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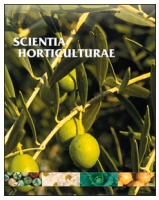

Research Paper

# Identification of genes involved in almond scion tree architecture influenced by rootstock genotype using transcriptome analysis

Álvaro Montesinos [a,b,c], María José Rubio-Cabetas [a,b], Jérôme Grimplet [a,b,*]

[a] Departamento de Ciencia Vegetal, Gobierno de Aragón, Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA), Avda. Montañana 930, Zaragoza 50059, Spain
[b] Instituto Agroalimentario de Aragón—IA2 (CITA-Universidad de Zaragoza), Calle Miguel Servet 177, Zaragoza 50013, Spain
[c] Centro de Biotecnología y Genómica de Plantas, Universidad Politécnica de Madrid, Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain

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ABSTRACT

The emergence of almond (*Prunus amygdalus* (L.) Batsch, syn *P. dulcis* (Mill.)) intensive and semi-intensive cropping systems has created a necessity for new almond cultivars with vigor and shape adapted to these new circumstances. Hence, it is important to unravel which mechanisms are behind the regulation of the tree three-dimensional structure, or tree architecture, and what factors may play a role, like the choice of rootstock. In this study, we have analyzed the rootstock influence on the scion transcriptome, regarding the biological processes that control almond tree architecture. Three commercial almond cultivars were grafted onto three hybrid rootstocks known to confer different architecture to the scion, resulting in nine combinations, whose gene expression in shoot tips was analyzed via RNA-Seq. We report that differences in tree architecture phenotype are correlated with differential expression of genes involved in hormonal and molecular responses associated with the regulation of apical dominance, branch formation, plant growth, cell wall formation, or nitrogen assimilation. These results highlight the importance of the rootstock choice in selecting a desirable scion architecture and in establishing almond orchards.

## 1. Introduction

Rootstocks are widely used in numerous fruit and nut orchards (Warschefsky et al., 2016). Their use allows to confer traits of agronomical interest to the cultivars and to independently select favorable traits for scion and rootstock. The rootstock influences the scion phenotype for multiple characters, such as tree vigor, yield, flowering time, or fruit quality (Aloni et al., 2010; Martínez-Ballesta et al., 2010; Albacete et al., 2015; Foster et al., 2015; Warschefsky et al., 2016; Font i Forcada et al., 2020; Reig et al., 2022). Almond (*Prunus amygdalus* (L.) Batsch, syn *P. dulcis* (Mill.)) cultivars are graft-compatible with both almond and peach (*P. persica* (L.) Batsch) rootstocks and their interspecific hybrids (Felipe, 2009; Rubio-Cabetas et al., 2017) are widely used in almond orchards, which almost exclusively consist of these scion/rootstock combinations.

Among these rootstock effects on the cultivar in various fruit tree species, researchers focused predominantly on scion vigor. Analysis in both apple (*Malus* × *domestica*) and *Prunus* species have determined a correlation between rootstock and vigor-related parameters such as scion height or trunk diameter (Tworkoski and Miller, 2007; Tworkoski and Fazio, 2015; Yahmed et al., 2016; Scalisi et al., 2018; Balducci et al., 2019; Lordan et al., 2019; Narandžić and Ljubojević, 2022). Although the effect on other traits related to tree architecture like shoot production and development has been reported in apple cultivars, the interaction is less clear (Tworkoski and Miller, 2007; Seleznyova et al., 2008; Van Hooijdonk et al., 2010).

Apical dominance is a crucial regulator of tree architecture. It defines the capacity exerted by the shoot apical meristem (SAM) to repress lateral bud outgrowth, redistributing resources towards the elongation of the main axis (Hollender and Dardick, 2015; Wang et al., 2018a). Numerous factors are behind the regulation of apical dominance and bud outgrowth with auxins acting as the core regulator, which are predominantly transported throughout the axis by specific efflux and influx carriers, promoting apical dominance (Cho and Cho, 2013;

* Corresponding author at: Departamento de Ciencia Vegetal, Gobierno de Aragón, Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA), Avda. Montañana 930, Zaragoza 50059, Spain.
*E-mail address:* jgrimplet@cita-aragon.es (J. Grimplet).

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Adamowski and Friml, 2015). Beside, auxin facilitates graft formation, and elevated levels in the rootstock promote callus and vascular cell development, proving that upward transport also happens at least over short distances (Zhai et al., 2021). The exact mechanism by which auxins repress bud outgrowth is yet under scrutiny, but strigolactones (SLs) are proven to act as auxin secondary messengers, inhibiting bud outgrowth (Dun et al., 2012; Shinohara et al., 2013; Bennett et al., 2016; Dierck et al., 2016a; Waldie and Leyser, 2018). Cytokinins (CKs) have the opposite effect, promoting bud outgrowth and shoot branching (Dun et al., 2012; Dierck et al., 2016b; Waldie and Leyser, 2018). Other hormones like gibberellic acid (GA) or brassinosteroids (BRs) are also involved in shoot development, but their effects are less characterized (Lo et al., 2008; Sun, 2010; Wei and Li, 2016). Sugars have been also described as an important regulator of bud outgrowth, promoting the formation of branches when there is high availability (Stokes et al., 2013; Mason et al., 2014). External stimuli such as light perception also control shoot development via photoreceptors phyA and phyB (Casal, 2012; Reddy and Finlayson, 2014; Holalu and Finlayson, 2017).

Tree vigor is mainly controlled by the hormonal response and nutrient availability. GA and BRs are involved in its regulation, primarily promoting cell elongation, although they have been described to stimulate cell proliferation too (Busov et al., 2008; Yamaguchi, 2008; Fridman and Savaldi-Goldstein, 2013). GA activity in cell elongation affects numerous aspects of plant growth, like seed germination, stem elongation, and flower development (White and Rivin, 2000; Ogawa et al., 2003; Griffiths et al., 2006; Gallego-Bartolomé et al., 2011). GA acts by connecting external clues such as light perception with molecular regulation of these processes (Alabadí et al., 2008; Filo et al., 2015). Furthermore, deficiencies in GA have been observed to affect tree vigor in several crops like poplar, apple, or peach (Hollender and Dardick, 2015; Hollender et al., 2016). CKs and auxins control plant vigor as well, regulating cell proliferation and cell elongation (Busov et al., 2008; Depuydt and Hardtke, 2011; Ma et al., 2016). Nutrient availability is crucial for plant development, especially nitrogen availability. Hormone synthesis and transport are tightly controlled by nitrogen supply (Krouk et al., 2011). Hence, nitrate acts as a signaling molecule, regulating gene expression, and controlling several developmental processes like root formation, shoot development, or flowering (Wang et al., 2018b).

In recent years, flowering has been linked with tree architecture. Hormones regulating tree architecture, like auxin or GA, are also part of flowering control, providing a possible crossroad between these developmental processes (Srikanth and Schmid, 2011). Studies in *Arabidopsis* and woody plants such as apple have proven that important flowering regulators like FLC or FT are involved in shoot development (Pin and Nilsson, 2012; Huang et al., 2013; Foster et al., 2014).

Characterization of all these processes affecting tree architecture using a collection of different rootstocks could help to a better understanding of how they influence scion phenotype. In a previous experiment (Montesinos et al., 2021), we grafted several almond cultivars onto various hybrid rootstocks observing that the rootstock influences parameters related to tree architecture like the number of shoots or shoot distribution through the trunk. Although several molecular processes have been linked to the regulation of tree architecture, little to none is known about the influence exerted by the rootstock genotype on the processes that are behind these changes in the scion. To unravel a cohesive view of the molecular mechanisms behind rootstock impact on the cultivar architecture, the transcriptome of nine scion/rootstock combinations, whose effect on scion traits was evaluated in a previous experiment, is here presented in a comparative analysis.

## 2. Materials and methods

### 2.1. Plant materials and growth conditions

In this study, a subset of nine scion/rootstock combinations from a previous trial with thirty combinations was chosen (Montesinos et al., 2021), comprising three almond cultivars of agronomic interests which were grafted onto three different commercial rootstocks. The following combinations were selected after analyzing rootstock influence on scion architecture: 'Densipac' (Rootpac® 20), 'Nanopac' (Rootpac® 40), and Garnem® (GN15) as rootstocks, and 'Isabelona' (syn. 'Belona'), 'Diamar' (syn. 'Mardía') and 'Lauranne' as cultivars. All rootstocks are hybrids from different origins. Garnem® is an almond × peach (*P. amygdalus* (L.) Batsch, syn *P. dulcis* (Mill.). × *P. persica* (L.) Batsch) hybrid rootstock, while the others come from the commercial Rootpac® series: Rootpac® 40 (*P. amygdalus* (L.) Batsch, syn *P. dulcis* (Mill.). × *P. persica* (L.) Batsch) and Rootpac® 20 (*P. cerasifera* × *P. besseyi*). Grafted plants were supplied by the Agromillora Iberia S.L. nursery in 2018 (Barcelona, Spain). Trees were planted in October 2018 at the Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA) experimental orchard El Vedado Bajo el Horno (Zuera, Zaragoza, 41°51′46.5″N 0°39′09.2″ W). Trees were planted in an open field as a single axis and supported by a wooden stick. Trees were then left without pruning so that, they could express their natural growth habit unaltered. Conventional orchard practices were used for weed, pest, and disease control and drip irrigation. The soil type was calcareous with a pH of around 7–8.

### 2.2. Data collection

Seven descriptors of tree architecture were measured in three trees per scion/rootstock combination. These parameters, previously depicted in Montesinos et al. (2021), belong to three different categories: (i) vigor, (ii) branch quantity, and (iii) branch distribution. (i) Length: trunk length; IN_L: mean length of trunk internodes. (ii) Nb_B: number of primary branches; BbyIN: proportion of branches per number of internodes; Nb_lB: number of long branches (> 200 mm); B_NbAS: number of secondary branches per primary branch. (iii) Dist_B; distribution of branches through the trunk.

### 2.3. RNA-Seq analysis

Samples from the nine combinations mentioned were collected in a single morning (between 10 am and 11 am) from shoot tips of two-year-old branches from three different individuals per combination during the summer of 2020. Plants were at stage 75 on the BBCH scale. RNA extraction was performed from these samples using the CTAB method described previously (Meisel et al., 2005) with some modifications (Chang et al., 1993; Salzman et al., 1999; Zeng and Yang, 2002). Stranded mRNA-Seq analysis was carried out at Centro Nacional de Análisis Genómico (CNAG-CRG) in Barcelona, Spain. Sequencing was performed by an Illumina NovaSeq 6000 System - with > 30 M PE reads per sample and a read length of 2 × 50 bp. FASTQ files were converted with FASTQ Groomer (Galaxy Version 1.1.1) (Blankenberg et al., 2010). Adapter sequences were removed by processing the reads sequences of the twenty-seven individual datasets with Trimmomatic (Galaxy Version 0.38.0) (Bolger et al., 2014). RNA-Seq data alignment was carried out by HISAT2 (Galaxy Version 2.2.1), with a maximum intron length of 20, 000 bp, (Kim et al., 2015) on the *P. dulcis* 'Texas' Genome v2.0 (Alioto et al., 2020). Duplicated molecules were located and mate-pairs were confirmed using the MarkDuplicates (Galaxy Version 2.18.2.2) and FixMateInformation (Galaxy Version 2.18.2.1) Picard tools respectively (http://broadinstitute.github.io/picard). featureCounts (Galaxy Version 2.0.1+galaxy2) was used to measure gene expression (Liao et al., 2014) using the gene annotation *P. dulcis* 'Texas' Genome v2.0 containing 27, 044 genes (https://www.rosaceae.org/analysis/295). Differential analysis of count data was performed by edgeR (Galaxy Version 3.36.0) with default settings (Robinson et al., 2009). Genes with a corrected p-value below 0.05 and a $\log_2$FC above 1 or below −1 were considered differentially expressed All procedures were carried out using the Galaxy platform. Recent reports have shown that RNA-Seq methods are robust enough and validation by qPCR would confirm its results for a vast majority of transcripts. Non-concordant results between both techniques

were observed in less than 2 % (Everaert et al., 2017; Coenye, 2021) appearing typically in short and low-expressed genes. As these data are related to the Fragments Per Kilobase of transcript per Million (FPKM), differentially expressed genes were filtered to assure that they belong to the 98 % transcripts with the highest FPKM.

### 2.4. RNA-Seq data structural and functional analysis

Principal component analysis (PCA) was carried out using the R stats package with default parameters on the gene expression values for all the genes in the nine combinations. Distance between genes was measured using its correspondent function from the R stats package. Hierarchical clustering and correlation networks were performed using the WGCNA package (Langfelder and Horvath, 2008). GO enrichment was carried out using the tool GOEnrichment (https://github.com/-DanFaria/GOEnrichment) with a p-value cut-off $< 0.1$ and Benjamin-Hochberg correction.

## 3. Results and discussion

### 3.1. Rootstock influence on scion architecture correlates with differences in gene expression

The phenotypic effect of the rootstock on the nine different scion/rootstock combinations was measured using seven architecture parameters (Supplementary Data 1), which had been previously proven to be affected by the rootstock (Montesinos et al., 2021). PCA (Principal Component Analysis) was carried out using the phenotypic data collected for the nine scion/rootstock combinations (Fig. 1a). The first two components explained more than two-thirds of the variability, with the first component explaining 55.1 %, and the second 22.22 %. For two of the cultivars, 'Isabelona' and 'Lauranne', we observed a stronger influence of the cultivar than the rootstock since combinations involving these cultivars can be observed indistinctively clustering together on each side of Fig. 1a. 'Isabelona' combinations present a strong apical dominance phenotype while those with 'Lauranne' as scion display numerous branching and high vigor (Fig. 2; Supplementary Data 1). The effect of the rootstock in aerial traits in these two cultivars seems to be limited. However, we observed more diversity between individuals for the 'Isabelona'/Rootpac® 40 combination (Fig. 1a). Contrarily to these two cultivars, 'Diamar' seemed more affected by the rootstock genotype. When grafted onto Rootpac® 20, which is a dwarfing rootstock, the plants showed high apical dominance and reduced branching similar to the plants carrying 'Isabelona' as the scion (Fig. 2; Supplementary Data 1). On the contrary, when grafted onto the vigor-inducing rootstock Garnem®, 'Diamar' combinations clustered with the 'Lauranne' combinations. Although Rootpac® 40 is a more vigor-inducing rootstock compared to Rootpac® 20, it does not reduce apical dominance at the same level as Garnem®. Therefore, 'Diamar'/Rootpac® 40 combinations are between 'Isabelona' and 'Lauranne' combinations, but closest to the former (Fig. 1a).

A second PCA was carried out, using the expression for each gene as variables for the nine combinations (Fig. 1b). The first two components explained 40 % of the variability, with 24.28 % and 10.76 % of the variability respectively. Data related to each cultivar grouped. As for phenotypic data, combinations involving both 'Lauranne' and 'Isabelona' did not present marked differential distribution linked to the rootstock genotype (Fig. 1b). As observed for the phenotypic data, 'Diamar' combinations presented a contrasted position in the PCA. Individuals grafted onto Rootpac® 20 were separated from individuals grafted onto Garnem® and Rootpac® 40 (Fig. 1b). Therefore, the absence of a rootstock effect in 'Isabelona' and 'Lauranne' combinations seems to be linked to a lack of differential gene expression under these conditions.

RNA-Seq data were then subjected to a hierarchical clustering analysis (Fig. 2). Data samples were separated according to the scion genotype, which was expected as the samples were taken from this part of the plant, showing the global gene expression variation between each genotype. Since these clusters depend on the complete gene expression profile and not only on the genes that may affect tree architecture, other processes not linked to the phenotype might also affect these results. It is not the objective of this study to draw conclusions on comparing varieties between each other since in these comparisons it is hard to separate the "cultivar effect" from the "rootstock effect". On the other hand, there is very limited research on the molecular influence of the rootstock genotype in a single cultivar. For the comparisons intra-cultivar, combinations with 'Lauranne' and 'Isabelona' as cultivars were clustered in one group each with no effect of the rootstocks and no clear gene expression differences when comparing the whole transcriptomes. In 'Diamar' we observed a clear separation of samples grafted onto Rootpac® 20 from the others. Transcriptomics data do not allow to clear separation of Garnem® and Rootpac® 40 unlike what was observed with the phenotypic data where 'Diamar'/Rootpac® 40 presented an intermediate phenotype between 'Diamar'/Rootpac® 20, which displayed low vigor and strong apical dominance, and 'Diamar'/Garnem® (Fig. 2).

Overall in the 'Diamar' case, the phenotypic profile of architecture characters is in accordance with the observed data for gene expression in shoot tips, which allows us to assume that the differentially expressed gene in this tissue might be related to differential architecture.

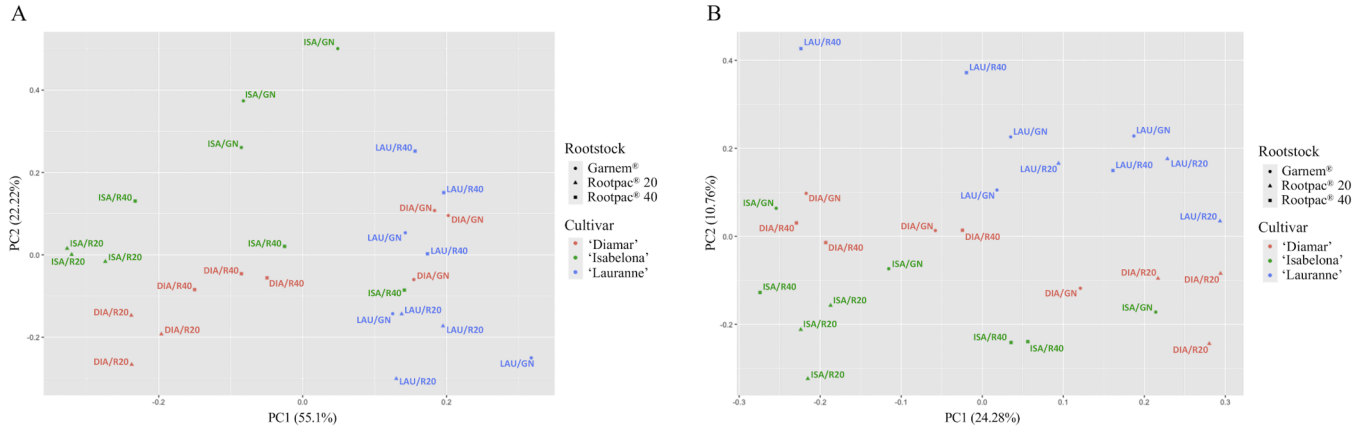


**Fig. 1.** Principal component analysis (PCA) of the nine scion/rootstock combinations. A. PCA of the phenotypic data. B. PCA of the global expression profile data. DIA/GN: 'Diamar'/Garnem®; DIA/R20: 'Diamar'/Rootpac® 20; DIA/R40: 'Diamar'/Rootpac® 40; ISA/GN:'Isabelona'/Garnem®; ISA/R20: 'Isabelona'/Rootpac® 20; ISA/R40: 'Isabelona'/Rootpac® 40; LAU/GN:'Lauranne'/Garnem®; LAU/R20: 'Lauranne'/Rootpac® 20; DIA/R40: 'Lauranne'/Rootpac® 40.

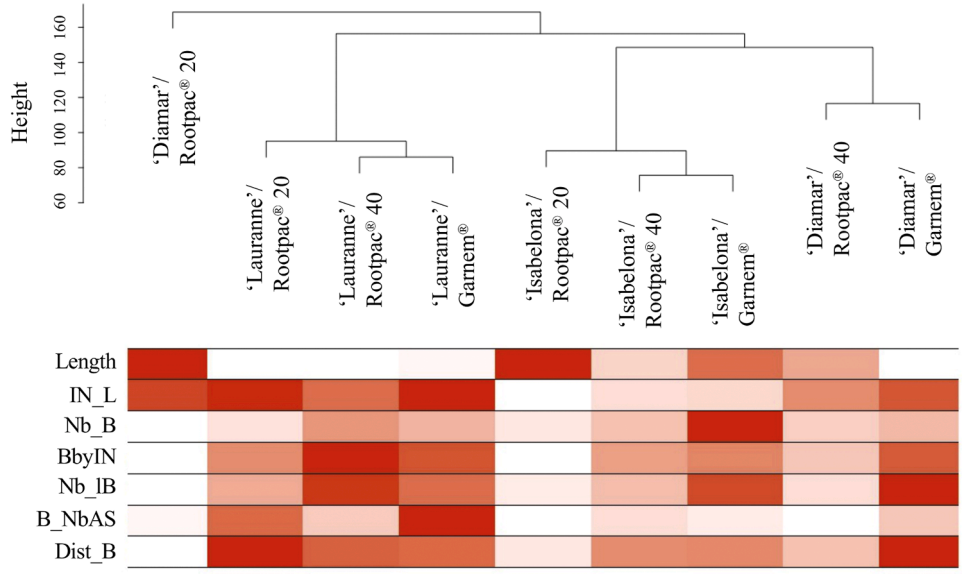


**Fig. 2.** Hierarchical clustering of the global transcriptome of the nine scion/rootstock combinations. The intensity of color in the heatmap below the clustering represents the values for each phenotypic trait. Length: trunk length; IN_L: mean length of trunk internodes; Nb_B: number of primary branches; BbyIN: proportion of branches per number of internodes; Nb_lB: number of long branches (> 200 mm); B_NbAS: number of secondary branches per primary branch; Dist_B; distribution of branches through the trunk.

### *3.2. Rootstock differentially affects metabolism genes in 'Diamar' combinations*

When comparing the same cultivar grafted onto different rootstocks, 'Lauranne' and 'Isabelona' combinations did not show any DEGs in any comparison (Supplementary Data 2, 3). As it was previously stated, the reduced rootstock effect on the scion architecture correlates with this absence of differences in gene expression. In the same way that we observed the impact of the rootstock on the scion phenotype, we did observe DEGs in 'Diamar' combinations (Supplementary Data 4). In these comparisons, DEGs were only observed when compared to individuals grafted onto the dwarfing rootstock Rootpac® 20, while we did not observe DEGs between Garnem® and Rootpac® 40. Both are hybrid almond × peach rootstocks which are described to confer vigor to the scion. This similar influence on phenotype exerted by the rootstock genotype would explain the lack of differences in gene expression observed here. We observed 311 DEGs more expressed with both vigor-inducing rootstocks than with Rootpac® 20 and 118 more expressed in Rootpac® 20. A total of 667 DEGs were found more expressed specifically with Rootpac® 40 than with Rootpac® 20 and 305 more with Rootpac® 20 than with Rootpac® 40. A total of 354 DEGs were detected comparing Garnem® with Rootpac® 20, with 297 DEGs more expressed with Garnem® and 52 with Rootpac® 20 (Fig. 3).

To characterize the biological processes and molecular functions associated with these DEGs, a GOenrichment analysis was carried out (Fig. 4). Since the majority of DEGs appeared more expressed in combinations with the vigor-inducing rootstocks Garnem® and Rootpac® 40, we focused on these genes. When analyzing molecular function terms (Fig. 4a), we observed an enrichment of those related to "catalytic activity" in Garnem® and Rootpac® 40 combinations, especially in the "oxidoreductase activity" category. In both combinations, 'Diamar' presented more vigor than when grafted onto Rootpac® 20, and the enrichment of DEGs belonging to these GO categories is probably due to higher metabolic activity in the shoot tips of these combinations, which are growing more actively. The term "transmembrane transport" was enriched in individuals grafted onto Garnem® (Fig. 4b). This might be due to the more active transport of nutrients or hormones linked to active growth (Park et al., 2017; Wang et al., 2018b). In individuals grafted onto Rootpac® 40, we observed an enrichment of DEGs belonging to the terms related to cell division. It is maybe linked to

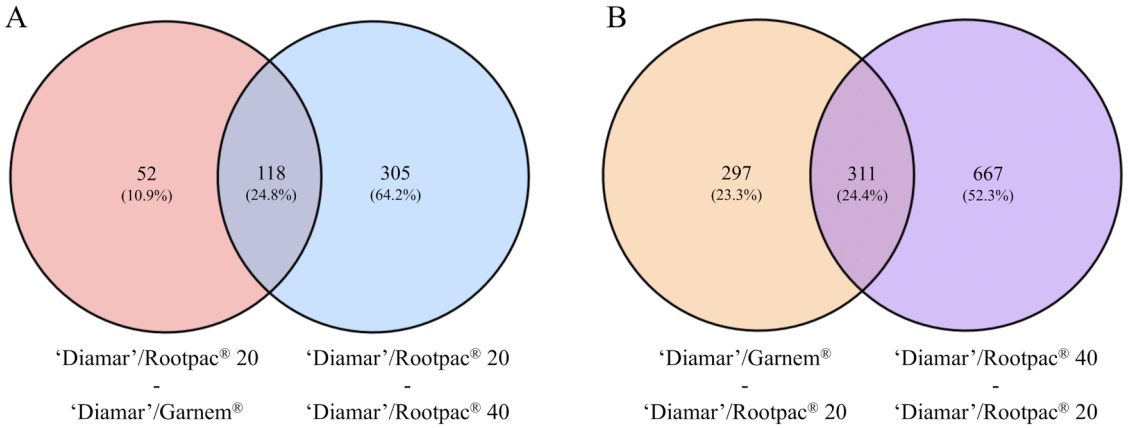


**Fig. 3.** Venn diagrams of differentially expressed genes (DEGs) in combinations with 'Diamar' as the scion. A. DEGs more expressed in combinations with Rootpac® 20 than with Rootpac® 40 or Garnem®. B. DEGs less expressed in combinations with Rootpac® 20 than with Rootpac® 40 or Garnem®.

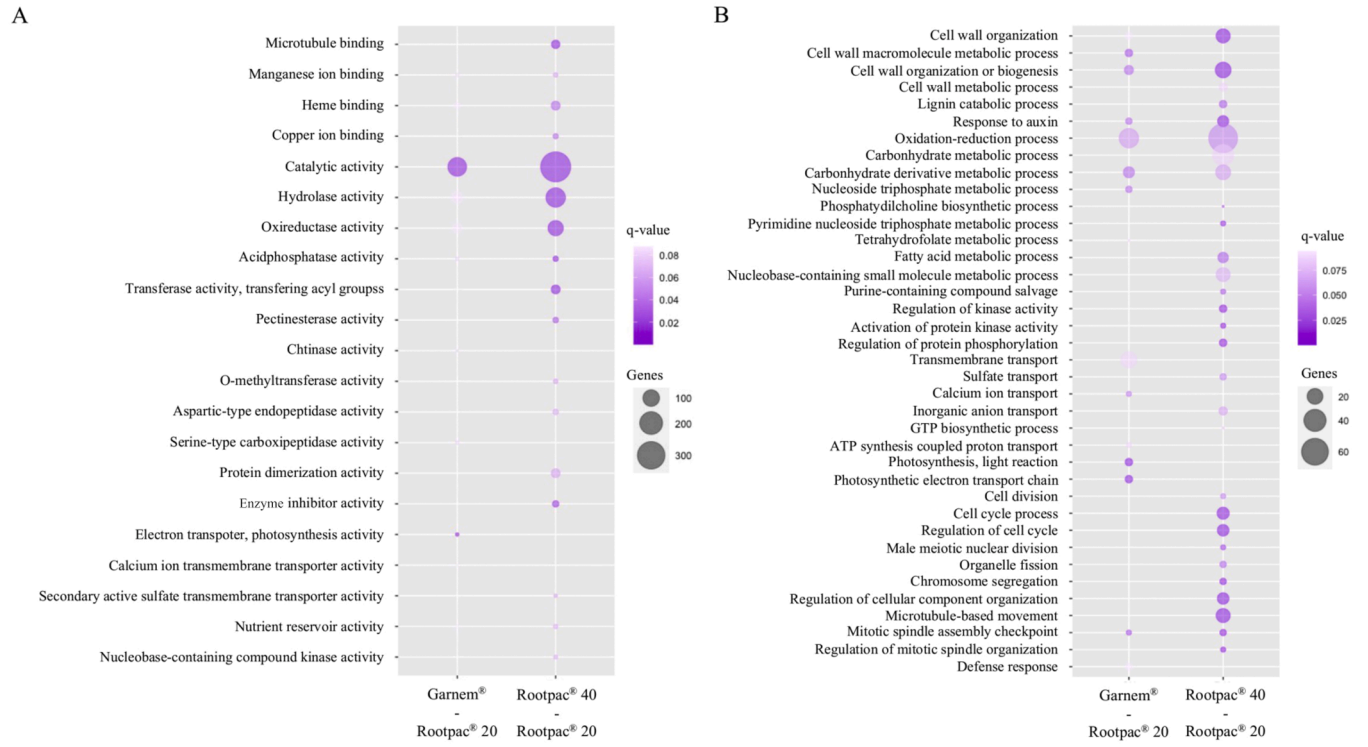


**Fig. 4.** GOenrichment of differentially expressed genes (DEGs) in combinations with 'Diamar' as the scion. A. Molecular function terms for 'Diamar' combinations in which DEGs were less expressed in combinations with Rootpac® 20 than with Rootpac® 40 or Garnem®. B. Biological process terms for 'Diamar' combinations in which DEGs were less expressed in combinations with Rootpac® 20 than with Rootpac® 40 or Garnem®.

promoting cell proliferation, or to cell elongation, which could therefore lead to its more vigorous phenotype (Sablowski, 2016).

For terms representing biological processes (Fig. 4b), we detected an enrichment of DEGs from the term "photosynthesis" in Garnem® combinations. The overrepresentation of these genes might be due to a higher photosynthetic rate and carbon assimilation that could be linked to the higher vigor displayed by 'Diamar' when grafted onto Garnem®. DEGs characterized by the term "carbohydrate derivative metabolic process" were enriched in individuals grafted onto Garnem®. While a more active metabolism is expected in scions grafted onto a vigor-conferring rootstock, like Garnem®; sugars are also an important regulator of branching, and the enrichments of DEGs associated with their pathways may be related to the low apical dominance and numerous branching observed in the 'Diamar'/Garnem® combination (Mason et al., 2014; Barbier et al., 2015). In both the 'Diamar'/Garnem® and the 'Diamar'/Rootpac® 40 combinations, terms associated with "cell wall organization" were enriched (Fig. 4b). Similar terms were enriched in previous transcriptomic analysis characterizing rootstock effect in grapevine and citrus (Cochetel et al., 2017; Liu et al., 2017b). Regulation and reorganization of the cell wall are crucial to allow plant growth, which explains why DEGs related to these processes are upregulated when individuals are grafted onto rootstocks that favor more active growth, like Rootpac® 40 and Garnem® (Cosgrove, 2016; Vaahtera et al., 2019). Several terms associated with cell cycle and cell division are enriched in the 'Diamar'/Rootpac® 40 combination (Fig. 4b). This reinforces the notion that growth is upregulated in individuals grafted onto Rootpac® 40 compared to those grafted onto Rootpac® 20.

In general, we observed an enrichment of terms linked to molecular functions and biological processes in vigor-inducing rootstocks that characterize a more active metabolism, likely due to a more active cell division. Since differences in gene expression are only detected when comparing combinations with vigorous rootstocks to the 'Diamar'/Rootpac® 20 and not between them, it seems that we are looking at a regulation of these processes that explained the low vigor conferred by Rootpac® 20 to the scion.

### 3.3. *DEGs associated with promoting apical dominance were upregulated in 'Diamar'/Rootpac® 20*

Multiple genes likely associated with establishing apical dominance and inhibiting bud outgrowth were upregulated in 'Diamar' individuals grafted onto Rootpac® 20. Auxin is the main regulator of these processes, being synthesized in apical leaves and transported through the axis (Barbier et al., 2019). *NF-YA10* (Prudul26A005445), which negatively regulates lateral root density and is likely involved in the regulation of the auxin-signaling regulatory pathway (Sorin et al., 2014; Zhang et al., 2017), was highly expressed in the 'Diamar'/Rootpac® 20 combination (Table 1). In *Arabidopsis, NF-YA10* is highly expressed in mature leaves in the expression atlas (Klepikova et al., 2016), while in grapevine (*Vitis vinifera*), its orthologue is over-expressed in woody stems and swelling buds (Fasoli et al., 2012). When grafted onto Rootpac® 20, scions present a phenotype with reduced branching and longer branches. Hence, *NF-YA10* expression in these shoot tips may be part of a regulation process in the formation of branches promoting cell growth or might be a marker of more mature tissues with reduced replication, but its involvement in the auxin pathway is uncertain. *CKX7* (Prudul26A024231) was upregulated in 'Diamar'/Rootpac® 20 (Table 1). Cytokinin oxidase/dehydrogenase enzymes negatively regulate CKs by inactivating them (Köllmer et al., 2014). Silencing of family members in rice leads to increase branching (Yeh et al., 2015), thus its highly expression, when grafted onto Rootpac® 20, may be related to its reduced branching phenotype. Another regulator of CKs, *PAN* (Prudul26A007859), which is associated with shoot control (Maier et al., 2011), was also highly expressed in this combination (Table 1). Orthologues of *MYB93* (Prudul26A029785) and *DRMH3* (Prudul26A007496), which participate in regulating root formation but are also expressed in aerial tissues in Arabidopsis and grapevine (Fasoli et al., 2012; Gibbs

**Table 1**
Differentially expressed genes (DEGs) associated with apical dominance and shoot formation.

| $log_2$FC Rootpac® 20 - 'Garnem' | $log_2$FC Rootpac® 20 - Rootpac® 40 | *P. dulcis* ID | Gene | GO term | Biological process |
|---|---|---|---|---|---|
| 1.269 | 0.679 | Prudul26A001569 | *ABCB15* | GO:0055085 | transmembrane transport |
| 1.255 | 1.350 | Prudul26A024231 | *CKX7* | GO:0009823 | cytokinin catabolic process |
| *2.126* | 2.071 | Prudul26A031352 | *CLAVATA3* | GO:0048507 | meristem development |
| *1.706* | 2.310 | Prudul26A007496 | *DRMH3* | GO:0009733 | response to auxin |
| *−4.372* | −5.185 | Prudul26A010631 | *ESR2* | GO:0009733 | response to auxin |
| −2.043 | −2.023 | Prudul26A017626 | *GH3.6* | GO:0009733 | response to auxin |
| *−0.666* | −2.747 | Prudul26A022681 | *GSO1* | GO:2000280 | regulation of root development |
| *−1.909* | −2.059 | Prudul26A032023 | *IAA16* | GO:0009733 | response to auxin |
| −2.915 | −2.680 | Prudul26A030184 | *IAA4* | GO:0009733 | response to auxin |
| *−0.628* | −1.204 | Prudul26A031522 | *LAX3* | GO:0060919 | auxin influx |
| *2.947* | 3.244 | Prudul26A029785 | *MYB93* | GO:1901332 | negative regulation of lateral root development |
| 3.565 | 3.185 | Prudul26A005445 | *NF-YA10* | GO:0006355 | regulation of transcription, DNA-dependent |
| *1.258* | 1.329 | Prudul26A007859 | *PAN* | GO:0006355 | regulation of transcription, DNA-dependent |
| *−2.262* | −2.696 | Prudul26A000568 | *PAR2* | GO:0009641 | shade avoidance |
| *−1.442* | −2.116 | Prudul26A009595 | *PIN6* | GO:0055085 | transmembrane transport |
| *−2.252* | −2.287 | Prudul26A005193 | *RALFL34* | GO:0019722 | calcium-mediated signaling |
| −1.645 | −1.424 | Prudul26A015967 | *SPL9* | GO:0006355 | regulation of transcription, DNA-dependent |
| *−1.672* | −2.060 | Prudul26A024821 | *SWEET17* | GO:0008643 | carbohydrate transport |

†$log_2$FC values in cursive represent genes that were not differentially expressed.

et al., 2014; An et al., 2020), were upregulated in 'Diamar'/Rootpac® 20 (Table 1).

Auxin is synthesized in the apex, but to carry out its function it needs to be transported through specific carriers (Titapiwatanakun and Murphy, 2009; Cho and Cho, 2013; Adamowski and Friml, 2015). Two genes involved in promoting auxin transport, *VAB* (Prudul26A002767) and *ABCB15* (Prudul26A001569) (Kaneda et al., 2011; Naramoto and Kyozuka, 2018), and therefore apical dominance, were upregulated in the 'Diamar'/Rootpac® 20 combination (Table 1).

Rootpac® 20 effect in 'Diamar' architecture is characterized by a reduced number of branches and high apical dominance. Here, we saw upregulation of genes related to auxin transport, which might promote apical dominance, and genes likely linked to the inactivation of CK, which promotes branch formation.

### 3.4. DEGs associated with shoot formation were downregulated in 'Diamar'/Rootpac® 20

CKs act in opposition to auxins, favoring bud outgrowth and shoot formation (Dun et al., 2012). The *GH3* family is a large group of genes involved in auxin homeostasis, but also in the synthesis of other hormones, such as jasmonic acid (JA) and salicylic acid (SA) (Zhang et al., 2007; Fu et al., 2011). A member of this family, *GH3.6* (Prudul26A017626), was downregulated in the 'Diamar'/Rootpac® 20 combination (Table 1). *GH3.6* has been described to be CK-dependent and to promote meristem development in roots, being also overexpressed in shoot apex in Arabidopsis (Pierdonati et al., 2019; Tian et al., 2019). Similar expression behaviors were observed for *ESR2* (Prudul26A010631), *RALFL34* (Prudul26A005193), and *GSO1* (Prudul26A022681) (Table 1). As for *GH3.6, RALFL34* and *GSO1* have been described participating in root development while being overexpressed in the shoot apex and inflorescences (Schmid et al., 2005; Racolta et al., 2014; Murphy et al., 2016). Therefore, its expression in the shoot apex could be linked to the presence of fewer branches in scions grafted onto Rootpac® 20. *ESR2* is a promoter of shoot formation and cell division in response to CKs (Ikeda et al., 2006).

Auxin carriers not only maintain the auxin flux to favor apical dominance but also can shape plant architecture by redistributing the auxin transport (Sauer et al., 2013). Two transporters expectedly engaged in this mechanism, like *PIN6* (Prudul26A009595) and *LAX3* (Prudul26A031522) (Revalska et al., 2015; Simon et al., 2016) were less expressed in the 'Diamar'/Rootpac® 20 combination (Table 1), likely provoking an inhibition of branch formation in this combination. *PIN6* localization and expression are mediated through phosphorylation in the plasma membrane and the endoplasmic reticulum influencing auxin homeostasis and stem elongation (Ditengou et al., 2017). Beside, overexpressing *PIN6* mutants display reduced apical dominance and improved root and shoot development (Cazzonelli et al., 2013).

Apart from its transport, auxin activity is controlled by numerous auxin response proteins, some of which are downregulated in the scions grafted onto Rootpac® 20 (Table 1). AUX/IAA proteins repress the expression of auxin response genes in absence of auxin. *IAA16* (Prudul26A032023) has been described as limiting auxin responses and its KO mutants show a reduction in the number of lateral roots in Arabidopsis (Rinaldi et al., 2012). Although its effect on bud outgrowth regulation is unclear, *IAA4* (Prudul26A030184) acts oppositely to auxin in *Populus* (Zhang et al., 2020). *SPL9* (Prudul26A015967) has been observed to act as regulating shoot branching in Arabidopsis, as both repressor and promoter (Jiao et al., 2010; Miura et al., 2010; Lu et al., 2013).

Sugars have been characterized to be a part of bud outgrowth positive regulation (Mason et al., 2014). *SWEET17* (Prudul26A024821) was less expressed in 'Diamar'/Rootpac® 20 (Table 1). *SWEET17* putatively acts by mobilizing fructose and glucose content (Chardon et al., 2013; Guo et al., 2014). Light availability also affects branching control (Finlayson et al., 2010; Casal, 2012). In Arabidopsis, *PAR1* and *PAR2* play a negative role in the shade avoidance syndrome, acting downstream of *COP1* and being repressed by *phyA* (Bou-Torrent et al., 2008; Zhou et al., 2014). *PAR2* (Prudul26A000568) was downregulated in the 'Diamar'/Rootpac® 20 combination (Table 1), matching with its repression by *phyA*, which arrests bud outgrowth (Finlayson et al., 2010; Rausenberger et al., 2011).

While auxin activity inhibits branch formation, other processes like CK activity, sugar content, or light perception may favor shoot formation. We observed a downregulation in 'Diamar'/Rootpac® 20 of genes involved in auxin homeostasis, as with the rest of the mechanisms that promote branch formation.

### 3.5. DEGs involved in plant growth were affected by rootstock in 'Diamar' combinations

GA has been largely known as the growth hormone. Its synthesis and activity are related to active growth and high vigor (Hedden and Thomas, 2012; Binenbaum et al., 2018). Downregulation of genes involved in GA regulation was observed in dwarfing rootstocks in citrus (Liu et al., 2017b). We found various genes associated with GA regulation downregulated in the low vigor 'Diamar'/Rootpac® 20 combination (Table 2). *YAB1* (Prudul26A023379) is a GA-responsive gene, which is part of regulatory feedback that controls GA levels, being overexpressed when GA levels are high and, thus, repressing its

**Table 2**
Differentially expressed genes (DEGs) associated with plant growth and vigor.

| $log_2$FC Rootpac® 20 - 'Garnem' | $log_2$FC Rootpac® 20 - Rootpac® 40 | *P. dulcis* ID | Gene | GO term | Biological process |
|---|---|---|---|---|---|
| *−1.989* | −2.382 | Prudul26A020015 | *ACL5* | GO:0006596 | polyamine biosynthetic process |
| *0.842* | 1.263 | Prudul26A009326 | *ARF16* | GO:0009733 | response to auxin |
| −1.303 | −1.591 | Prudul26A012411 | *CAX3* | GO:0006816 | calcium ion transport |
| 1.544 | 1.341 | Prudul26A022494 | *DAG1* | GO:0006355 | regulation of transcription, DNA-dependent |
| −2.597 | −2.970 | Prudul26A027852 | *ELP* | GO:0009664 | plant-type cell wall organization |
| *−0.578* | −1.446 | Prudul26A006427 | *EXL5* | GO:0009741 | response to brassinosteroid |
| 4.663 | 5.974 | Prudul26A026745 | *EXLB1* | GO:0019953 | sexual reproduction |
| *−1.033* | −1.860 | Prudul26A015374 | *EXT2* | GO:0009664 | plant-type cell wall organization |
| −1.746 | −2.019 | Prudul26A005909 | *FBL17* | GO:0051302 | regulation of cell division |
| 3.769 | 3.085 | Prudul26A017080 | *GA2OX8* | GO:0009686 | gibberellin biosynthetic process |
| *−3.055* | −3.876 | Prudul26A015013 | *GASA1* | GO:0009739 | response to gibberellin |
| −2.475 | −2.565 | Prudul26A023277 | *GASA6* | GO:0009740 | gibberellic acid mediated signaling pathway |
| *−1.374* | −1.960 | Prudul26A011751 | *GASA9* | GO:0009739 | response to gibberellin |
| *−3.275* | −3.699 | Prudul26A010439 | *GAST1* | GO:0009739 | response to gibberellin |
| *−0.914* | −1.776 | Prudul26A009189 | *NCED5* | GO:0009688 | abscisic acid biosynthetic process |
| *−0.626* | −1.189 | Prudul26A025913 | *NPH3* | GO:0009638 | phototropism |
| −1.258 | −1.575 | Prudul26A012618 | *RPT2* | GO:0009638 | phototropism |
| *0.820* | 1.614 | Prudul26A006348 | *SAUR36* | GO:0009733 | response to auxin |
| *−0.991* | −1.919 | Prudul26A025556 | *SAUR50* | GO:0009733 | response to auxin |
| −2.035 | −2.794 | Prudul26A030325 | *SAUR50* | GO:0009733 | response to auxin |
| −2.986 | −3.692 | Prudul26A003964 | *SAUR50* | GO:0009733 | response to auxin |
| *−1.303* | −1.401 | Prudul26A023379 | *YAB1* | GO:1902183 | regulation of shoot apical meristem development |
| −1.625 | −1.960 | Prudul26A020640 | *YAB5* | GO:1902183 | regulation of shoot apical meristem development |

†$log_2$FC values in cursive represent genes that were not differentially expressed.

biosynthesis (Dai et al., 2007). Another member of the same family, *YAB5* (Prudul26A020640), presented a similar expression profile. *GASA6* (Prudul26A023277) is thought to be a positive regulator of GA-dependent processes, which affect growth positively. It is also up-regulated by numerous growth hormones (Qu et al., 2016). *ACL5* (Prudul26A020015) is a crucial part of internode elongation and shoot growth, probably acting downstream of GA responses (Hanzawa et al., 1997). *GASA1* (Prudul26A015013), *GASA9* (Prudul26A011751), or *GAST1* (Prudul26A010439) have been described as inhibiting GA response in Arabidopsis (Zhang and Wang, 2008). Therefore, they could be acting here in a feedback regulatory way, being less expressed in combinations with the dwarfing rootstock Rootpac® 20, and expectedly, with lower levels of GA (Table 2).

On the other hand, two genes expected to affect GA biosynthesis were more expressed in the 'Diamar'/Rootpac® 20 combination (Table 2). In Arabidopsis, *GA2OX8* (Prudul26A017080) participates in the GA biosynthetic pathway deactivating bioactive GA, while *DAG1* inhibits GA biosynthesis genes (Gabriele et al., 2010; Zhou et al., 2012; Liu et al., 2021). A homolog of this gene in citrus, *GA2OX1*, was also upregulated when grafted onto dwarfing rootstocks (Liu et al., 2017b). Therefore, the low vigor observed in combinations with Rootpac® 20 as rootstock compared to those with Rootpac® 40 or Garnem® may be in part due to reduced GA activity.

Genes related to other hormonal responses were downregulated when grafted onto the dwarfing Rootpac® 20 rootstock (Table 2). *NCED5* (Prudul26A009189) participates in maintaining basal abscisic acid (ABA) levels in Arabidopsis, which are necessary to promote plant growth (Frey et al., 2012). *CAX3* (Prudul26A005365) participates in $Ca^{2+}$ transport and interacts with auxin response, promoting growth and development in Arabidopsis (Cheng et al., 2005; Cho et al., 2012). The *EXORDIUM* family is a group of genes that are involved in BR-mediated responses (Coll-Garcia et al., 2004; Schröder et al., 2011). A member of this family, *EXL5* (Prudul26A006427), was less expressed in the 'Diamar'/Rootpac® 20 combination, which might indicate lower BR activity in scions grafted onto dwarfing rootstocks (Table 2).

Light response is an important regulator of plant growth (Molas and Kiss, 2009; Casal, 2012; Yadav et al., 2020). Several homologs to the auxin-induced gene *SAUR50* (Prudul26A025556, Prudul26A030325, Prudul26A003964) were downregulated when grafted onto the dwarfing rootstock Rootpac® 20 (Table 2). *SAUR50* promotes cell expansion and is positively regulated by light (Wang et al., 2020a). A similar expression profile was presented by other genes associated with light responses (Table 2). *NPH3* (Prudul26A025913) and *RPT2* (Prudul26A012618), which in Arabidopsis act by linking phototropism and auxin response, modifying polar auxin transport, and promoting growth (Wan et al., 2012; Christie et al., 2018). Oppositely, *SAUR36* (Prudul26A006348) and *ARF16* (Prudul26A009326), which in Arabidopsis have been described to inhibit cell elongation in response to light or auxin (Hou et al., 2013; Dai et al., 2021), were found being upregulated in 'Diamar'/Rootpac® 20.

At the tissue level, cell proliferation and cell elongation define plant growth. Some effectors of cell proliferation were less expressed in the least vigorous 'Diamar'/Rootpac® 20 combination (Table 2). *FBL17* (Prudul26A005909) is a crucial regulator of the cell cycle in Arabidopsis, targeting a negative regulator and hence, promoting cell division (Gusti et al., 2009). Loss-of-function mutants display reduced growth due to decreased cell proliferation, being necessary to keep meristem activity (Noir et al., 2015). *ELP* (Prudul26A027852) and *EXT2* (Prudul26A015374) are homologs of *EXT1*, whose expression is correlated to tip growth in the roots of Tomato, maybe with a function also in shoot tips (Bucher et al., 2002).

Here, we observed a general downregulation of diverse processes promoting growth in the Diamar'/Rootpac® 20 combination. Specially, we have seen that GA regulation is affected by the rootstock.

### *3.6. DEGs associated with cell wall formation and reorganization were downregulated in combinations with dwarfing rootstock Rootpac® 20*

The cell wall defines the ultimate shape of the plant cell, restricting its capacity to elongate or divide (Cosgrove, 2016). Hence, for plants to grow and develop, cells must carry out remodeling of the cell wall. There were multiple genes associated with cell wall reorganization that were downregulated in the 'Diamar'/Rootpac® 20 combination (Table 3). It is indeed plausible that these plants, being less vigorous and thus undergoing fewer cell division and cell elongation cycles, will present reduced cell wall remodeling processes. *EXP1* (Prudul26A014459), *EXP3* (Prudul26A015151), *EXP8* (Prudul26A032368, Prudul26A002026), *EXP15* (Prudul26A028987), and *EXPB3* (Prudul26A000148) are all members of the expansin family, which acts mediating cell wall loosening, allowing then cell expansion (Cosgrove, 2015; Ramakrishna et al., 2019; Otulak-Kozieł et al., 2020). LRR-extensin proteins like LRX4 (Prudul26A018014) are part of the cell wall formation and deficiencies in

**Table 3**
Differentially expressed genes (DEGs) associated with cell wall formation and cell wall reorganization.

| $log_2$FC Rootpac® 20 - 'Garnem' | $log_2$FC Rootpac® 20 - Rootpac® 40 | *P. dulcis* ID | Gene | GO term | Biological process |
|---|---|---|---|---|---|
| *−1.346* | −2.772 | Prudul26A016569 | *4CLL9* | GO:0009809 | lignin biosynthetic process |
| *−1.795* | −1.876 | Prudul26A026119 | *CSLB4* | GO:0030244 | cellulose biosynthetic process |
| −1.147 | −1.209 | Prudul26A023496 | *CSLC5* | GO:0071555 | cell wall organization |
| *−1.481* | −1.777 | Prudul26A005669 | *CSLC5* | GO:0071555 | cell wall organization |
| *−2.225* | −2.391 | Prudul26A026490 | *CSLC5* | GO:0071555 | cell wall organization |
| *−1.510* | −1.954 | Prudul26A019715 | *CSLD3* | GO:0030244 | cellulose biosynthetic process |
| −2.628 | −3.405 | Prudul26A014459 | *EXP1* | GO:0009664 | plant-type cell wall organization |
| −3.417 | −4.109 | Prudul26A028987 | *EXP15* | GO:0009664 | plant-type cell wall organization |
| *−1.174* | −1.528 | Prudul26A015151 | *EXP3* | GO:0009664 | plant-type cell wall organization |
| *−4.341* | −5.406 | Prudul26A032368 | *EXP8* | GO:0009664 | plant-type cell wall organization |
| *−2.370* | −2.994 | Prudul26A002026 | *EXP8* | GO:0009664 | plant-type cell wall organization |
| −2.202 | −2.566 | Prudul26A000148 | *EXPB3* | GO:0009828 | plant-type cell wall loosening |
| −2.638 | −3.705 | Prudul26A015935 | *FLA9* | GO:0009834 | plant-type secondary cell wall biogenesis |
| *−1.534* | −1.898 | Prudul26A000195 | *GRF4* | GO:0006355 | regulation of transcription, DNA-dependent |
| *−1.963* | −2.516 | Prudul26A000315 | *LAC11* | GO:0009809 | lignin biosynthetic process |
| *−3.545* | −3.917 | Prudul26A001608 | *LAC11* | GO:0009809 | lignin biosynthetic process |
| *−1.718* | −2.205 | Prudul26A010009 | *LAC17* | GO:0009809 | lignin biosynthetic process |
| *−1.858* | −2.763 | Prudul26A019505 | *LAC17* | GO:0009809 | lignin biosynthetic process |
| *−0.818* | −1.191 | Prudul26A018014 | *LRX4* | GO:0009664 | plant-type cell wall organization |
| *−1.248* | −1.602 | Prudul26A021520 | *PME3* | GO:0042545 | cell wall modification |
| *−0.738* | −1.412 | Prudul26A004552 | *PME34* | GO:0042545 | cell wall modification |
| *−1.406* | −1.778 | Prudul26A029274 | *PME54* | GO:0042545 | cell wall modification |
| *−1.629* | −2.260 | Prudul26A018663 | *PMR5* | GO:0042545 | cell wall modification |
| −2.460 | −2.728 | Prudul26A012896 | *TBL19* | GO:1990937 | xylan acetylation |
| *−2.204* | −2.828 | Prudul26A009187 | *TBL19* | GO:1990937 | xylan acetylation |
| −2.513 | *−1.785* | Prudul26A011091 | *TBL19* | GO:1990937 | xylan acetylation |
| *−2.599* | −2.896 | Prudul26A009872 | *XTH5* | GO:0010411 | xyloglucan metabolic process |
| −2.889 | −2.911 | Prudul26A002835 | *XTH6* | GO:0010411 | xyloglucan metabolic process |
| −2.358 | −2.763 | Prudul26A000404 | *XTH8* | GO:0010411 | xyloglucan metabolic process |

†$log_2$FC values in cursive represent genes that were not differentially expressed.

this gene family lead to reduced plant growth (Draeger et al., 2015).

The plant cell wall is formed by numerous components, whose regulation affects cell wall formation and reorganization (Cosgrove, 2016; Meents et al., 2018; Voiniciuc et al., 2018). Various DEGs putatively related to the positive regulation of these processes displayed less expression when 'Diamar' was grafted onto Rootpac® 20 (Table 3). More vigor entails tissue growth and a more active cell wall metabolism and reorganization. Lignification is a crucial aspect of the secondary cell wall formation, with laccases like *LAC11* (Prudul26A000315, Prudul26A0016089, and *LAC17* (Prudul26A010009, Prudul26A019505) playing an important role in assuring proper cell structure, controlling lignin deposition (Ranocha et al., 2002; Berthet et al., 2011; Zhao et al., 2013; Liu et al., 2018a). *4CLL9* (Prudul26A016569) is a regulator of lignin biosynthesis in rice, both promoting and repressing it (Liu et al., 2017a). Cell wall hemicellulose is formed by several molecules, including xyloglucans, which in case of cell wall reorganization are hydrolyzed or remodeled (Park and Cosgrove, 2015). *XTH5* (Prudul26A009872), *XTH6* (Prudul26A002835), and *XTH8* (Prudul26A000404) are involved in loosening the cell wall, allowing cell elongation in Arabidopsis (Liu et al., 2007; Muñoz and Calderini, 2015; Takahashi et al., 2021). *CSLC5* (Prudul26A026490, Prudul26A005669) is part of the xyloglucan biosynthetic pathway, while *TBL19* (Prudul26A012896, Prudul26A009187, Prudul26A011091) controls xylan acetylation (Gao et al., 2017; Kim et al., 2020).

Cellulose and pectins are major cell wall components and their synthesis and organization are crucial aspects of cell wall formation (Meents et al., 2018; Saffer, 2018). FLA proteins, like *FLA9* (Prudul26A015935), are associated with wood formation, affecting secondary cell wall formation and structure (Wang et al., 2015; He et al., 2019). They participate in the organization of cell wall polysaccharides like cellulose and pectins, with mutants presenting reduced cellulose content (Liu et al., 2020). *CSLD3* (Prudul26A019715) plays a role in the cellulose biosynthetic pathway (Park et al., 2011; Yang et al., 2020). Although its specific role is yet to be characterized, *CSLB4* (Prudul26A026119) seems to be also required for cellulose biosynthesis (Youngs et al., 2007). *GRF4* (Prudul26A000195) is expected to positively regulate cellulose biosynthesis and biomass accumulation, controlling *MYB61* transcription. A member of its family in citrus has been characterized as being more expressed in vigor-inducing rootstocks (Liu et al., 2017b; Gao et al., 2020). *PMR5* (Prudul26A018663) is a member of the TBL family, likely participating in pectin acetylation (Chiniquy et al., 2019). Pectin methylesterases like *PME3* (Prudul26A021520) and *PM34* (Prudul26A004552, Prudul26A029274) affect cell wall composition and cell expansion in Arabidopsis (Kohorn et al., 2014).

When grafted onto Rootpac® 20, 'Diamar' displayed a broad downregulation of mechanisms involved in cell wall formation and reorganization compared to vigor-conferring rootstock combinations. Lower expression in this combination may be associated with a less active metabolism, likely due to a less active cell division, which translates into a less cell wall modifications.

### *3.7. Nitrogen metabolism was less active in the 'Diamar'/Rootpac® 20 combination*

Nitrogen assimilation is vital for plant growth and development as it is an indispensable nutrient for the mechanisms involved in tree vigor (Krouk et al., 2011). The rootstock effect in nitrogen assimilation has been described in grapevine, where changes in nitrogen availability affect the expression profile of genes in dwarfing rootstocks (Cochetel et al., 2017). *NIR1* (Prudul26A012711) and *NIA1* (Prudul26A000078) perform two crucial successive steps in nitrate assimilation, converting NO into assimilable molecules for plant metabolism (Solomonson and Barber, 1990; Tanaka et al., 1994). Deficiencies in these genes lead to severely impaired growth in Arabidopsis (Costa-Broseta et al., 2020). In Arabidopsis, *TIP2;3* (Prudul26A020819) mediates $NH_3$ transport and is upregulated under conditions of high nitrogen availability (Loqué et al., 2005). These three genes were downregulated in the 'Diamar'/Rootpac® 20 combination, evidencing that nitrogen metabolism is less active in scions grafted onto dwarfing rootstocks (Table 4). Various homologs to the *NRT1.1* (Prudul26A015004, Prudul26A008539, and Prudul26A010496) transporter were also less expressed when grafted

**Table 4**
Differentially expressed genes (DEGs) associated with nitrogen assimilation and flowering meristem development.

| $log_2$FC Rootpac® 20 - 'Garnem' | $log_2$FC Rootpac® 20 - Rootpac® 40 | *P. dulcis* ID | Gene | GO term | Biological process |
|---|---|---|---|---|---|
| −1.025 | −1.616 | Prudul26A005648 | *CIB1* | GO:0009908 | flower development |
| 2.863 | 3.562 | Prudul26A019427 | *DAM5* | GO:0009910 | negative regulation of flower development |
| 2.081 | 2.128 | Prudul26A006108 | *FD* | GO:0009909 | regulation of flower development |
| *1.615* | 2.472 | Prudul26A024273 | *NF-YA3* | GO:0006355 | regulation of transcription, DNA-dependent |
| −2.401 | −1.542 | Prudul26A000078 | *NIA1* | GO:0042128 | nitrate assimilation |
| −3.929 | −2.589 | Prudul26A012711 | *NIR* | GO:0042128 | nitrate assimilation |
| −1.422 | −1.460 | Prudul26A015004 | *NRT1* | GO:0010167 | response to nitrate |
| *−2.414* | −3.720 | Prudul26A008539 | *NTL1* | GO:0055085 | transmembrane transport |
| −1.550 | −1.799 | Prudul26A010496 | *NTL1* | GO:0055085 | transmembrane transport |
| *0.819* | 2.080 | Prudul26A030680 | *SIP1* | GO:0005975 | carbohydrate metabolic process |
| *−2.104* | −2.610 | Prudul26A021958 | *TFL1* | GO:0009910 | negative regulation of flower development |
| *−5.937* | −9.422 | Prudul26A020819 | *TIP2;3* | GO:0055085 | transmembrane transport |

†$log_2$FC values in cursive represent genes that were not differentially expressed.

onto Rootpac® 20 (Table 4). NRT1.1 carriers participate in the regulation of architecture processes like root branching, slowing down their development in response to auxin, which they seem able to transport (Krouk et al., 2010; Wang et al., 2020b). This function would not match the observed phenotype, since individuals grafted onto Rootpac® 40 or Garnem® displayed reduced apical dominance and numerous branches in comparison to those grafted onto Rootpac® 20, a different regulatory function in the nitrogen metabolism cannot be excluded for these homologs.

Nitrogen availability is crucial for tree growth and development. Here we detected a downregulation of genes involved in nitrogen assimilation and transport in the reduced vigor 'Diamar'/Rootpac® 20 combination.

### *3.8. Characterization of DEGs associated with meristem differentiation in 'Diamar' combinations*

Flowering has been previously linked to the regulation of tree architecture, though the relation between them is not fully characterized (Seleznyova et al., 2008; Foster et al., 2014). We observed mixed results, with genes promoting and repressing flowering being more expressed in both combinations with the dwarfing rootstock Rootpac® 20 and the vigor-inducing rootstocks Rootpac® 40 and Garnem®. Various flowering inductors were less expressed when grafted onto Rootpac® 20 (Table 4). *CIB1* (Prudul26A005648) activates *FT* transcription in Arabidopsis, thus regulating flowering positively (Liu et al., 2018b). Nevertheless, the flowering repressor *TFL1* (Prudul26A021958) was downregulated in 'Diamar'/Rootpac® 20 (Table 4). TFL1 acts antagonistically to *FT*, repressing flowering and increasing vegetative growth (Moraes et al., 2019). The effect of *TFL1* in growth promotion may concur with the reduced vigor observed in the 'Diamar'/Rootpac® 20 combination compared with 'Diamar'/Rootpac® 40. A gene encoding a homolog of *DAM5* (Prudul26A019427) was upregulated in the 'Diamar'/Rootpac® 20 combination (Biswajit et al., 2011Table 4). *DAM5* and *DAM6* participate in flowering by negatively regulating bud dormancy release in *Prunus* (Biswajit et al., 2011). Several flowering inductors were also upregulated in the 'Diamar'/Rootpac® 20 combination (Table 4). *FD* (Prudul26A006108) performs a pivotal step in flowering development, being required for *FT* activity, which regulates directly forming a complex (Wigge et al., 2005; Collani et al., 2019). Upstream of this step, *NF-YA3* (Prudul26A024273) interacts with the flowering regulator *CO*, positively affecting floral organ development in Arabidopsis (Fornari et al., 2013; Su et al., 2018). Lastly, *SIP1* (Prudul26A030680) has been described in rice to promote early flowering in response to light signaling (Kim et al., 2013; Kang et al., 2015; Jiang et al., 2018).

Given these results, it is unclear how genes associated with flowering interact with the regulatory pathways involved in the tree architecture. Instead of an overall interaction between these two biological processes, individual genes may carry out specific functions that affect both pathways.

## 4. Conclusions

Tree architecture is dependent on numerous processes such as light perception, gravity sensing, sugar availability, or nutrient supply that take part in the tree's physiological and hormonal regulation. Rootstock interaction with the scion may transform how cultivars respond to the same environmental cues. Previous studies had described how the rootstock effect can alter scion architecture traits like the number of branches or axis height in tree species, including Almond. After carrying out a transcriptome analysis in nine cultivar/rootstock combinations, we report our results and considerations of the biological processes that are affected by scion/rootstock interaction possibly affecting tree architecture. As a prospect, the evaluation of these hormones and metabolites concentrations would help to support our hypothesis based on phenotypic and molecular observations of the rootstock effect on tree architecture. Our results show that while the expression profile of cultivars with strong scion phenotypes is not significatively altered by the rootstock, that of cultivars whose phenotype is affected by the rootstock presents a strong modification. Regulation of genes associated with hormones involved in apical dominance and branch formation, like auxin and CKs, are in this case influenced by the rootstock. Moreover, mechanisms associated with vigor control, such as GA response or nitrogen assimilation, were shown to also be affected by the rootstock, being limited when grafted onto dwarfing rootstocks. Rootstock interaction can also modify the expression of genes involved in cell wall formation and reorganization, being less active in combinations with dwarfing rootstocks. In conclusion, described effects on scion architecture correlate with significatively differences in the transcriptome of those combinations, affecting several hormonal responses and molecular mechanisms.

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## CRediT authorship contribution statement

**Álvaro Montesinos:** Investigation, Writing – original draft, Methodology, Formal analysis, Writing – review & editing. **María José Rubio-Cabetas:** Investigation, Writing – original draft, Writing – review & editing. **Jérôme Grimplet:** Investigation, Writing – original draft, Formal analysis, Writing – review & editing.

## Declaration of Competing Interest

The authors declare the following financial interests/personal

relationships which may be considered as potential competing interests:

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## Data availability

The datasets generated and/or analyzed during the current study are available in the European Nucleotide Archive and are accessible through the accession number PRJEB47633.

## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2023.112628.

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