ResearchGate

See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/337645633

Buds of "Italia melhorada" grapevines grown under tropical conditions develop a quiescent state

Article *in* Environmental and Experimental Botany · November 2019

DOI: 10.1016/j.envexpbot.2019.103951

CITATIONS
0

READS
56

4 authors, including:

Debora Dantas
Universidade Federal Rural do Semi-Árido - UFERSA
10 PUBLICATIONS **111** CITATIONS

SEE PROFILE

Ricardo Bressan-Smith
Universidade Estadual do Norte Fluminense
66 PUBLICATIONS **1,147** CITATIONS

SEE PROFILE

Francisco J. Pérez
University of Chile
66 PUBLICATIONS **1,881** CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:

Plant hormones in fruit species View project

All content following this page was uploaded by Ricardo Bressan-Smith on 05 December 2019.

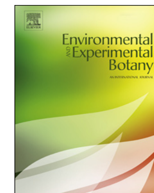
The user has requested enhancement of the downloaded file.

Environmental and Experimental Botany 171 (2020) 103951

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot



Buds of "Italia melhorada" grapevines grown under tropical conditions develop a quiescent state

Débora Dantas[a], Ricardo Bressan-Smith[a], Ximena Noriega[b], Francisco J. Pérez[b,*]

[a] Centro De Ciencias e Tecnologia Agropecuarias, Universidade Estadual Do Norte Fluminense, Av Alberto Lamego 2000, Campos Dos Goytacazes, RJ, Brazil

[b] Laboratorio De Bioquímica Vegetal, Facultad De Ciencias, Universidad De Chile, Casilla 653, Santiago, Chile

ARTICLE INFO

Keywords:
Grapevine buds
Dormancy
Quiescence
Photoperiod
Phytochromes

ABSTRACT

A double cropping system for the grapevine (*Vitis vinifera* L) has been commercially adopted for use in regions where the tropical climate is characterized by high temperatures and small variations in daylength throughout the year. Under these climatic conditions, the use of hydrogen cyanamide (HC), a compound that breaks bud dormancy, is mandatory to produce homogeneous budbreak. However, it is unknown whether grapevine buds are capable of developing endodormancy (ED) under these climatic conditions. In this study, typical signals of ED, such as the number of nodes per cane, the development of periderm and the thickening of the cell wall of the bud meristematic cells, were analysed in vines of "Italia melhorada" grown in Mossoró, Brazil (5°12′16″S), under a natural (ND) photoperiod (12/12 h), a short-day (SD) photoperiod (10/14 h) and a long-day (LD) photoperiod (14/10 h). The abundance of phytochrome A (*VvPHYA*) and B (*VvPHYB*) and *FLOWERING LOCUS T* (*VvFT*) transcripts in the leaves and buds was also determined. The results showed a reduced number of nodes per cane and development of the periderm in the shoots of grapevines grown under ND and SD photoperiods. In addition, compared with that under the LD photoperiod, the expression of *VvPHYA* and *VvFT* under the ND and SD-photoperiod decreased, and the expression of *VvPHYB* increased. However, the thickness of the cell wall of the bud meristematic cells increased only in the grapevines exposed to the SD photoperiod. Therefore, we hypothesize that cell wall thickening is a characteristic of ED, while decreased expression of *VvPHYA* and *VvFT* and increased expression of *VvPHYB* are characteristic of quiescence. Consequently, under a tropical conditions, the grapevine buds would be in a quiescent state and not in a dormant state.

1. Introduction

The reproductive cycle of the grapevine (*Vitis vinifera* L) cultivated in temperate climates span two consecutive seasons, separated by a period of dormancy or recess between late summer and early spring (Carmona et al., 2008; Li-Mallet et al., 2016). On the basis of data concerning the factors that inhibits bud outgrowth, dormancy has been divided into paradormancy (PD) in which bud outgrowth is inhibited by apical dominance or correlative inhibition, endodormancy (ED) in which bud outgrowth is inhibited by intrinsic factors located within the bud, and ecodormancy (ECD) in which bud outgrowth is inhibited by environmental cues such as low temperatures (Lang, 1987). However, Considine and Considine (2016) recently suggested the use of the terms "quiescence" and "dormancy" instead of para-, endo- and ecodormancy, and to look for association of these terms with physiological factors. In grapevine buds, ED is induced by the decreasing photoperiod during late summer (Kühn et al., 2009; Grant et al., 2013; Cragin et al., 2017), and is characterized by growth inhibition, arrested cell division (Vergara et al., 2017), reduced respiratory activity (Parada et al., 2017), cell wall thickening of meristematic cells (Rubio et al., 2016) and starch accumulation (Rubio et al., 2019). Although there are no visual signs indicating the state of bud ED (Lavee and May, 1997), the inhibition of cane growth and periderm development has been associated with the development of bud ED (Fennell and Hoover, 1991). The development of bud ED is part of the process by which the buds adapt to the unfavorable conditions of the winter, and its main functions is to avoid budbreak in response to a transient warm spell during the winter (Jian et al., 1997), and to promote cold acclimation induced by low temperatures (Cragin et al., 2013; Rubio et al., 2016). In a previous study, large differences in the sprouting of para- and endodormant grapevine buds were detected under forced conditions, and it was concluded that the paradormant buds are in a quiescent state, in which sprouting and growth can resume rapidly, while the endodormant buds are in a state of recess, which they have to leave before

* Corresponding author.
E-mail address: frperez@uchile.cl (F.J. Pérez).

https://doi.org/10.1016/j.envexpbot.2019.103951
Received 19 August 2019; Received in revised form 14 November 2019; Accepted 17 November 2019
Available online 29 November 2019
0098-8472/ © 2019 Elsevier B.V. All rights reserved.

they can sprout (Pérez and Noriega, 2018).

In tropical climates, where variations in daylength and temperatures are minor throughout the year, budbreak can be achieved during the current growing season by pruning and applications of hydrogen cyanamide (HC), resulting in a double cropping system (Lin et al., 1985; Bai et al., 2008; Gu et al., 2012). The production of two crops of table grapes per year was achieved in Taiwan by combining pruning, defoliation and chemical treatment (Lin et al., 1985). Similarly, in the Brazilian Southeast Region and in southern China, double cropping strategies have been introduced (Favero et al., 2011; Chen et al., 2017). In Brazil, grape production is distributed from the southern extreme to the Northeast Region (Pommer et al., 2009). This double cropping strategy allows a geographical redistribution of viticulture in Brazil with the incorporation of new producing states such as Ceará (Camargo et al., 2011). However, a better understanding of bud dormancy, and other physiological aspects of the vine will help to effectively implement this new production strategy.

The light signals perceived by phytochromes (Phys) and cryptochromes (Crys) play a key role in the growth and development of plants, and in photoperiod-dependent processes such as flowering, tuberization, seasonal growth cessation and dormancy. In the vine, ED is induced by decreasing photoperiod (Kühn et al., 2009; Grant et al., 2013; Cragin et al., 2017), and Phys together with the *FLOWERING LOCUS T* (*VvFT*) gene play a crucial role in the development of bud-ED (Pérez et al., 2009, 2011).

In the double cropping system, the use of hydrogen cyanamide (HC), a compound that breaks bud dormancy, is mandatory (Bai et al., 2008; Gu et al., 2012). However, the underlying biochemical and molecular events that justify this agronomic management practice are unknown. In this study, we hypothesize that grapevine buds grown under tropical conditions develop ED, which would explain the need to apply HC to release the buds from ED (Shulman et al., 1983). To test this hypothesis, "Italia melhorada" grapevines grown in Mossoró, Brasil (5°12′16″S latitude) were subjected to different photoperiod regimens: natural (ND, 12/12 h), short day (SD, 10/14 h) and long day (LD, 14/10 h) photoperiods. After eight weeks of treatment, typical ED signals such as the number of nodes per cane, periderm development in the shoots and cell wall thickening of bud meristematic cells were assessed. Furthermore, because phytochromes and *FLOWERING LOCUS T* (*VvFT*) play a crucial role in the perception of the photoperiod, the transcript abundance of phytochrome A (*VvPHYA*) and B (*VvPHYB*) and of *VvFT* were in the leaves and buds of grapevines was determined.

2. Materials and methods

2.1. Plant material and experimental conditions

Vitis vinifera L. "Itália melhorada" scions atop IAC 572 rootstock were grown at the Federal University of Rural Semi-arid (UFERSA), located in Mossoró, Brazil (5°12′16″S latitude, 18 m altitude). The seedlings were planted into a 1:1:1 (v:v:v) soil:sand:peat mixture in 5 L pots. As growth started, one shoot was allowed to develop on each plant. The plants were grown in an unshaded glasshouse, with a 31/29 °C temperature and 63/79 % relative humidity and a photosynthetic photon flux (PPF) density of 600–1400 $\mu mol\, s^{-1}\, m^{-2}$ from October to December. The temperature and the relative humidity were recorded by an automatic meteorological station located at the UFERSA, and the PPF was measured using an LI-190SA quantum sensor.

2.2. Photoperiod treatments

On October 15th, vines displaying uniform growth with 12–16 leaves at EL stage 17 or 18 according to the phenological scale of Eichhorn and Lorenz (Lorenz et al., 1995), were selected and randomly assigned to each photoperiod treatment for 8 weeks. The photoperiod treatments included a natural photoperiod (ND 12/12 h day/night), a LD photoperiod (14/10 h day/night) and a SD photoperiod (10/14 h day/night). The LD and SD treatments were imposed with opaque plastic material, the same used to make blackout curtains. Two layers of this material were used in the construction of the unshaded greenhouse to prevent the passage of light. Two unshaded greenhouses were built, one for the SD photoperiod and the other for the LD photoperiod that contained an artificial light system (Supplementary data Fig. 1S). During the night, the plants in both treatments were kept inside the unshaded greenhouse with the curtains extended. The SD photoperiod was imposed by keeping the curtains extended until 7:30 a.m., while for the LD photoperiod, the curtains were raised at 4:30 a.m. before dawn (5:08 a.m.) and the lights turned on automatically at 5:30 pm and remained on until 7:30 pm. The control treatment had no coverage. The supplemental light was provided by a fluorescent 100 W tube, and the treatments were imposed for 8 weeks, because that is reportedly the time needed for grapevine buds to reach the endodormancy state under a SD photoperiod (Fennell and Hoover, 1991). The temperatures were measured separately in both treatments with a thermometer.

2.3. Photoperiod effect on the growth and periderm development

Cane length, node number, and periderm development were measured twice per week on 10 plants from each of the ND, LD, and SD photoperiod treatments for 8 continuous weeks. Periderm development was estimated visually by monitoring the progression of external cane browning by counting the number of brown internodes from the base of the cane.

2.4. Photoperiod effect on the cell wall (CW) thickness of bud meristematic cells

Axillary buds located on the third node of the branches were collected from plants at the beginning (zero time) and after 8 weeks of the photoperiodic treatments (three replicates per treatment). The buds were fixed in 100 mM phosphate buffer (pH 7.2) and 2 % glutaraldehyde (v:v) and then were post-fixed in excess of OsO_4 for 1 h. After post-fixation, the buds were washed twice in phosphate buffer containing 2 % potassium antimonate and then washed twice with distilled water pH 10 adjusted with KOH. Thereafter, they were dehydrated in a graded series of ethanol for at least 1 h and subsequently embedded in LR White resin (Agar Scientific, Stansted Essex, UK). The embedded samples were cut in sections of 90 nm by an ultramicrotome MT4000, after which they were collected in copper grids and stained with uranyl acetate and lead citrate. Afterwards they were placed in an aqueous solution of 2.5 % uranyl acetate for 20 min and protected from light. The samples were then washed in distilled water and placed on filter paper. After washing, they were incubated in Petri dishes that contained parafilm, and citrate drops were placed along with sodium NaOH pellets to decrease the CO_2 concentration for 3 min. Finally, the thickness of the cell wall of the bud meristematic cells was examined by transmission electron microscopy (TEM) operated at 80 kV at the Laboratory of Cell Biology and Tissue (LBCT) at the State University of Norte Fluminense Darcy Ribeiro (UENF).

2.5. Photoperiod effect on the expression of the VvPHYA, VvPHYB and VvFT genes

For the photoperiod experiments, total RNA was isolated from lyophilized buds and leaves (0.05 –0.1 g) located on the third node of the branches of *V. vinifera* cv. "Italia melhorada". The total RNA was extracted and purified using a modified method of Chang et al. (1993), as described by Noriega et al. (2007). DNA was removed by treatment with RNAase-free DNAase (1 U/μg) (Invitrogen, CA, USA) at 37 °C for 30 min. First-strand cDNA was synthesized from 5 μg of purified RNA with 1 μL oligo(dT)12–18 (0.5 μg 9 μL^{-1}) as primers, 1 μL of dNTP mix (10 mM), and Superscript II RT (Invitrogen, USA). Gene expression

analysis was performed by quantitative real-time PCR, and carried out in an Eco Real-Time PCR system (Illumina, Inc. SD, USA), in conjunction with Kapa SYBR FAST mix (KK 4602) and Kapa Taq DNA Polymerase. Primers were obtained from (Kühn et al., 2009). The amplification of cDNA was performed under the following conditions: denaturation at 94 °C for 2 m followed by 40 cycles at 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 45 s. Three biological replicates with three technical repetitions were included for each treatment. The sampling was carried out five times during the day: at 06:00, 10:00, 14:00, 18:00, and 22:00 h. Transcript levels were calculated by the ΔΔCq method (Livak and Schmittgen, 2001) using *VvUBIQUITIN* as the reference gene. *VvUBIQUITIN* was selected as a reference gene because the transcript level was stable across treatments (Rubio et al., 2016).

3. Results

3.1. Effects of photoperiod on node number

Vitis vinifera L. cv. Italia melhorada plants grown under different photoperiod regimens: ND (12/12 h day/night), SD (10/14 h day/night) and LD (14/10 h day/night) differed in terms of the number of nodes that developed after eight weeks of treatment. It was observed that the average number of nodes developed by grapevines exposed to the ND and SD photoperiod was 26, while for grapevines exposed to the LD photoperiod, the number was 29; this difference was statistically significant ($p < 0.05$). (Table 1).

3.2. Effects of photoperiod on periderm development

The development of the periderm in the internodes of the lateral shoots of *Vitis vinifera* L. cv. Italia melhorada plants grown under different photoperiod regimens for eight weeks is shown in Fig. 1. The beginning of the development of the periderm occurred from the fourth week onwards. The ND and SD treatments did not differ significantly until the fourth week; subsequently, the SD treatment exceeded the ND treatment in terms of the number of internodes in which periderm had formed. In both cases, there was a progressive increase in periderm development until the end of the eighth week, while in the LD treatments, no periderm development was observed during the 8 weeks (Fig. 1).

3.3. Effects of photoperiod on the thickness of the cell wall of bud meristematic cells

Cytological changes in axillary bud meristems of Italia melhorada after eight weeks of exposure to the ND, SD and LD photoperiod treatments are shown in Fig. 2. The axillary buds collected before starting the photoperiodic treatments (time zero) and those of plants exposed to ND and LD photoperiods have thin cell walls and innumerable small vacuoles, and there were no differences between among (Fig. 2A, B, D). However, the meristematic cells of the axillary buds of grapevines exposed to the SD photoperiod showed a thicker cell wall than did those exposed to the ND and LD photoperiods (Fig. 2C). The thickness measurements of the axillary bud meristem cells assessed by the Image J program confirmed the differences detected with the transmission electron microscopy images (Fig. 2).

Table 1
Number of nodes per cane in *Vitis vinifera* L. cv. 'Itália melhorada' after eight weeks of growth under ND (12/12 h day/night), SD (10/14 h day/night) and LD (14/10 h day/night) photoperiod. Average follows by the same letter do not differ statistically according to Tukey test ($P < 0.05$ $N = 10$).

Treatments	Average
ND	26,5 b
SD	26,2 b
LD	28,9 a

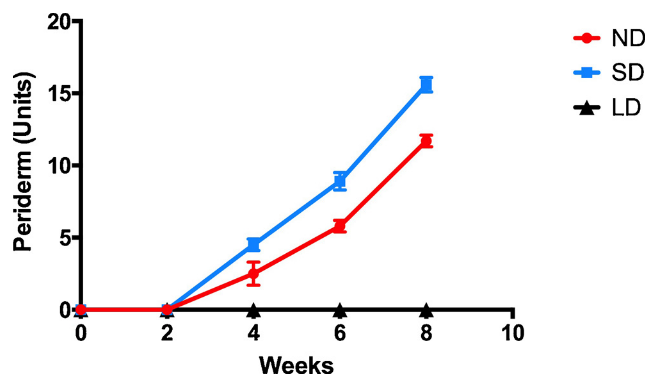


Fig. 1. Number of internodes with periderm in *V. vinifera* cv. "Italia melhorada" plants after eight weeks of the following photoperiod treatments ND (12/12 h day/night), SD (10/14 h day/night) and LD (14/10 h day/night). The values represent the averages ± S.Ds of 10 replicates.

3.4. Effects of photoperiod on the expression of VvPHYA and VvPHYB in the leaves and buds of V. vinifera

The relative abundance of *VvPHYA* and *VvPHYB* transcripts in leaves and buds of *Vitis vinifera* L. "Itália melhorada" oscillated with a daily rhythm that differed for the different photoperiod treatments. In the leaves, compared with LD photoperiod the ND and SD photoperiods significantly reduced the relative abundance of *VvPHYA* transcripts. This phenomenon was observed at all hours of the day, except at 14:00 (Fig. 3). Compared with the LD photoperiod, the ND and SD photoperiods also reduced the relative abundance of *VvPHYA* transcripts in the buds, and this reduction was highest at 14:00 and 18:00 (Fig. 3). In contrast, the ND and SD photoperiods significantly increased the relative abundance of *VvPHYB* transcripts in both the leaves and the buds (Fig. 3), compared with that under the LD photoperiod, and the greatest increase was observed at 14:00.

3.5. Effects of photoperiod on the expression of VvFT in leaves and buds of V. vinifera

The daily expression pattern of *VvFT* transcripts in the buds and leaves of "Italia melhorada" was similar. In both cases, a major abundance of *VvFT* transcripts was observed under the LD-photoperiod, reaching a maximum at 22:00 h in the leaves and at 18:00 h in the buds (Fig. 4). Under the ND and SD photoperiods, the level of *VvFT* remained at a low level, without large variations throughout the day.

4. Discussion

In tropical regions, where variations in daylength are small and temperatures are high throughout the year, a double cropping system have been adopted for grapevines (Chen et al., 2017). However, the use of HC, a compound that breaks bud ED (Or, 2009; Pérez et al., 2009), is mandatory for their commercial production under these climatic conditions. This agronomic management practice suggests that the grapevine buds under tropical conditions may develop ED since HC advances bud sprouting by releasing the buds from the ED (Shulman et al., 1983). The role of abscisic acid (ABA) in the release of grapevine buds from ED and in their cold acclimation/deacclimation process has been studied recently (Zheng et al., 2015; Vergara et al., 2017; Rubio and Pérez, 2019). Furthermore, HC upregulated the expression of *VvA8H-CYP707A4*, which encodes ABA 8´-hydroxylase, which catabolizes ABA

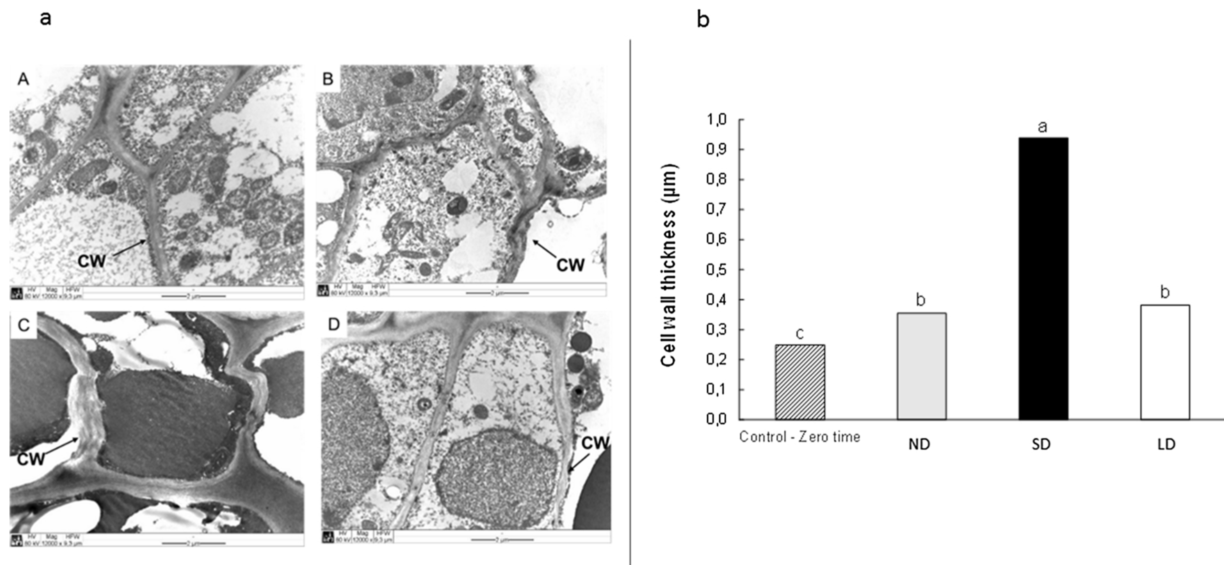


Fig. 2. a) Electron microscopy images of bud meristematic cells of *V.vinifera* cv. "Italia melhorada" plants after eight weeks of different photoperiod treatments, A) control, time zero (day of the start of treatments), B) natural photoperiod (ND; 12/12 h day/night), C) short-day photoperiod (SD; 10/14 h day/night) and C) long-day photoperiod (LD; 14/10 h day/night). Images scales = 2 μm; 12000 × cell wall. b) Cell-wall thickness of bud meristematic cells of *V. vinifera* cv. "Italia melhorada" after eight weeks of the above treatments. The different lowercase letters indicate statistically significant differences (Tukey´s test, $P < 0.05$, $N = 16$).

(Zheng et al., 2015; Vergara et al., 2017), and transgenic grapevines overexpressing *VvA8H-CYP707A4* exhibit increased ABA catabolism and significant enhancement of budbreak in both controlled and natural environments (Zheng et al., 2018). Therefore, the reduction in ABA content seems to be a possible mechanism by which HC releases the ED of buds. In accordance with this proposal, we have shown that, under forced conditions, ABA levels decreased significantly before bud break in both paradormant (quiescent) and endodormant grapevine buds (Pérez and Noriega, 2018). From the results reported here, it is clear that, although the buds of grapevines grown under tropical conditions

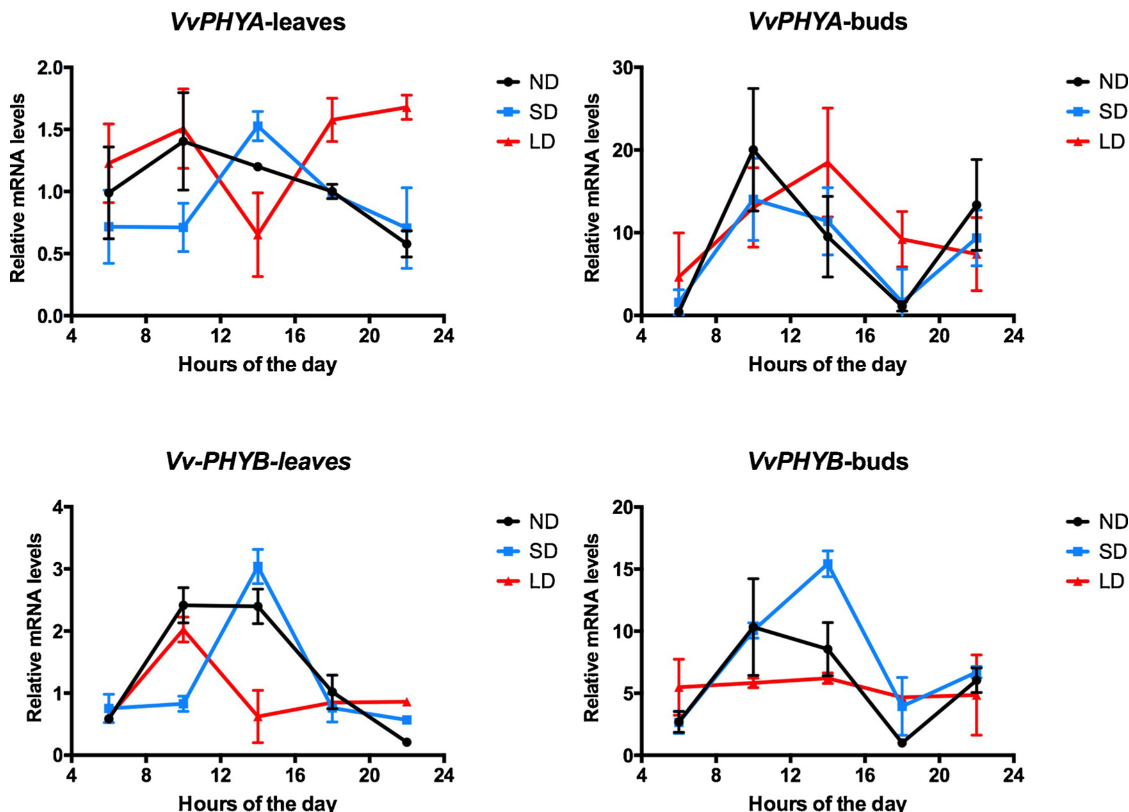


Fig. 3. Daily expression profile of *VvPHYA* and *VvPHYB* in the leaves and buds of *V.vinifera* cv."Italia melhorada" plants after eight weeks of the following photoperiod treatments: ND (12/12 h day/night), SD (10/14 h day/night) and LD (14/10 h day/night). Gene expression analysis was performed by RT-qPCR normalized against the expression of *VvUBIQUITIN* The values are expressed relative to those of samples collected at 6:00 a.m., and correspond to the average of three biological replicates and three technical repetitions ± S.Ds.

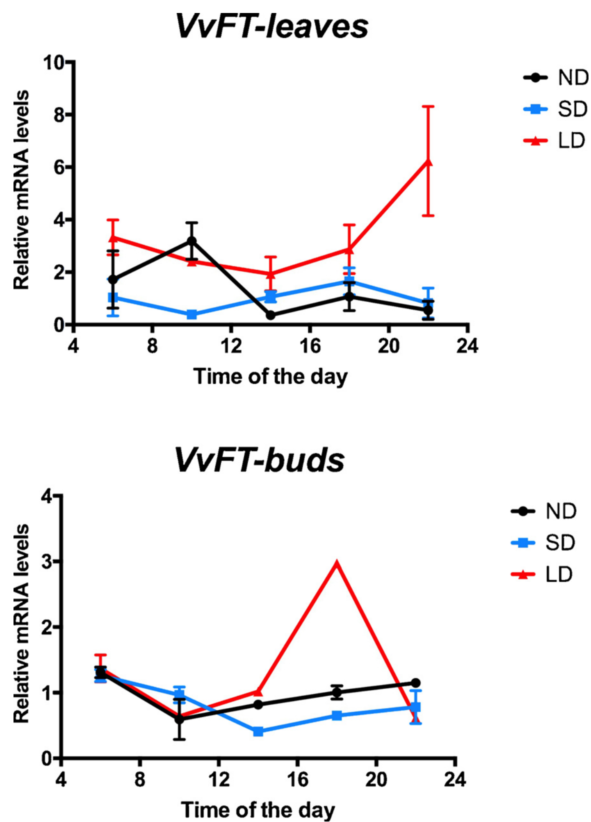


Fig. 4. Daily expression profile of *FLOWERING LOCUS T* (*VvFT*) in the leaves and buds of *V.vinifera* cv."Italia melhorada" plants after eight weeks of the following photoperiod treatments: ND (12/12 h day/night), SD (10/14 h day/night) and LD (14/10 h day/night). Gene expression analysis was performed by RT-qPCR normalized against the expression of *VvUBIQUITIN* The values are expressed relative to those of the samples collected at 6:00 a.m., and correspond to the average of three biological replicates and three technical repetitions ± S.Ds.

develop some typical signs of ED, such as a reduction in the number of nodes, the development of periderm and a reduction in the expression of *VvPHYA* and *VvFT* transcripts, they do not enter into ED since the thickness of the cell wall of their meristematic cells did not increase, as occurred with the buds of grapevines exposed to the SD photoperiod. It is well known that SD photoperiods induce bud ED in grapevines (Kühn et al., 2009; Grant et al., 2013; Cragin et al., 2017) and that the thickening of the cell wall of meristematic cells is characteristic of bud endodormancy in grapevines (Rubio et al., 2016). Therefore, in accordance with Considine and Considine (2016) suggestions, we thought that the buds of grapevines grown under tropical conditions are in a quiescent state, which, in poplar, is characterized by growth cessation, and repression of *VvPHYA* and *VvFT* expression (Maurya and Bhalerao, 2017). Moreover, the rapid growth resumption of quiescent buds compared with dormant buds under forced growth conditions (Pérez and Noriega, 2018), is consistent with the idea that buds are quiescent under tropical conditions, since after pruning and HC applications, they sprout quickly. In hybrid poplars, Tylewicz et al. (2018) showed that the photoperiod regulation of dormancy is mechanistically distinctive from the cessation of growth. Those authors postulated that dormancy is established when intercellular communication through plasmodesmata is blocked by an ABA-dependent process, and therefore, closed plasmodesmata would be associated with dormancy. In the case of the grapevines, dormancy would be associated with the thickening of the cell wall of bud meristematic cells, which could also involve a blockage of intercellular communication. Because quiescence and dormancy in grapevine buds is reached under a 12/12 (L/D) photoperiod and under a 10/14 (L/D) photoperiod, respectively, we postulate that quiescence and dormancy are sequential events that respond to a gradual shortening of the length of the day.

It has been suggested that a common signaling pathway involving *PHYA* and the floral integrator gene *FT* participates in the regulation of photoperiod-dependent processes, such as flowering and ED induction in perennial species (Horvath, 2009). Poplar responds to SD photoperiods by cessation of growth, the establishment of terminal buds and the initiation of ED (Olsen et al., 1997; Welling et al., 2002). Overexpression of oat *PHYA* in the hybrid poplar (*P. tremula x P. tremuloide*), causes the transgenic plants to not respond to SD photoperiod and to continue to grow without establishing terminal buds and entering ED (Olsen et al., 1997). On the other hand, overexpression of *PtFT1*, the poplar orthologue of *Arabidopsis FT*, renders no cessation of seasonal growth or transition of the buds towards ED under conditions of a SD photoperiod (Böhlenius et al., 2006). In addition, the expression of *PTFT1* was not reduced by a SD photoperiod in transgenic poplar overexpressing the oat *PHYA* gene (Böhlenius et al., 2006). These results suggest that *PHYA* and *FT* are involved in the SD photoperiod induction of ED and that the negative regulation of *PtFT1* by the SD photoperiod is mediated by *PHYA*. In *Vitis*, the development of the ED is not associated with growth cessation and bud set, as it is in poplar (Carmona et al., 2008). However, despite these differences in morphology and growth habit between *Vitis* and *Poplar*, in both species, the expression of the *PHYA* and *FT* genes is downregulated during growth cessation and ED development, suggesting that the downregulation of these genes form part of the SD photoperiod signaling pathway leading to growth cessation and ED. In this study, the ND and SD photoperiods reduced the expression of *VvFT* and *VvPHYA* in the leaves and buds of "Italia melhorada, suggesting that this reduction is related to growth cessation and quiescence but not to ED.

Although phytochrome B is involved in regulating seed dormancy (Botto et al., 1995; Donohue et al., 2007; Finch-Savage et al., 2007), the underlying molecular mechanism is unknown. Recently, it has been shown that the expression of *REV1, REV2* and DOG1 transcription factors, which promote seed dormancy, is reduced by *PHYB*, and it was also demonstrated that *REV1* directly inhibits the expression of *GIBBERELLIN 3- OXIDASE 2* (*GA3ox2*), and subsequently suppresses bioactive GA biosynthesis (Jiang et al., 2016). In grapevine buds, the expression of *VvPHYB* was induced by the ND and SD-photoperiods, indicating that this increase is related to the development of a quiescent state; however, how *VvPHYB* contributes to growth cessation and quiescence is unknown.

5. Conclusions

Our results provide evidence that the ND and SD-photoperiods reduce the expression of the *VvPHYA* and *VvFT* genes and increase the expression of *VvPHYB* in the leaves and buds of "Italia melhorada", a phenomenon that was associated with the cessation of growth and quiescence, while the SD-photoperiod was the only treatment that produced a thickening of the cell wall of the meristematic cells of the buds, a phenomenon that was associated with ED. Additionally, our results also indicated that under tropical conditions (the ND photoperiod), the buds of "Italia melhorada" developed a state of quiescence and not ED.

Author statements

DD mounted the photoperiod experiments and performed the morphological physiological and gene expression analysis. RBS contribute to plan the experiments. XN contribute to the gene expression analysis. FJP contribute to plan the experiments and wrote the manuscript.

Declaration of competing interest

There is no conflict interest.

Acknowledgements

The financial support of Fondo Nacional de Ciencia y Tecnología (FONDECYT), Chile Proyecto # 1190057 is gratefully acknowledged.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.envexpbot.2019.103951.

References

Bai, X.J., Li, Y., Huang, J.J., Peng, H.X., Xie, T.L., 2008. One year two harvest cultural technique for Kyoho grape in southern region of Guanxi. Southwest China J. Agric. Sci. 21, 953–955.
Böhlenius, H., Huang, T., Charbonnel-Campaa, L., Brunnet, A.M., Jansson, S., 2006. Regulatory module controls timing of flowering and seasonal growth cessation in trees. Science 312, 1040–1043.
Botto, J.F., Sanchez, R.A., Casal, J.J., 1995. Role of phytochrome B in the induction of seed germination by light in Arabidopsis thaliana. J. Plant Physiol. 146, 307–312.
Camargo, U.A., Tonietto, J., Hoffmann, A., 2011. Progressos na viticultura brasileira. Rev. Bras. Frutic. 33, 618–624.
Carmona, M.J., Chaib, J., Martínez-Zapater, J.M., Thomas, M.R., 2008. A molecular genetic perspective of reproductive development in grapevine. J. Exp. Bot. 59, 2579–2596.
Considine, M.J., Considine, J.A., 2016. On the language and physiology of dormancy and quiescence in plants. J. Exp. Bot. 67, 3189–3203.
Chang, S., Puryear, J., Cairney, J., 1993. A simple and efficient method for isolating RNA from pine trees. Plant Mol. Biol. Rep. 11, 113–116.
Chen, W., Bai, X., Cao, M., Cheng, G., Cao, X., Guo, R., Wang, Y., He, L., Yang, X., He, F., Duan, C., Wang, J., 2017. Dissecting the variations of ripening progression and flavonoid metabolism in grape berries grown under double cropping system. Front. Plant Sci. 8, 1912.
Donohue, K., Heschel, M., Butler, C.M., Barua, D., Sharrock, R.A., Whitelam, G.C., Chiang, G.C.K., 2007. Diversification of phytochrome contributions to germination as a function of seed-maturation environment. New Phytol. 177, 367–379.
Favero, A.C., Amorim, D., Mota, R., Soares, A.M., Souza, C.R., Regina, M., 2011. Double pruning of Syrah grapevine, a management strategy to harvest wine during the winter in the Brazilian Southeast. Vitis 50, 151–158.
Fennell, A., Hoover, E., 1991. Photoperiod influences growth, bud dormancy and cold acclimation of *Vitis labruscana* and V. *riparia*. J. Am. Soc. Hortic. Sci. 116, 270–273.
Finch-Savage, W.E., Cadman, C.S., Toorop, P.E., Lynn, J.R., Hilhorst, H.W., 2007. Dormancy release in Arabidopsis cvi by dry after ripening, low temperature, nitrate and light shows common quantitative patterns of gene expression directed by environmentally specific sensing. Plant J. 51, 60–78.
Cragin, J., Serpe, M., Keller, M., Shellie, K., 2017. Dormancy and cold hardiness transition in wine grape cultivars chardonnay and cabernet sauvignon. Am. J. Enol. Vitic. 68, 195–202.
Grant, T.N.L., Gargrave, J., Dami, I.E., 2013. Morphological physiological, and biochemical changes in *Vitis* genotype in responses to photoperiod regimes. Am. J. Enol. Vitic. 64, 466–475.
Gu, S., Jacobs, S., Mc Carthy, B.S., Gohil, H.L., 2012. Forcing vine regrowth and shifting fruit ripening in warm region to enhance fruit quality in Cabernet Sauvignon grapevine (*Vitis vinifera* L). J. Hortic. Sci. Biotechnol. 87, 287–292.
Horvath, D., 2009. Common mechanisms regulate flowering and dormancy. Plant Sci. 177, 523–531.
Jian, L., Li, P.H., Sun, L., Chen, T.H., 1997. Alterations in ultrastructure and subcellular localization of Ca^{2+} in poplar apical bud cells during the induction of dormancy. J. Exp. Bot. 48, 1195–1207.
Jiang, Z., Xu, G., Jing, Y., Tang, W., Lin, R., 2016. Phytochrome B and REVEILLE ½-mediated signaling controls seed dormancy and germination in *Arabidospis*. Nat. Commun. 7, 12377.
Kühn, N., Ormeño-Nuñez, J., Jaque-Zamora, G., Pérez, F.J., 2009. Photoperiod modifies the diurnalexpression profile of VvPHYA and VvPHYB transcripts in field grown grapevine leaves. J. Plant Physiol. 166, 1172–1180.
Lang, G.A., 1987. Dormancy: a new universal terminology. Hort. Science 22, 817–820.
Lavee, S., May, R., 1997. Dormancy of grapevine buds-facts and speculation. Aust. J. Grape Wine Res. 3, 31–46.
Lin, C.H., Lin, J.H., Chang, L.R., Lin, H.S., 1985. The regulation of the Golden Muscat grape production season in Taiwan. Am. J. Enol. Vitic. 36, 114–117.
Li-Mallet, A., Rabot, A., Geny, L., 2016. Factors controlling inflorescence primordia formation ofgrapevine: their role in latent fruitfulness? A review. Botany 94, 147–163.
Livak, K.J., Schmittgen, T.D., 2001. Analysis of relative gene expression data using real time quantitative PCR and the ΔΔCT method. Methods 25, 402–408.
Lorenz, D.H., Eichhorn, K.W., Bleiholder, H., Klose, R., Meier, U., Weber, E., 1995. Growth stages of the grapevines. Aust. J. Grape Wine Res. 1, 100–110.
Maurya, J.P., Bhalerao, P., 2017. Photoperiod- and temperature-mediated control of growth cessation and dormancy in trees: a molecular perspective. Ann. Bot. 120, 351–360.
Noriega, X., Burgos, B., Pérez, F.J., 2007. Short-day photoperiod triggers and low temperatures increase expression of peroxidase RNA transcripts and basic peroxidase isoenzyme activity in grapevine-buds. Phytochemitry 68, 1376–1383.
Olsen, J., Juntilla, O., Nilson, J., Eriksson, M.E., Martinussen, I., Olsson, O., 1997. Ectopic expression of oat phytochrome A in hybrid aspen change critical daylength to growth and prevent cold acclimatization. Plant J. 12, 1339–1350.
Or, E., 2009. Grape bud dormancy release, the molecular aspects. In: Roubelakis-Angelakis, K.A. (Ed.), Grapevine Molecular Physiology and Biotechnology. Springer, Berlin, pp. 1–9.
Parada, F., Noriega, X., Dantas, D., Bressam-Smith, R., Pérez, F.J., 2017. Differences in respiration between dormant and non-dormant buds suggest the involvement of ABA in the development of endodormancy in grapevines. J. Plant Physiol. 201, 71–78.
Pérez, F.J., Vergara, R., Or, E., 2009. On the mechanism of dormancy release in grapevine buds: a comparative study between hydrogen cyanamide and sodium azide. Plant Growth Regul. 59, 145–152.
Pérez, F.J., Kühn, N., Vergara, R., 2011. Expression analysis of phytochromes A,B and floral integrator genes during the entry and exit of grapevine-buds from endodormancy. J. Plant Physiol. 168, 1659–1666.
Pérez, F.J., Noriega, X., 2018. Sprouting of paradormant and endodormant grapevine buds under conditions of forced growth: similarities and differences. Planta 248, 837–847.
Pommer, C.V., Mendes, L.S., Hespanhol-Viana, L., Bressan-Smith, R., 2009. Potencial climático para a produção de uvas em Vampos dos Goytacazes, regiao norte. Rev. Bras. Frutic. 31, 1076–1083.
Rubio, S., Dantas, D., Bressan-Smith, R., Pérez, F.J., 2016. Relationship between endodormancy and cold-hardiness in grapevine buds. J. Plant Growth Regul. 35, 266–275.
Rubio, S., Noriega, X., Pérez, F.J., 2019. Abscisic acid (ABA) and low temperatures synergistically increase the expression of CBF/DREB1 transcription factors and cold-hardiness in grapevine dormant buds. Ann. Bot. 123, 681–689.
Rubio, S., Pérez, F.J., 2019. ABA and its signaling pathway are involved in the cold acclimation and deacclimation of grapevine buds. Sci. Hortic. 256, 108565.
Shulman, Y., Nir, G., Fanberstein, L., Lavee, S., 1983. The effect of cyanamid on the release from dormancyof grapevine buds. Sci. Hortic. 19, 97–104.
Tylewicz, S., Petterle, A., Marttila, S., Miskolczi, P., Azeez, A., Singh, R.K., Immanen, J., Mähler, N., Hvidsten, T.R., Eklund, D.M., Bowman, L., Helariutta, Y., Bhalerao, R.P., 2018. Photoperiodic control of seasonal growth is mediated by ABA acting on cell-cell communication. Science. https://doi.org/10.1126/science.aan8576.
Vergara, R., Noriega, X., Pérez, F.J., 2017. ABA represses the expression of cell cycle genes an may modulate the development of endodormancy in grapevine buds. Front. Plant Sci. 8, 812.
Welling, A., Moritz, T., Palva, E.T., Juntilla, O., 2002. Independent activation of cold acclimation by low temperatures and short photoperiod in hybrid aspen. Plant Physiol. 129, 1633–1641.
Zheng, C., Halaly, T., Acheampong, A.K., Takebayashi, Y., Jikumaru, Y., Kamiya, Y., Or, E., 2015. Abscisicacid (ABA) regulates grape bud dormancy, and dormancy release stimuli may act through modification of ABA metabolism. J. Exp. Bot. 66, 1527–1542.
Zheng, C., Acheampog, A.K., Shi, Z., Mugzech, A., Halaly-Basha, T., Shaya, F., Sun, Y., Colova, V., Mosquna, A., Ophir, R., Galbraith, D.W., Or, E., 2018. Abscisic acid catabolism enhances dormancy release of grapevine buds. Plant Cell Environ. 1, 14.

View publication stats