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ORIGINAL ARTICLE

Relationship between endodormancy, *FLOWERING LOCUS T* and cell cycle genes in *Vitis vinifera*

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Abstract

Main conclusion **In grapevines, the increased expression of *VvFT*, genes involved in the photoperiodic control of seasonal growth (*VvAP1*, *VvAIL2*) and cell cycle genes (*VvCDKA*, *VvCDKB2*, *VvCYCA1*, *VvCYCB*, *VvCYCD3.2*) in the shoot apex relative to the latent bud, suggests a high mitotic activity of the apex which could prevent them to enter into endodormancy. Additionally, the up-regulation of these genes by the dormancy-breaking compound hydrogen cyanamide (H_2CN_2) strongly suggests that *VvFT* plays a key role in regulating transcriptionally cell cycle genes.**

At the end of the growing season, short-day (SD) photoperiod induces the transition of latent grapevine buds (*Vitis vinifera* L) from paradormancy (PD) to endodormancy (ED), which allows them to survive the cold temperatures of winter. Meanwhile, the shoot apex gradually decreases its growth without entering into ED, and as a result of the fall of temperatures at the beginning of autumn, dies. To understand developmental differences and contrasting responses to environmental cues between both organs, the expression of cell cycle genes, and of genes involved in photoperiodic control of seasonal growth in trees, such as *FLOWERING LOCUS T* (*FT*), *APETALA1* (*AP1*) and *AINTEGUMENTA-like* (*AIL*) was analyzed at the shoot apex and latent buds of vines during the transition from PD to ED. After shift to SD photoperiod, increased expression of cell cycle genes in the shoot apex suggests a high mitotic activity in this organ which could prevent them from entering into ED. Additionally, the increased expression of *VvFT*, *VvAP1*and *VvAIL2* in the shoot apex, and the up-regulation of *VvFT*, *VvAP1*and cell cycle genes *VvCDKA*, *VvCDKB2*, *VvCYCA.1*, by the dormancy-breaking compound hydrogen cyanamide (H_2CN_2), strongly suggests that *VvFT* plays a key role in regulating transcriptionally cell cycle genes, giving thus, more support to the model for photoperiodic control of seasonal growth in trees. Furthermore, downregulation of *VvFT* by the SD photoperiod detected in leaves and buds of grapevines highlights the importance of *VvFT* in the induction of growth cessation and in ED development, probably by regulating the expression of cell cycle genes.

Keywords Apex · Buds · Dormancy · Grapevines

Abbreviations

AIL	*AINTEGUMENTA-like*
AP1	*APETALA1*
CDK	Cyclin-dependent kinase
ED	Endodormancy
FT	*FLOWERING LOCUS T*
PD	Paradormancy
SD	Short day

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Introduction

In contrast to poplar and other tree species, *Vitis* does not set a terminal bud in response to short day (SD) photoperiod signal, and the shoot apex does not enter into endodormancy (ED) nor cold acclimates, as a result growth always terminates by the death of the shoot apex after the fall of the temperatures at the beginning of autumn; however, upon reaching a critical day length (CDL), other hallmark phenotypes such as periderm development, growth cessation and development of bud ED are induced (Fennell and Hoover 1991; Wake and Fennell 2000; Sreekantan et al. 2010; Grant et al. 2013). The shoot apex, through apical dominance inhibits the outgrowth of latent buds in woody perennial plants (Crabbé 1984; Suzuki 1990; Blazková et al. 1999) and this phase of bud development is termed paradormancy (PD) (Lang 1987). Recently, in *V. riparia* it has been shown that the shoot apex, summer lateral buds and leaves in addition to node position, contribute to the inhibition of latent bud outgrowth during PD (He et al. 2012). In *Populus*, the CO/FT module plays a central role in sensing the SD photoperiod signal, and the rapid down-regulation of *FLOWERING LOCUS T* (*FT*) expression after the perception of the SDs signal is a key event in the induction of growth cessation and ED establishment (Böhlenius et al. 2006). In *V. vinifera*, *VvFT* is downregulated during ED (Díaz-Riquelme et al. 2012) and is up-regulated naturally prior to budbreak, and by hypoxia (Vergara et al. 2012). Downstream of the CO/FT module, the *AINTEGUMENTA-like 1* (*AIL1*) transcription factor is the target of the SDs signal (Resman et al. 2010; Karlberg et al. 2011). Because *AIL1* and related transcription factors are positive regulators of the expression of core cell cycle genes, the repression of *AIL1* expression by SDs results in the cessation of growth (Mizukami and Fischer 2000; Karlberg et al. 2011). Recently, in hybrid aspen the MAD-box transcription factor called *Like-AP1* (*LAP1*), which is highly similar to the *Arabidopsis* floral identity gene *APETALA 1* (*AP1*) was identified as the target of *FT* which mediates the regulation of *AIL1* expression; this finding led to a model for the photoperiodic control of seasonal growth in trees (Azeez et al. 2014). Recently, Tylewicz et al. (2015) showed that the interaction of FT with FD is crucial for the transcriptional regulation of *LAP1* in hybrid aspen. In order to test whether the module CO/FT mediates the induction of ED by SD photoperiod, and to analyze the role of this module in the absence of ED at the shoot apex, the effect of SD photoperiod on *VvFT* expression was analyzed in leaves and latent buds of vines. In addition, the expression of cell cycle genes (CCG) and genes involved in the model for photoperiodic control of seasonal growth (*VvFT*, *VvAP1* and *VvAIL*) was analyzed at the shoot apex and latent buds during the transition from PD to ED. Finally, in order to get more insight in the possible regulation of cell cycle genes by *VvFT*, the effect of the dormancy-breaking compound hydrogen cyanamide (H_2CN_2) on the expression of *VvFT*, *VvAP1*, *VvAIL2* and CCG was analyzed in dormant grapevine buds.

Materials and methods

Gene expression analysis at the shoot apex and latent buds of grapevines

Eight-year-old *Vitis vinifera* cv. Thompson seedless grown at the experimental station of the Chilean National Institute of Agriculture Research (INIA) in Santiago, Chile (33°34′S latitude) were used as plant material for gene expression analyses. Latent buds and shoot apex were harvested on the same dates; samples were frozen in liquid nitrogen and stored at −80 °C until used. Samples were harvested between December 27 and March 7 because it has been previously reported that in this grape cultivar grown at the same location, the transition from PD to ED occurs in mid-January (Kühn et al. 2009).

Photoperiod treatments

In a collaborative project with colleagues from Brazil, the effect of different photoperiod regimes on the expression of *VvFT* was performed. Photoperiod experiments were carried out in Messoró, Brazil due to small variations in photoperiod and temperature in the area, making it easier to conduct this type of experiments. Cuttings of *V. vinifera* cv. Italia melhorada on rootstock IAC 572 grown at the Federal University of Rural Semi-Arid (UFERSA), located in Messoró, Brazil (5°12′16″S), where the natural photoperiod during the whole year is (12/12 h day/night) and temperature fluctuates between 29 and 31 °C, were used as plant material for photoperiod experiments (3 replicates per treatment). Rooted cuttings (15 per treatment) were planted into mix 1:1:1 (by vol.) soil, sand and muck in 5 L pots. As growth commenced, one shoot was allowed to develop on each cutting. Cuttings having uniform growth with 12–16 leaves were selected and randomly assigned to each photoperiod treatment for 8 weeks. Photoperiod experiments were conducted in a greenhouse under LD (14/10 h day/night) and SD photoperiod (10/14 h day/night), since the critical day length (CDL) for dormancy transition in *V. vinifera* is about 13 h (Kühn et al. 2009). Supplemental light was provided automatically in the afternoon at 17:30 h using 100 W fluorescent tube; light restriction was

imposed with black plastic sheet in the early morning at 5:30 h. After the treatments, buds were lyophilized for gene expression analysis.

Hydrogen cyanamide treatments

Canes of grapevines cv. Thompson seedless collected at the state of ED (28 April 2015) (Kühn et al. 2009) were used to prepare two groups of 30 single-node cuttings each (10× replicate). One group was sprayed with 2.5 % (w/v) hydrogen cyanamide (Sigma-Aldrich) and the other with tap water and served as control. The treated cuttings were mounted in polypropylene sheet and floated in water in a plastic tray which was placed in a growth chamber (LGC-5201, Daihan labtech CO, ltda. Korea) set at 23 ± 2 °C under 14 h light (forcing conditions). Samples were retired after 24 and 48 h of treatments and total RNA for gene expression analysis was extracted immediately.

RNA purification and cDNA synthesis

For gene expression analysis in different organs of grapevines, total RNA was isolated and purified from the latent buds (0.5–0.7 g^{-1}FW) and shoot apex (0.1 g^{-1}FW) of *Vitis vinifera* cv Thompson seedless. For photoperiod experiments total RNA was isolated from lyophilized leaves and buds (0.05–0.1 g) of *V. vinifera* cv. Italia melhorada. In both cases, total RNA was extracted and purified using a modification of the method of Chang et al. (1993), as described in Noriega et al. (2007). DNA was removed by treatment with RNAase-free DNAse (1 U/μg) (Thermo Scientific) at 37 °C for 30 min. First-strand cDNA was synthesized from 1 μg of purified RNA with 1 μL oligo$(dT)_{12–18}$ (0.5 μg μL^{-1}) as primer, 1 μL dNTP mix (10 mM) and Superscript ® II RT (Invitrogen).

Quantitative real-time PCR

Quantitative real-time PCR was carried out in an Eco Real-Time PCR system (Illumina) using KAPA SYBR FAST mix (KK 4602) qPCR Master Mix (2×). Primers suitable for the amplification of 80-200 bp products from each of the genes being studied were designed using PRIMER3 software (Rozen and Skaletsky 2000) (Suppl. Table S1), primers for *VvFT* have been described previously (Vergara et al. 2012). cDNA was amplified under the following conditions: denaturation at 94 °C for 2 min and 40 cycles at 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 45 s. Relative changes in gene expression levels were determined using the $2^{-\Delta\Delta CT}$ method (Livak and Schmittgen 2001). Each reaction was performed in at least three biological replicates, each with three technical replicates, and *VvUBIQUITIN* was used as a reference gene for normalization.

Results

VvFT is down-regulated by SD photoperiod

In grapevine latent buds, the transition from PD to ED is triggered by SD photoperiod (Kühn et al. 2009; Grant et al. 2013) and the expression of *VvFT* is down-regulated during ED (Díaz-Riquelme et al. 2012). In order to verify whether *VvFT* is down-regulated by SD photoperiod, we analyzed throughout the entire day the expression of *VvFT* in both, leaves and buds of grapevines cv. Italia melhorada after 8 weeks of exposure to LD photoperiod (14/10 h day/night) and SD photoperiod (10/14 h day/night). Results showed significant variations in the expression of *VvFT* throughout an entire day in leaves (Fig. 1b) and buds (Fig. 1a) of grapevines. Under LD conditions, the level of *VvFT* peaked earlier in the buds (at dusk) than in leaves (at night). Under SD conditions, *VvFT* in both leaves and buds, remained at lower levels than under LD conditions throughout the entire day, and no clear peak was observed in both organs (Fig. 1a, b).

VvFT, *VvAP1* and *VvAIL2* are expressed more in the shoot apex than in latent buds during the transition from PD to ED

In order to analyze whether the genes involved in the photoperiodic control of seasonal growth are responsible for the different behavior of the shoot apex and latent bud, the expression levels of these genes were compared in both organs. A single sequence coding for *VvFT* (GSVIVT000 12870001) and for *VvAP1* (GSVIVT01012250001) and nine genes belonging to subgroup *AINTEGUMENTA* (*AI*) or *AINTEGUMENTA-like* (*AIL*) of the *APETALA 2* family were identified in the genome of *V. vinifera* GENOSCOPE (http://www.genoscope.cns.fr). Three of these genes *VvAI* (GSVIVT01007388001), *VvAIL1* (GSVIVT01009293001) and *VvAIL2* (GSVIVT01016764001) belong to the same clade that *Arabidopsis AINTEGUMENTA* (at4g37750) (Suppl. Fig. S1). Gene expression analysis carried out by qRT-PCR revealed that the expression level of *VvFT* is about tenfold higher in the shoot apex than in latent buds, and as expected, its expression level decreased in both organs with the transition from PD to ED (Fig. 2a). Of the three floral related genes acting downstream of *VvFT*, only *VvAP1* were expressed differently in both organs. Transcript abundance of *VvAP1* was significantly higher at the shoot apex than at the latent bud (Fig. 2b), while the other floral related genes *VvSOC1* and *VvLFY* did not exhibit a

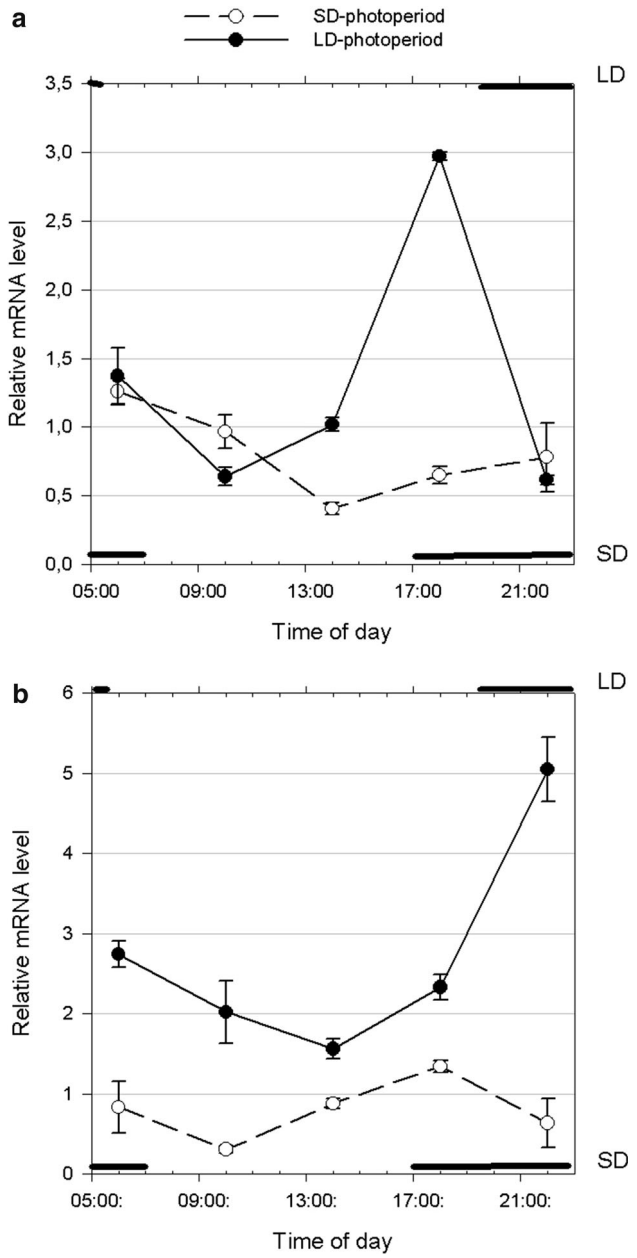

Fig. 1 Effect of LD photoperiod (14/10 h day/night) and SD photoperiod (10/14 h day/night) on the expression of *VvFT* in buds (**a**) and leaves (**b**) of *V. vinifera* cv. Italia melhorada after 8 weeks of treatment. Gene expression analysis was performed by qRT-PCR normalized against *VvUBIQUITIN*. *Values* are expressed relative to samples collected at 6 a.m., and correspond to the average of three biological replicates with three technical repetitions ± SD

different expression level between both organs (results not shown). The expression of *VvAIL2* was significantly higher in the shoot apex than in the latent bud (Fig. 2c), while *VvAI* expressed slightly more in the shoot apex than in the latent bud and *VvAIL1* did not exhibit differential expression between both organs (results not shown).

Cell cycle genes are expressed more in the shoot apex than in latent buds of grapevines during the transition from PD to ED

Bioinformatics analyses of the public database of *V. vinifera* allowed the identification of one gene coding for cyclin-dependent kinase A *VvCDKA* (GSVIVT01026 700001) and one for type B2-cyclin-dependent kinase, *VvCDKB2* (GSVIVT01013440001). Expression analysis of *VvCDKA* in the shoot apex and in latent buds of vines showed similar expression levels, and no significant differences were detected during transition into ED in both organs (Fig. 3a). In contrast, the expression level of *VvCDKB2* was significantly higher at the shoot apex than at the latent bud, and transcript abundance increased with transition into ED especially in the shoot apex (Fig. 3b). Cyclins genes *VvCYCA1* (GSVIVT01008823001), *VvCYCB* (GSVIVT01023978001) and in a lesser extent *VvCYCD3.2* (GSVIVT01030175001) were also expressed more in the apex than in the latent bud (Fig. 3c–e); however, contrasting with the above results, the cyclin-dependent kinase inhibitor *VvICK5* (GSVIVT01021078001) expressed more in the latent bud than in the shoot apex (Fig. 3f).

Hydrogen cyanamide up-regulated the expression of *VvFT*, *VvAP1* and cell cycle genes in grapevine buds

As a way to get more insight on *VvFT* relationship with ED and with cell cycle genes, the effect of hydrogen cyanamide (H_2CN_2), a compound widely used for the release of ED in grapevines (Or 2009), on the expression of *VvFT* and genes downstream in the signaling cascade for the photoperiodic control of seasonal growth in trees (*VvAP1*, *VvAIL*) and cell cycle genes was analyzed in grapevine buds. In grapevine buds, H_2CN_2 treatment increased significantly the expression of *VvFT* 24 and 48 h after treatment (Fig. 4a). The expression of *VvAP1*increased significantly only 48 h after treatment (Fig. 4b), while the expression of *VvAIL2* showed no major differences with respect to the control (Fig. 4c). On the other hand, the expression of the two cyclin-dependent kinases *VvCDKA* and *VvCDKB.2* was up-regulated by H_2CN_2 48 h after treatment (Fig. 5a, b). Of the three cyclins analyzed, only *VvCYCA1* (Fig. 5c) increased its expression after treatment, while *VvCYCB* expression was downregulated 24 h after treatment (Fig. 5d) and *VvCYD3.2* expression was downregulated 48 h after treatment (Fig. 5e). It is interesting to remark that H_2CN_2 treatments showed no effect on *VvAIL2* and on *VvICK5* gene expression.

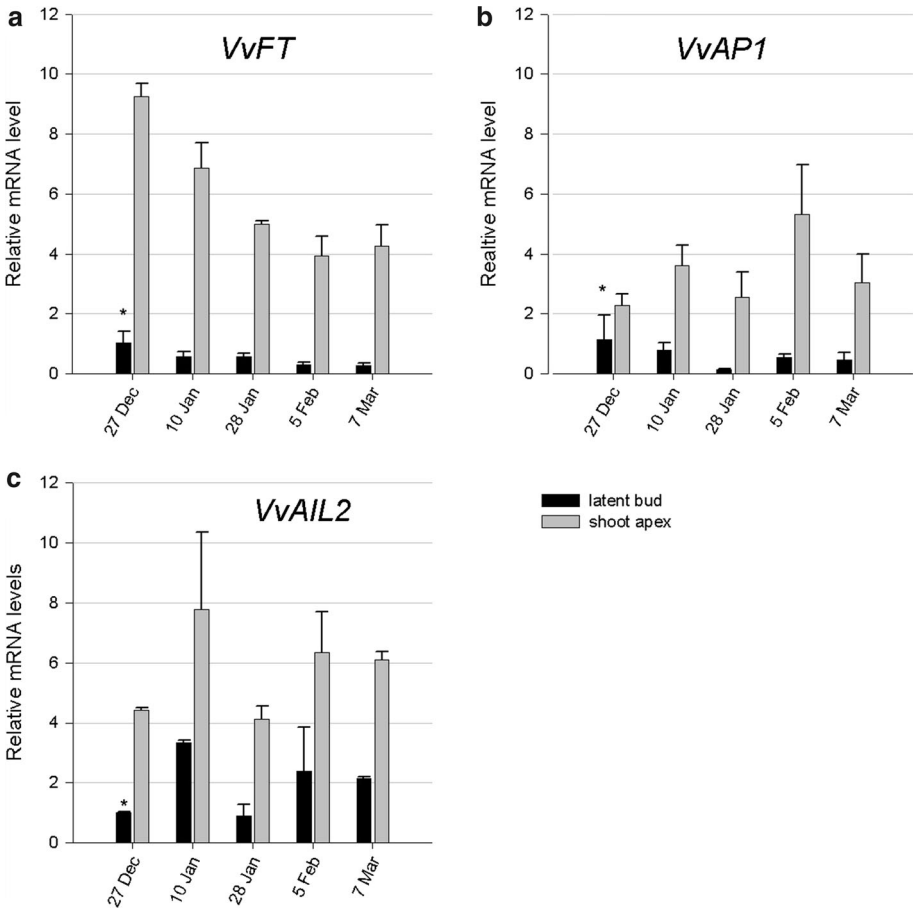

Fig. 2 Expression analysis of genes related with photoperiodic regulation of seasonal growth at the shoot apex and at the latent bud of *V. vinifera* cv. Thompson seedless during the transition from PD to ED. Gene expression analysis was performed by qRT-PCR normalized against *VvUBIQUITIN*. *Values* are referred to control sample marked with (*asterisk*), and are the average of three biological replicates with three technical repetitions ± SD

Discussion

Apical meristems are specialized regions found at the extremity of the stem and root, where cells remain in a non-differentiated state and have the potential to proliferate indefinitely (Gegas and Doonan 2006). Axillary and adventitious meristems are also major participants in the control of the overall plant form, but their outgrowth is controlled in various ways including the arrest of development and dormancy. In *Vitis vinifera*, both organs the shoot apex and the latent bud contain a meristem; nevertheless, the behavior of the meristem differs depending on the organ. In the latent bud, as a result of the shortening of day length in late summer, the meristematic cell division stops and the buds enter into a recess period or ED (Kühn et al. 2009; Grant et al. 2013), while in the shoot apex, the meristematic cell division continues and stops gradually with the onset of decreasing temperatures in autumn, and finally dies without entering into ED. In *Populus*, growth arrest of terminal bud is the first event in the process of initiation of ED in response to shortening photoperiods (Rohde and Bhalerao 2007; Petterle et al. 2013), and the same module that controls the photoperiodic flowering of *Arabidopsis* (CO/FT) is likely to be responsible for growth cessation in *Populus* (Böhlenius et al. 2006; Horvath 2009). Moreover, the rapid down-regulation of *FT* after perception of SD is a key event in the induction of growth cessation and ED development in *Populus* (Böhlenius et al. 2006). Recently, a model which provides insights into the molecular mechanism from SD photo-perception to growth arrest and ED development by inactivation of cell growth regulators has been proposed in hybrid aspen (Azeez et al. 2014). In this model, *FT* responds to photoperiod signals and through the mediation of *AP1* and *AIL* genes regulates cell cycle genes which control cell division activity and growth. In *V. vinifera* as in *Populus*, SD photoperiod downregulated the expression of *VvFT*, indicating that a similar signal cascade that integrates photoperiod signals with growth cessation and dormancy development could operate in both species. The greatest expression of *VvFT*, *VvAP1* and *VvAIL2* at the shoot apex is consistent with an increased mitotic activity of this organ. Therefore, this result could explain the different responses of both organs to SD photoperiod, because when *VvFT* level is high, as in the shoot apex, growth cessation is hindered because the level of *VvFT* is not low enough. Conversely, when *VvFT*

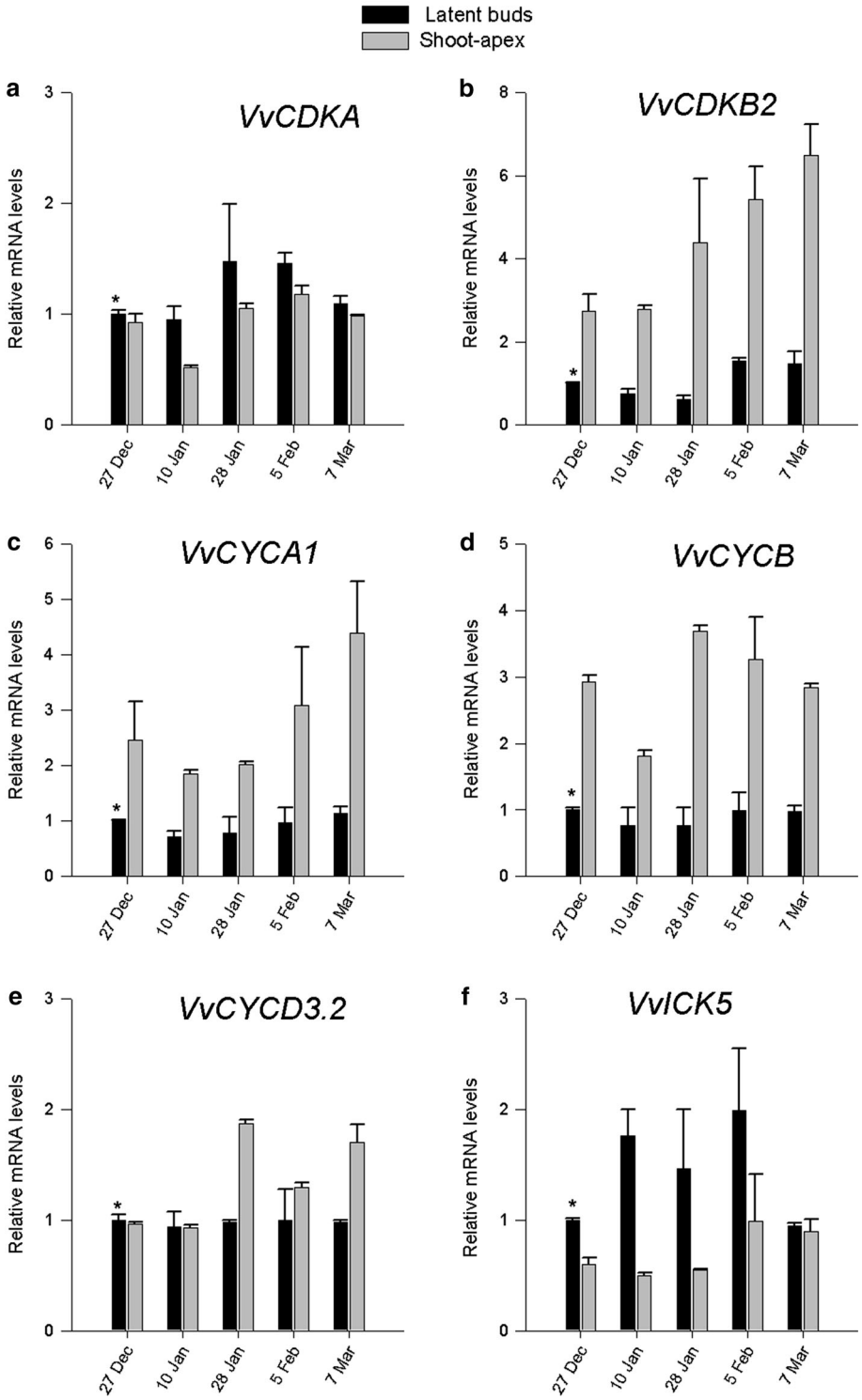

Fig. 3 **a–f** Expression analysis of cell cycle genes at the shoot apex and at the latent buds of *V. vinifera* cv. Thompson seedless during the transition from PD to ED. Gene expression analysis was performed by qRT-PCR normalized against *VvUBIQUITIN*. Values are referred to control sample marked with (*asterisk*), and are the average of three biological replicates with three technical repetitions ± SD

level is low, as in the latent buds, SD photoperiod induce growth cessation and ED and *VvFT* are not detectable during this period.

Plants contain two main types of cyclin-dependent kinase (CDK) involved in primary control of the mitotic cell cycle, the CDKA which is equivalent and functionally interchangeable with CDK1, the CDK of yeast and animals (Joubés et al. 2000), and the CDKB which is present in higher plants in two sub-types called CDKB1 and CDKB2. The remarkable feature of the *CDKB* genes is that they are expressed only in mitotic cells, from the S-phase until the M-phase of the cell

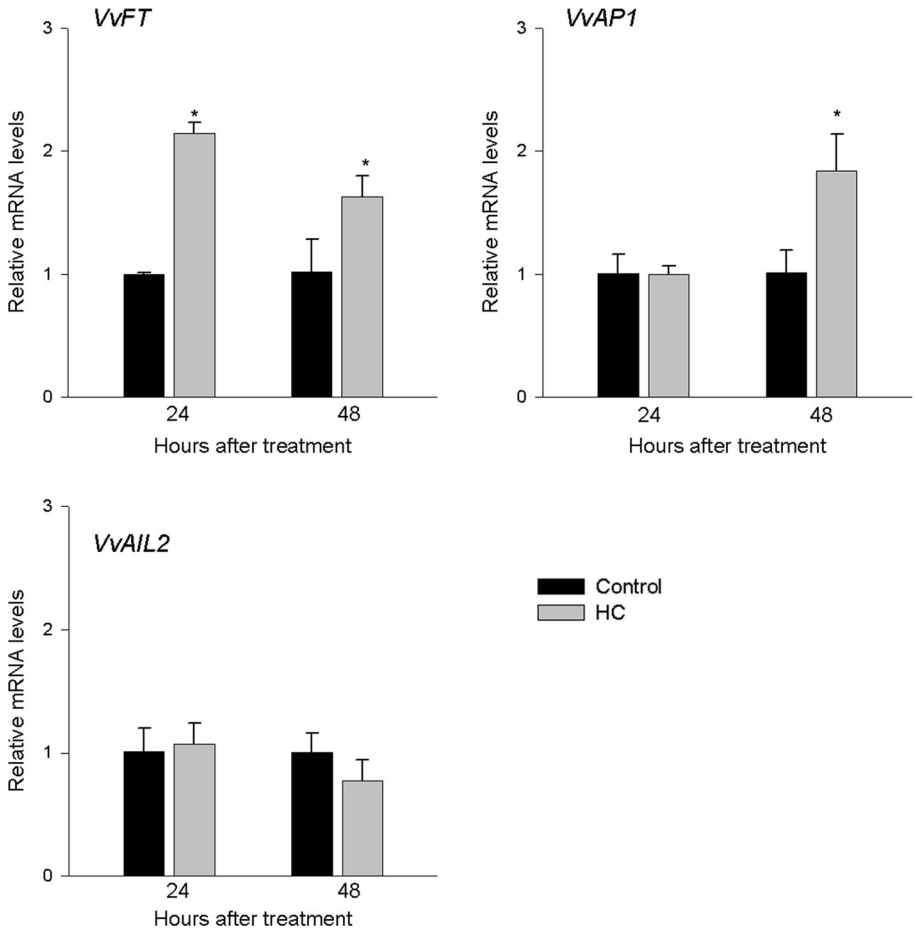

Fig. 4 Effect of hydrogen cyanamide (H_2CN_2) on the expression of genes related with photoperiodic regulation of seasonal growth in dormant buds of *V.vinifera* cv. Thompson seedless. Gene expression analysis was performed 24 and 48 h after treatments by qRT-PCR normalized against *VvUBIQUITIN*. *Values* are the average of three biological replicates with three technical repetitions ± SD (*asterisk*) Student's *t* test ($\alpha = 0.05$)

cycle. The *CDKB1* are expressed from the S-phase and peak in G2, whereas the *CDKB2* genes are expressed somewhat latter from G2-M (Menges et al. 2005). The increased expression of *VvCDKA*, *VvCDKB2* and cyclins *VvCYCA1*, *VvCYCB* and *VvCYCD3.2* in the shoot apex than in latent buds, and on the contrary, the higher expression of the inhibitor of cyclin-dependent kinase *VvICK5* in the latent bud than in the shoot apex, is consistent with a higher mitotic activity of the apex. The high mitotic activity of the shoot apex due to the high expression of *VvFT* could be the reason that explains the lack of growth cessation and the development of ED in the apex in response to SD photoperiod.

Analyzing microarray data for developmental transition in grapevine buds (Díaz-Riquelme et al. 2012), it was found that *VvFT* co-expressed with cell cycle genes. Thus, during the transition from PD to ED the level of *VvFT* decreased similarly to cell cycle regulators *VvCDKA*, *VvCDKB2*, *VvCYCA1*, *VvCYCD3.2*, while during the transition from ED to bud-break, *VvFT* level increased together with cell cycle genes. This finding suggests that *VvFT* could transcriptionally regulate cell cycle genes, and by means of them, regulates the development of ED. The development of ED is an adaptive trait that has a profound effect on cell proliferation. Previous studies have suggested that endodormant cells are predominantly arrested in the G1 phase of the cell cycle. Changes in cell-specific gene expression occur during release of axillary buds of pea (Devitt and Stafstrom 1995) potato (Campbell et al. 1996) adventitious buds of leafy spurge (Horvarth et al. 2002) and Jerusalem artichoke (Freeman et al. 2003) from dormancy. Here, it was found that the dormancy releasing compound hydrogen cyanamide (H_2CN_2) up-regulates the expression of *VvFT* and *VvAP1* together with the expression of cell cycle genes *VvCDKA*, *VvCDKB2* and *VvCYCA1* in dormant grapevine buds, suggesting that the release of dormancy is accompanied by an increase in mitotic activity of meristematic cells, and cell cycle genes may be transcriptionally regulated by *VvFT* through the mediation of *VvAP1*. However, *VvAIL2* participation in the *VvFT* signaling cascade is questioned, since their expression is not affected by H_2CN_2. To reach a definitive conclusion on the regulation of cell cycle genes by *VvFT*, analyzing the effect of *VvFT* overexpression on the expression of cell cycle

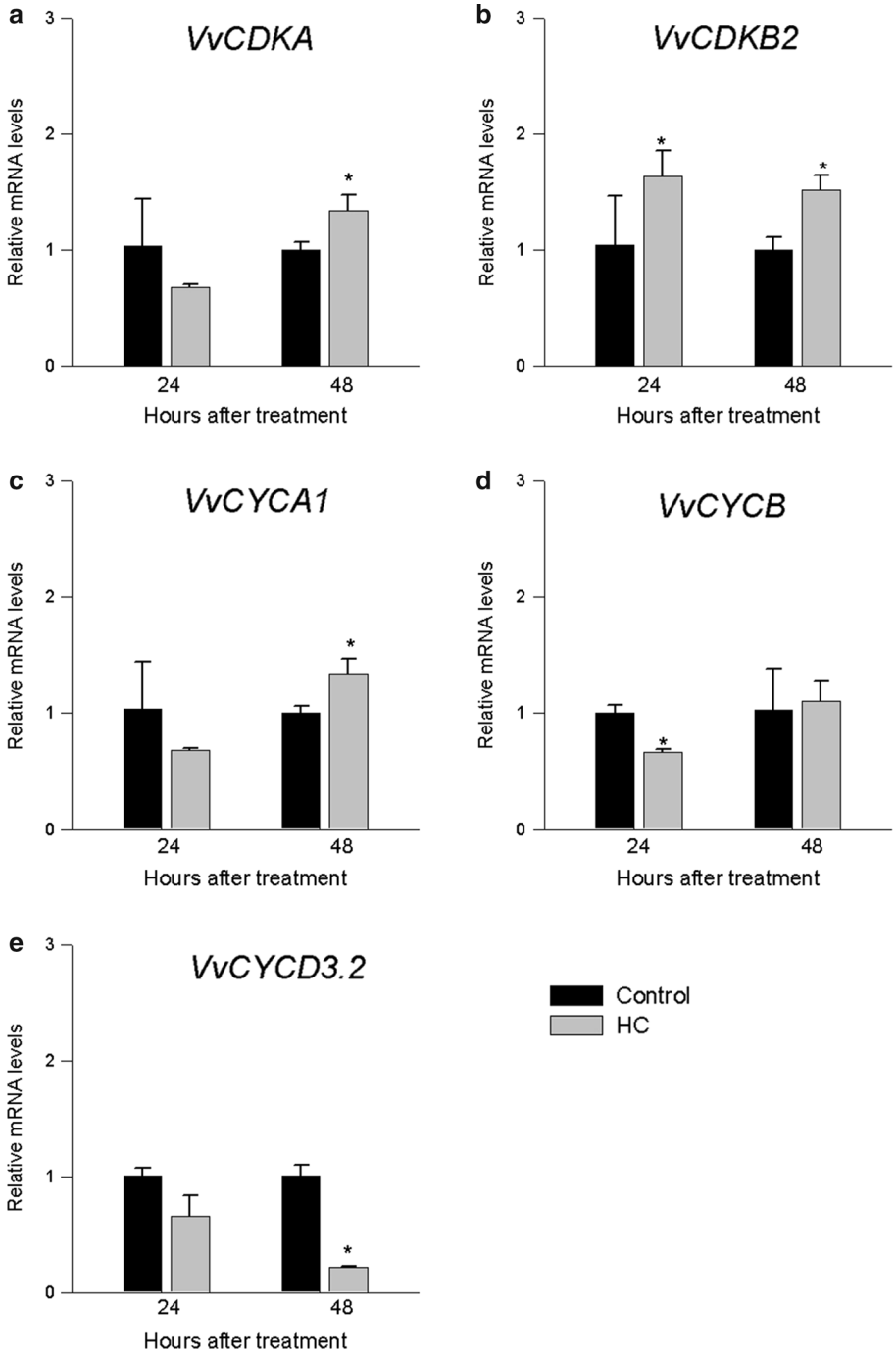

Fig. 5 **a–e** Effect of hydrogen cyanamide (H_2CN_2) on the expression of cell cycle genes in dormant buds of *V.vinifera* cv. Thompson seedless. Gene expression analysis was performed 24 and 48 h after treatment by RT-qPCR normalized against *VvUBIQUITIN*. *Values* are the average of three biological replicates with three technical repetitions ± SD (*asterisk*) Student's *t* test ($\alpha = 0.05$)

genes (CCG), either in a homologous or heterologous system is needed.

Author contribution statement RV and FJP designed research; RV, XN, FP and DD performed research; FJP analysed data; RV and FJP wrote the paper.

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