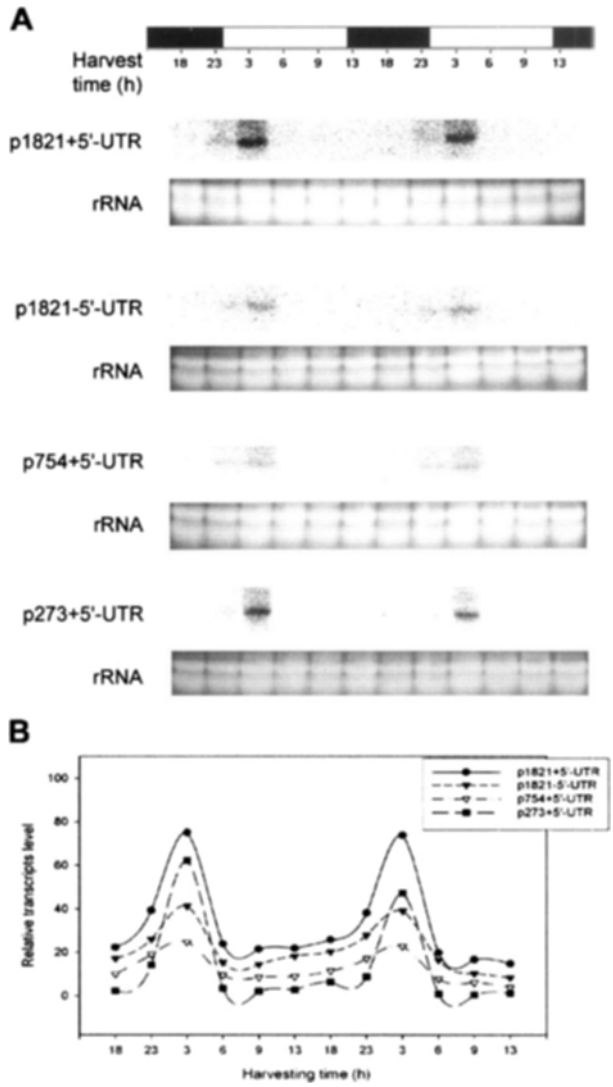

Figure 4. Rhythmic accumulation of transcripts for *GUS* gene under control of deleted mutations of *SAMDC* 5′-flanking region from transgenic tobacco plants. Northern blot analysis of *GUS* mRNA accumulation was performed with *GUS* cDNA probe (**A**). Equal amounts of total RNA were loaded on each lane as adjusted by ethidium bromide staining of rRNA bands. Solid and open bars represent dark and light periods, respectively. Results in **A** are quantitatively presented in **B**. Experiment was performed twice with nearly identical results; one representative data set is shown.

respectively (Fig. 5; see also Terzaghi and Cashmore, 1995; Piechulla et al., 1998).

DISCUSSION

Plants utilize light as a major signal for modulating growth and development throughout their life span. Given the periodicity of light/dark cycles in the environment, it is not surprising that a circadian clock affects several important physiological aspects. This clock regulates the expression of many genes involved in such processes as photosynthesis, hypocotyl elongation, and flowering (Schultz and Kay, 2003). Polyamines are growth regulators that participate in cell division, vascular differentiation, flower development, and fruit ripening (Evans and Malmberg, 1989). Based on

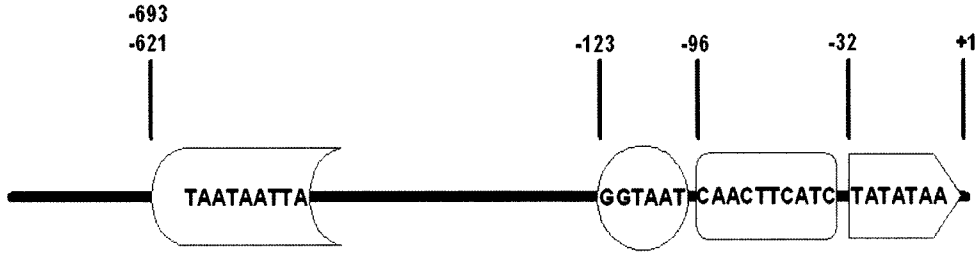

Figure 5. Putative structure of *gCSDC9* proximal promoter. The 754-bp region upstream of transcription start site was analyzed using PLACE database. HD-Zip-2 binding consensus sequences (TAATAATTA) are present at positions -693 and -621. GT-1 consensus sequence (GGTAAT), another sequence necessary for circadian expression (CAACTTCATC), and TATA box are present at positions -123, -96, and -32, respectively.

the results from previous research, it is reasonable to conclude that expression of the *SAMDC* gene, a known rate-limiting step of PA biosynthesis, might be regulated by a circadian clock.

In carnation, circadian-controlled SAMDC activity may follow the circadian-regulated expressions of *CSDC9* and *CSDC16* at the transcriptional level. Although clock-controlled *SAMDC* mRNA accumulation has been reported in tritordeum and *P. nil* (Dresselhaus et al., 1996; Yoshida et al., 1999), circadian-regulated SAMDC activity has not been studied in those species. In tritordeum, levels of *SAMDC* mRNA increase at the end of the 8-h dark period, reaching a maximum during the first 8 h of light exposure. These *SAMDC* transcripts then decline at the end of that light phase, attaining their lowest mRNA level in the middle of the dark period. This periodicity also persists when plants are treated with constant light. Under continuous darkness, oscillation apparently occurs over a long period (Dresselhaus et al., 1996). In *P. nil*, the level of mRNA for *SAMDC* begins to increase in the dark, then peaks after 1 h following lights-on. The oscillation of *SAMDC* mRNA level persists when plants are shifted to continuous light, showing a circadian periodicity of approximately 24 h (Yoshida et al., 1999). Here, the circadian expression pattern of *CSDC16* was similar to that of the *SAMDC* genes reported in tritordeum and *P. nil*, but that pattern differed for *CSDC9* in terms of the timing at which the maximum levels of their transcripts were reached. These results might suggest differential regulation of circadian rhythm between *CSDC9* and *CSDC16*. The fact that the *CSDC9* mRNA level was highest at the end of the dark period implies the presence of an evening element (EE; AAAATATCT), which has been reported for a catalase 3 promoter of *Arabidopsis* in the *gCSDC9* promoter region (Michael and McClung, 2002). However, although we found no EE in our analysis, a putative circadian clock-associated 1-binding site (CBS; AAAAAATCT) is critical for morning-specific transcription, and is located at position -1360 in the *gCSDC9* promoter region (Michael and McClung, 2002). Therefore, we hypothesized that the element essential for dark-specific transcription also is present in that promoter region. To investigate whether that was true, we performed a promoter assay using tobacco plants transformed with the constructs described in Figure 3. Maximum levels of *GUS* mRNA were detected during the first 3 h of the light phase, even though *GUS* accumulations were periodically regulated in the transgenic plants containing the p1821+5′-UTR (Fig. 4A, B). This distinction between the expression pattern of *CSDC9* in carnation leaves and that of *GUS* in transgenic tobacco may have resulted from either our utilization of a hetero-system in the transformation experiment or because of variations in the stability of *GUS* versus *SAMDC* mRNA. Except for quantitative differences, the periodicity for mRNA accumulation of *GUS* persisted in transgenic plants containing five types of constructs. Therefore, a 273-bp region of the *SAMDC* promoter might be sufficient for the circadian regulation of gene expression. We suggest that the promoter region involved with diurnal SAMDC expression be thoroughly examined.

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