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Exploring the Molecular Mechanisms Underlying Mulberry Bud Break : Insights from an *In-silico* Expression Analysis

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Abstract

Mulberry (*Morus* spp.) is a perennial tree species that are commercially exploited for its leaves. Rapid regrowth after foliage harvest is important in the sericulture industry and re-growth is dependent on uniform bud break. While previous research has characterized bud break stages and tried to induce uniform bud break, the underlying mechanisms behind this process are largely unknown. The present study aims to investigate the potential involvement of the genes responsible for mulberry bud break using an in-silico expression analysis. This research is motivated by the observed similarities between the process of bud break in tree systems and the germination process in annual plants, including the overlap of pathways and mechanisms. The study used existing transcriptome data generated on the bud break process in mulberry and the genes belonging to different regulatory pathways were selected. The Arabidopsis homologues of the select genes were then analyzed for their expression patterns during the seed germination process using the e-Northern expression browser from the Botany Array Resource. The results indicate that the selected genes, particularly those involved in hormonal pathways, symplastic connectivity, antioxidant and redox processes and the cell cycle, are represented in seed germination datasets and play a role in growth induction. These findings provided insight into the molecular mechanisms underlying bud break in mulberry plants and indicated that some of the mechanisms might be similar to those involved in seed germination.

Keywords : Mulberry, Bud break, Phytohormones, Arabidopsis, *In-silico* analysis

Mulberry (*Morus alba* L.) is a tree species cultivated as the primary food source for silkworm (*Bombyx mori* L.) larvae (Rohela *et al.,* 2020). One important phenological stage of mulberry trees is the bud break process, which determines the production of leaves and ultimately impacts the sustainability of the sericulture industry. Timely availability of leaf production, a multifaceted trait that depends on the number of shoots and opened buds, is a major constraint in meeting the demands of the industry (Vijayan *et al.,* 2014). Hence inducing early and rapid bud break and thereby increasing leaf yield is crucial for growth in the silk industry. A study has shown that exposing mulberry plants to mild drought stress followed by rehydration can result in uniform and early bud break (Dhanyalakshmi *et al.,* 2020). The role of phytohormones, specifically Abscisic acid (ABA) and Gibberellic acid (GA), in controlling the bud break process has recently been reported (Thomas and Nataraja, 2022). However, the mechanism behind bud break in mulberry trees is not fully understood and further research is needed to manipulate the trait for improved foliage yield (Shangguan *et al.,* 2020).

The process of bud break in trees is similar to that of seed germination in annual plants, as both involve the initiation of growth and development in response to

specific environmental cues (Chao *et al.,* 2015). These factors play a crucial role in determining the timing of dormancy and growth induction stages, ultimately leading to growth in buds and seeds. Phytohormones play a crucial role in regulating seed germination and bud break. ABA and GAs are key regulators of these processes with ABA delaying germination and GAs stimulating it (Nambara and Marion-Poll, 2003). Recent research has revealed that the genes and regulatory pathways controlling bud break and seed germination are similar (Yan *et al.,* 2015). ABA and GAs act antagonistically, with ABA repressing and GAs inducing the biosynthesis and signalling of down stream genes. Phytochromes, MADS-box genes, circadian clock genes, cell cycle genes and reactive oxygen species play important roles in regulating the timing and release of dormancy in seeds and buds.

The process of bud break in mulberry trees, which is crucial for leaf growth, is not fully understood. However, by comparing the genes involved in mulberry bud break to those involved in seed germination of the model organism *Arabidopsis thaliana*, we attempted to uncover the genes responsible for this process. To achieve this goal, the data available from Arabidopsis research, such as The Arabidopsis Information Resource (TAIR) and the Gene Expression Omnibus (GEO) (Edgar *et al.,* 2002) have been utilized. This approach has the potential to greatly facilitate the interpretation of large data sets and uncover new insights into the molecular mechanisms underlying various biological processes in plants. By uncovering the similarities and representation of mulberry genes in Arabidopsis seed germination, we can gain a deeper understanding of the mechanisms underlying bud break in mulberry trees. Therefore, *In-silico* based expression analysis was conducted to indirectly assess bud break process using Arabidopsis seed germination data.

Material and Methods

Selection of Genes from Mulberry Transcriptome

A transcriptome specific to mulberry bud break was curated to identify genes associated with the bud break process. These genes were selected based on literature references from other tree species and belong to various regulatory pathways.

Retrieval of Arabidopsis Genome Initiative Id (AGI)

To assess the relevance of the genes, the nucleotide gene sequence was analyzed using various data bases. The sequence from mulberry was first blasted against the NCBI non-redundant protein sequence database (https://www.ncbi.nlm.nih.gov) using blastx with default parameters to confirm its annotation. Then, to identify the Arabidopsis homologues, the sequence was blasted against the Arabidopsis genome using blastx, resulting in the identification of the Arabidopsis Genome Initiative Id (AGI). The AGI Id was then verified using TAIR (https:/ www.arabidopsis.org).

In-silico Expression Analysis and Selection of Condition

One of the most comprehensive databases for gene expression analysis is the Botany Array Resource (BAR) (http://bar.utoronto.ca/), which makes data generated from experiments publicly available through its web interface. This database follows the guidelines outlined in the Minimum Information About a Microarray Experiment (MIAME) (Toufighi *et al.,* 2005 and Brazma *et al.,* 2001). The retrieved AGI IDs were then queried against the e-Northern expression browser (http://bar.utoronto.ca/affydb/cgi-bin/affy_db_exprss_browser_in.cgi), using the seed germination process database. The data available through the *e-Northern* expression browser was collected (Boyes *et al.,* 2001). The expression pattern of the selected genes was studied in the seed series during the germination time course at 0, 1, 3, 6, 12 and 24 hours. The overall workflow followed for the *In-silico* expression analysis is presented in Fig. 1. The relative expression data at various time points was presented using Graph Pad Prism V.8 software.

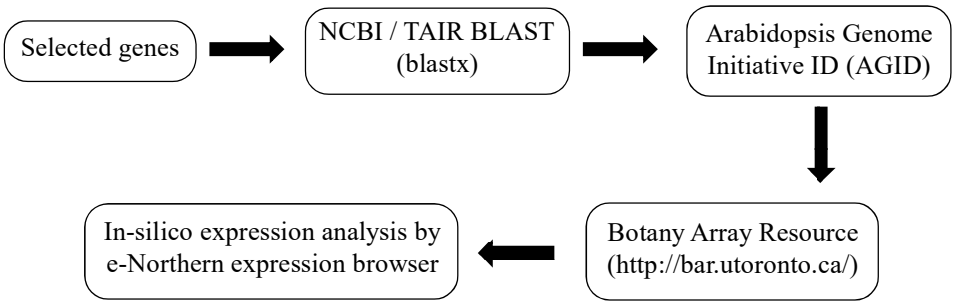

Fig. 1 : Overall workflow of *In-silico* gene expression analysis

Gene Network Analysis

To predict the gene regulatory network of genes involved in dormancy release and growth induction, the STRING database (STRING v.11.5) (https://string-db.org/) was utilized. It was employed as the search tool for retrieval of interacting genes in the STRING database to identify potential interactions between genes involved in growth induction. To construct the gene networks, active interaction sources were applied, including text mining, experiments, databases and co-expression. The species was limited to *Arabidopsis thaliana*. Interactions with a score greater than 0.4 were considered the cut-off value for reliable predictions.

Results and Discussion

Gene Selection and AGI Retrieval

Dormancy release and bud break are associated with numerous physiological and biochemical processes that are shown to be involved under the influence of energy metabolism (Khalil-Ur-Rehman *et al.,* 2019), phytohormones (Qiu *et al.,* 2019), cell division and growth (Mathiason *et al.,* 2009), carbohydrate metabolism (Min *et al.,* 2017), reactive oxygen species (Takemura *et al.,* 2015) and oxidative stress (Sudawan *et al.,* 2016). Genes belonging to different regulatory pathways were selected and were blasted against NCBI and AGI Id was obtained. The obtained AGI Id's are grouped and listed in Table 1.

e-Expression Analysis of Mulberry Homologues during Seed Germination in Arabidopsis

Comparative analysis of the bud break and seed germination processes has shown that the genes and pathways involved in these events are similar. To determine if this relationship also applies to mulberry bud break, an analysis was performed using data on seed germination. The expression patterns of Arabidopsis homologues of mulberry genes were studied at different time points after seed germination (growth induction) events in Arabidopsis.

Phytohormone-related genes : ABA metabolism and signaling-linked genes play an important role in dormancy onset and release (Zheng *et al.,* 2015). The expression levels of genes involved in the ABA signalling pathway varied over time during the process of inducing growth. The *In-silico* expression analysis of specific genes in the ABA pathway showed that the gene involved in regulating ABA levels (CYP707A2) increased during growth induction (Fig. 2c). In contrast, the downstream gene RAB15 decreased (Fig. 2b). Additionally, the expression of the ABA signalling components SnRK.2 and PP2C were also altered, with SnRK.2 getting down regulated and PP2C upregulated, suggesting that ABA signalling is suppressed during growth induction. This shows that ABA levels go down during growth induction and ABA levels are reported to drop in tree systems during dormancy release towards induction of growth (Arora *et al.,* 2003). Hence, ABA, as reported earlier, acts as a negative regulator of seed germination and bud break.

GA play a critical role in regulating seed germination and bud break. The computational analysis revealed that the gene responsible for the synthesis of GA (GA20 oxidase) increased activity during the growth induction while the genes involved in the degradation

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TABLE 1

List of Arabidopsis Genome Initiative (AGI) Id of selected genes from mulberry bud transcriptome representing different regulatory pathway

Metabolic pathway	Annotation (Mulberry)	Annotation (Arabidopsis)	AGI Id
Abscisic acid (ABA)	ABSCISIC ACID-INSENSITIVE 5-like protein 5	ABF2 (ABSCISIC ACID RESPONSIVE ELEMENTS-BINDING FACTOR 2)	AT1G45249
	PP2C domain-containing protein	PP2C (Protein phosphatase 2C)	AT2G40860
	Dehydrin Rab15	RAB15 (Responsive to ABA 15)	AT5G66400
	Abscisic acid 8'-hydroxylase 2	CYP707A2	AT2G29090
	Sucrose non-fermenting-1-related protein kinase 2-1	SnRK 2.4 (Sucrose nonfermenting 1(SNF1)-related protein kinase 2.4)	AT1G60940
Gibberellic acid (GA)	Gibberellin 2-beta-dioxygenase 2	GA2-oxidase 6 (Gibberellin 2 oxidase 6)	AT1G02400
	Gibberellin receptor GID1C	GID1C (Gibberellic acid Insensitive Dwarf 1C)	AT5G27320
	DELLA2	RGL1 (RGA-like 1)	AT1G66350
	Gibberellin 20 oxidase 1	GA20-oxidase 2 (Gibberellin 20 oxidase 1)	AT5G51810
	Putative UDP-N-acetylglucosamine—peptide N-acetylglucosaminyltransferase SPINDLY	SPY1 (Spindly1)	AT3G11540
	Transcription factor GAMYB	GAMYB65	AT3G11440
Symplast connectivity	Endo-1,3(4)-beta-glucanase 1	GH81 (Glycosyl hydrolases81)	AT5G15870
	Callose synthase 9	CALS9 (CALLOSE SYNTHASE9)	AT3G07160
Antioxidant system	L-ascorbate peroxidase, cytosolic	APX (Ascorbate Peroxidase)	AT1G07890
	Superoxide dismutase	SOD1 (Superoxide dismutase1)	AT3G10920
	Catalase	CAT2 (Catalase2)	AT4G35090
Cell cycle regulation	Cyclin-dependent kinase	CDKB2 (Cyclin Dependent Kinase 2)	AT1G76540
	CHD3-type chromatin-remodelling factor PICKLE	PKL (PICKLE)	AT2G25170
	D6-type cyclin	D6 Cyclin	AT4G03270
	AP2-like ethylene-responsive transcription factor ANT	ANT (AINTEGUMENTA)	AT4G37750

of GA (GA2 oxidase) showed reduced expression levels. Additionally, one of the regulators of GA signalling, RGL1, showed an initial increase in activity followed by a subsequent decrease (Fig. 3). This suggests that GA acts as a positive regulator of growth induction and may regulate bud dormancy. Additionally, the highest expression of the GA receptor gene (GID1C) was observed during the initial hours of the process, which may initiate downstream events (Fig. 3a). This pattern of GID1C expression has also been observed in tea plants during bud break (Yue *et al.,* 2018). Therefore, GA

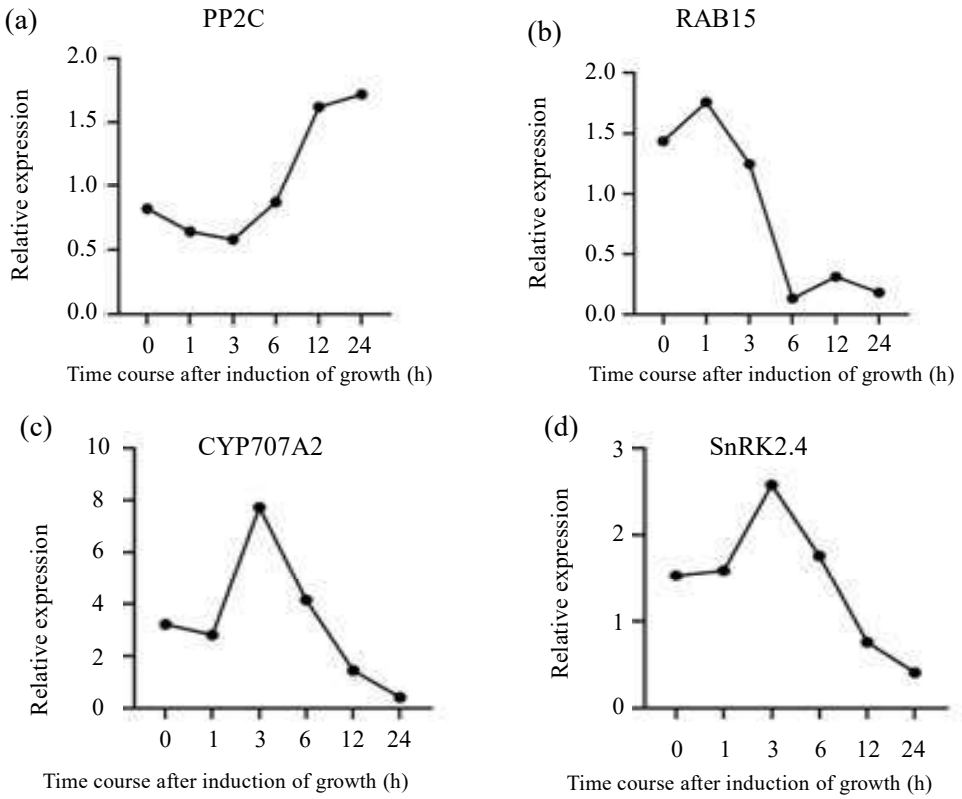

Fig. 2. *In-silico* expression analysis of ABA biosynthesis and signalling related genes identified from mulberry bud transcriptome [PP2C (Protein phosphatase 2C), RAB15 (Responsive to ABA 15), CYP707A2 (CYTOCHROME P450), SnRK2.4 (Sucrose non-fermenting 1(SNF1)-related protein kinase 2.4)]

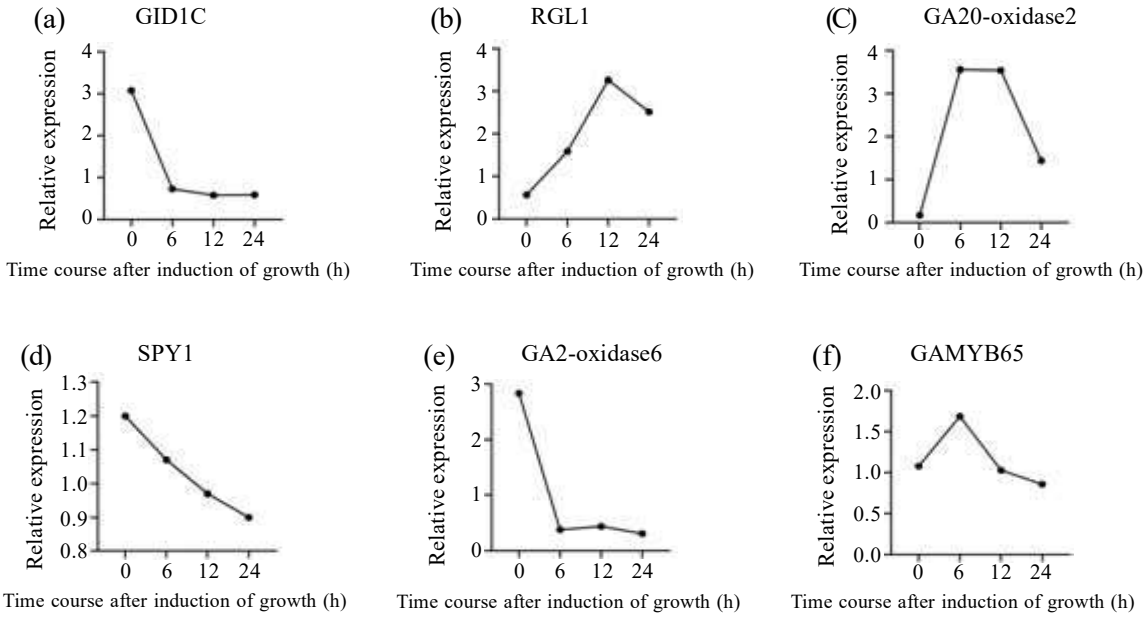

Fig. 3. *In-silico* expression analysis of GA biosynthesis and signalling related genes identified from mulberry bud transcriptome [GID1C (Gibberellic acid Insensitive Dwarf 1C), RGL1 (REPRESSOR OF GA1-like), GA20-oxidase 2 (Gibberellin 20 oxidase 1), SPY1 (Spindly1), GA2-oxidase 6 (Gibberellin 2 oxidase 6), GAMYB65 (MYB DOMAIN PROTEIN 65)]

may be a potential positive regulator driving growth induction during germination and bud break.

Symplast connectivity genes : Symplastic connectivity refers to the interconnected network of plasmodesmata, small channels that allow for the movement of small molecules and macromolecules between cells in plants (Wu *et al.,* 2018). This network plays a crucial role in the communication and coordination of various developmental processes, including bud break, which marks the beginning of the growing season in woody plants. *In-silico* expression analysis of GH81, a key gene involved in restoring symplastic connectivity and callose degradation, showed a steady increase in expression with a high at three hours during the growth induction process (Fig. 4 a). On the other hand, the expression pattern of the callose synthase gene (CALS9) showed a reduction during the initial hours (Fig 4b). Upregulation of β-1,3-glucanase, which degrades callose by cleaving 1,3-β-D-glucosidic linkages, has also been reported during bud break (Gao *et al.,* 2021). These findings suggest that the opening of symplastic connections is necessary for connectivity and growth induction during seed germination and bud break.

Antioxidant and redox cues related genes : Reactive oxygen species (ROS) have been shown to play a role in the process of bud break in plants (Vergara *et al.,* 2012). ROS serves as a crucial signaling molecule and can actively promote the production of hormones such as auxin and cytokinin. These hormones play significant roles in initiating bud break, as well as facilitating cell division and differentiation, among other essential processes involved in the growth and development of plants. *In-silico* expression of genes linked to the antioxidant system showed that the genes encoding Ascorbate Peroxidase (APX) and Superoxide Dismutase 1 (SOD1) showed increased transcript levels at 24 hours, while catalase 2 (CAT2) was significantly down regulated post induction of bud break (Fig. 5). This suggests that the decreased expression of CAT2 may be necessary to maintain redox stress, which is important for growth induction and bud break (Viti *et al.,* 2012). Previous research has also shown that ascorbate peroxidase levels increase during the transition from dormancy and that peroxidase isoenzyme and ascorbate peroxidase activity are upregulated in Peach and Japanese pear during dormancy release, potentially playing a role in maintaining redox status (Takemura *et al.,* 2015). These findings highlight the complex and varied responses of ROS scavenging enzymes, such as ascorbate peroxidase, peroxidase, and catalase during dormancy release and seed germination, which are critical for the proper regulation of reactive oxygen species (ROS) levels.

Cell cycle-related genes: Activation of the cell cycle is crucial for plant growth and development

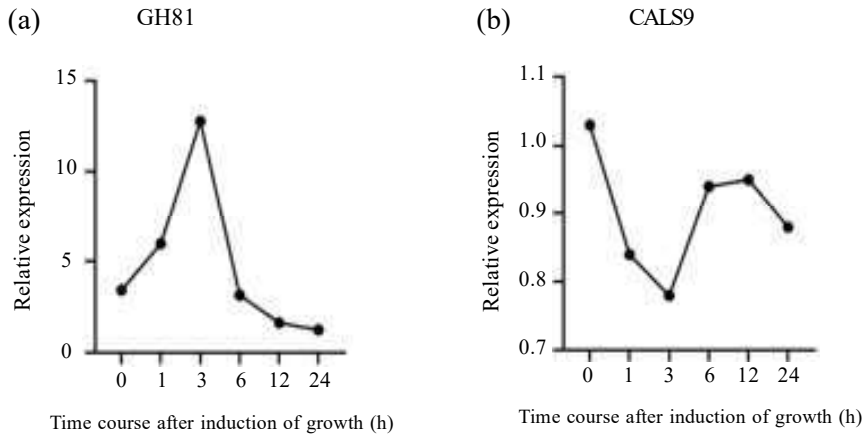

Fig. 4 : *In-silico* expression analysis of Symplast connectivity linked genes identified from mulberry bud transcriptome [GH81 (Glycosyl hydrolases81), CALS9 (CALLOSE SYNTHASE9)]

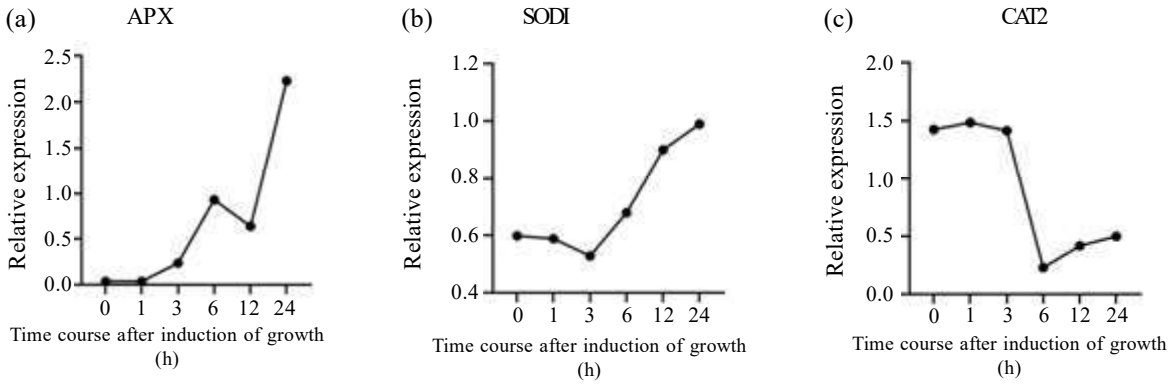

Fig. 5 : *In-silico* expression analysis of Antioxidant and redox cue linked genes identified from mulberry bud transcriptome [APX (Ascorbate peroxidase), SOD1 (Superoxide dismutase1), CAT2 (Catalase2)]

(Noriega *et al.,* 2017). *In-silico* analysis of genes related to the cell cycle revealed that their expression was increased during the initiation of growth (Fig. 6). This suggests that the cell cycle plays an important role in the process of growth induction. PICKLE (PKL), chromatin remodeling factor showed up-regulation throughout the induction of growth, and D6 Cyclin showed peak upregulation at 12 and 24h post-induction of growth. This increase in expression is in line with the activation of cell cycle-related genes during bud break (Pines, 1995). Hence, cell cycle-related genes are regulated similarly during bud break and germination.

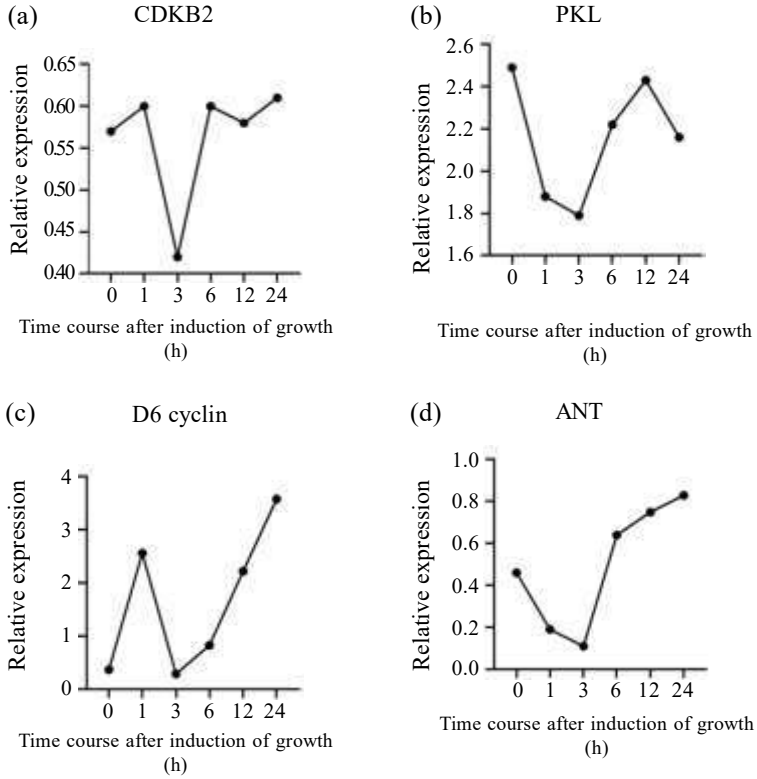

Fig. 6 : *In-silico* expression analysis of Cell cycle linked genes identified from mulberry bud transcriptome [CDKB2 (Cyclin Dependent Kinase 2), PKL (PICKLE),D6 Cyclin, ANT (AINTEGUMENTA)]

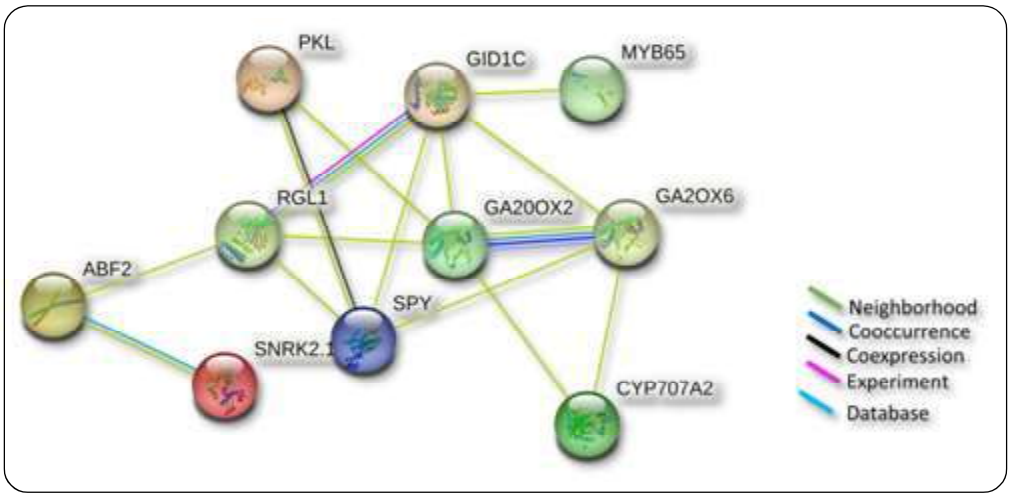

Fig. 7. Gene regulatory network analyzed with string-db (http://string-db.org) set to medium confidence of 0.400. [GID1C (Gibberellic acid Insensitive Dwarf 1C), RGL1 (REPRESSOR OF GA1-like), GA20-oxidase 2 (Gibberellin 20 oxidase 1), SPY1 (Spindly1), GA2-oxidase 6 (Gibberellin 2 oxidase 6), GAMYB65 (MYB DOMAIN PROTEIN 65), PKL (PICKLE), SnRK2.4 (Sucrose non-fermenting 1(SNF1)-related protein kinase 2.4]

Gene Regulatory Network Analysis :

In the present study, we utilized STRING to map lists of genes to the global Arabidopsis protein association network. Our study showed that the majority of genes required for growth induction were related to the biosynthesis and signalling of GA. We also found that these GA-related genes interacted with genes involved in the breakdown of ABA and genes related to the cell cycle, such as PICKLE (Fig. 7). The interaction between GA-related genes and multiple pathways suggests that GA plays a crucial role in regulating growth induction.

The study investigated the expression patterns of various genes involved in mulberry bud break in the context of seed germination in the model organism Arabidopsis. The results showed that plant hormones, mainly ABA and GA, play important roles in early developmental events. The analysis also showed that the genes in mulberry that play a role in symplast connectivity, antioxidant and redox regulation and the cell cycle, also have similar functions in both the seed germination and bud break processes. Based on the *In-silico* analysis and gene network analysis we propose a model of dormancy release and growth induction (Fig. 8). These findings provided additional insight into the molecular mechanisms underlying bud break in mulberry plants.

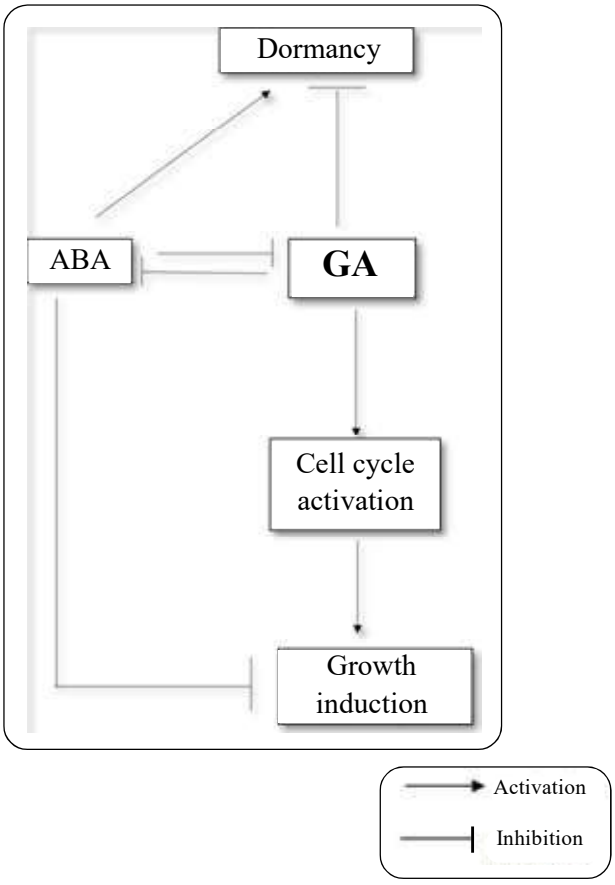

Fig. 8 : Proposed model of dormancy release and growth induction as evidenced through *in-silico* expression analysis and string gene regulatory network analysis [ABA (Abscisic acid), GA (Gibberellic acid)]

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