Leaf growth – complex regulation of a seemingly simple process

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SUMMARY

Understanding the underlying mechanisms of plant development is crucial to successfully steer or manipulate plant growth in a targeted manner. Leaves, the primary sites of photosynthesis, are vital organs for many plant species, and leaf growth is controlled by a tight temporal and spatial regulatory network. In this review, we focus on the genetic networks governing leaf cell proliferation, one major contributor to final leaf size. First, we provide an overview of six regulator families of leaf growth in Arabidopsis: DA1, PEAPODs, KLU, GRFs, the SWI/SNF complexes and DELLAs, together with their surrounding genetic networks. Next, we discuss their evolutionary conservation to highlight similarities and differences among species, because knowledge transfer between species remains a big challenge. Finally, we focus on the increase in knowledge of the interconnectedness between these genetic pathways, the function of the cell cycle machinery as their central convergence point, and other internal and environmental cues.

INTRODUCTION

Increasing the biomass production of plants is one strategy to meet the increasing demands for food and biofuels (Alexandratos and Bruinsma, 2012; International Energy Agency, 2021), and the efficient use of the available arable land. Leaves contribute to biomass either directly during harvesting, or indirectly as the main sites of photosynthesis and thus also carbon fixation and energy production. Understanding leaf growth and development is therefore of particular interest to plant breeders. In *Arabidopsis thaliana* (Arabidopsis), final leaf size is dependent on at least six different intrinsic factors: the number of initial founder cells at the leaf primordium, the rate and duration of cell division, the rate and duration of cell expansion, and the extent of meristemoid cell division (Gonzalez *et al.*, 2012; Hepworth and Lenhard, 2014). Leaves originate from the sides of the shoot apical meristem where leaf primordia are formed by founder initial cells (Reinhardt *et al.*, 2000; Efroni *et al.*, 2010; Kalve *et al.*, 2014). These cells undergo cell division within a predefined time window, after which cell proliferation ceases and cells start to expand and differentiate in a leaf tip to base direction (Andriankaja *et al.*, 2012; Gonzalez *et al.*, 2012). Meristemoids, precursor cells of the stomatal lineage, are dispersed throughout the leaf epidermis and continue dividing after the initial cell division phase is finished, giving rise to the stomata and additional pavement cells (Bergmann and Sack, 2007).

Recently, much progress has been made in the further identification of leaf growth regulators and the elucidation of growth regulatory pathways in Arabidopsis and other plant species (Liebsch and Palatnik, 2020; Vercruysse *et al.*, 2020; Strable and Nelissen, 2021; Wang *et al.*, 2021a). It has become apparent that a number of growth regulatory pathways are key players in governing leaf growth and that these modules are highly interconnected with each other, as well as with other developmental processes and external factors (Vercruysse *et al.*, 2020). Furthermore, computational approaches have shown that gene function is more likely to be conserved when entire gene networks rather than individual gene homologs are maintained across species (Curci *et al.*, 2022).

In this review, we give an overview of the recent advances in the field of leaf size control by discussing six cell division-regulating pathways with a focus on the increasing knowledge on the interconnections among them in Arabidopsis. Furthermore, we discuss the translatability of the current understanding of Arabidopsis leaf growth into other plant species by providing an overview of their general evolutionary conservation across different plant species based on the PLAZA platform (Van Bel *et al.*, 2022) (see Methods for details) and discussing specific examples of similarities and differences in leaf size control among species.

DA1 PATHWAY

DA1 is a ubiquitin-activated protease (Dong *et al.*, 2017) that acts as a negative regulator of leaf size by cleaving its targets, such as TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL NUCLEAR ANTIGEN FACTOR 14 (TCP14), TCP15 and TCP22 (Peng *et al.*, 2015; Dong *et al.*, 2017), which are positive regulators of cell division duration (Martín-Trillo and Cubas, 2010), and UBIQUITIN SPECIFIC PROTEASE 15/SUPRESSOR OF DA1 2 (UBP15/SOD2, hereafter UBP15), a deubiquitinating enzyme that also acts as a promoter of cell proliferation (Liu *et al.*, 2008) (Figure 1A). Overexpression of *DA1* (*35S::GFP-DA1*) or ectopic expression of a dominant-negative allele (*da1-1*) leads to smaller and bigger plant organs, respectively, including leaves, seeds and flowers (Li *et al.*, 2008; Dong *et al.*, 2017; Vanhaeren *et al.*, 2017). In contrast, ectopic expression of *UBP15* enhances leaf growth, whereas *ubp15* loss-of-function mutants show decreased leaf growth. Furthermore, *ubp15* can repress the *da1-1* organ size phenotypes, indicating that *UBP15* is epistatic to *DA1* for seed, petal and potentially also leaf size (Du *et al.*, 2014).

DA1 itself is also subject to an intricate regulatory network. CUP-SHAPED COTYLEDON2 (CUC2) and CUC3, two transcription factors (TFs) positively regulating shoot apical and axillary meristem formation (Hibara *et al.*, 2006; Raman *et al.*, 2008), have been shown to directly activate *DA1* transcription (Li *et al.*, 2020b). Whereas *cuc2* loss-of-function mutants display leaves with less-pronounced or even without serrations, plants carrying the degradation-resistant *cuc2-2D* allele overall show bigger leaves with more pronounced serrations. Meanwhile, ectopic induction of a *CUC2-glucocorticoid receptor* fusion construct leads to overall smaller leaves, suggesting overall negative effects of CUC2 on cell division (Sieber *et al.*, 2007; Hasson *et al.*, 2011; Li *et al.*, 2020a). Similarly, CUC3 maintains leaf serration by negatively regulating cell division, although no drastic leaf phenotypes have been described (Hasson *et al.*, 2011; Serra and Perrot-Rechenmann, 2020). *DA1* expression is also negatively regulated by OTUBAIN-LIKE CYSTEINE PROTEASE 1 (OTU1), a histone deubiquitinase, and *otu1* mutants accumulate histone 2B mono-ubiquitylations and other transcription-enhancing histone modifications in the chromatin regions of *DA1* and *DA2* (Keren *et al.*, 2020). Furthermore, *otu1* mutants display a reduced rosette size phenotype (Keren *et al.*, 2020). DA2 and BIG BROTHER/ENHANCER OF DA1 (BB/EOD1, hereafter EOD1) are two RING-type E3 ligases that monoubiquitinate DA1 and its homologs DA1-RELATED1 (DAR1) and DAR2, thereby activating their protease activity (Xia *et al.*, 2013; Dong *et al.*, 2017). Accordingly, DA2 and EOD1 act synergistically with DA1 and their mutations enhance the *da1* mutation (Li *et al.*, 2008; Xia *et al.*, 2013). DA1, in turn, targets DA2 and EOD1 for proteasomal degradation, forming a negative feedback loop (Dong *et al.*, 2017). In contrast, UBP12 and UBP13 deubiquitinate DA1, DAR1 and DAR2 to lower their protease activity (Vanhaeren *et al.*, 2020). Ectopic expression of *UBP12* or *UBP13* results in an overall reduced rosette size characterized by smaller and rounder leaves and shorter petioles (Vanhaeren *et al.*, 2020). Additionally, DA1 activity can be inhibited through phosphorylation (Dong *et al.*, 2020).

Core components of the DA1 pathway are widely distributed among plant species (Figure 1B) and there is increasing knowledge about their function, especially in crops. Although these studies often focus on agronomic traits such as seed size, general conclusions about the functionality of the DA1 pathway can still be drawn. In *Populus alba* × *P. glandulosa,* the DA2 orthologs PagDA2a/b control the activity of the DA1 orthologs PagDA1a/b by regulating their ubiquitination status (Tang *et al.*, 2022). In turn, PagDA1a/b can destabilize their targets, including the WUSCHEL-RELATED HOMEOBOX 4 (WOX4) ortholog PagWOX4 to restrict cambium activity (Tang *et al.*, 2022). *DA1* and *DAR* orthologs have been identified in several *Brassica* species (Wang *et al.*, 2017; Karamat *et al.*, 2022) and ectopic expression of the dominant-negative allele *AtDA1*^{R358K} (*da1-1*) leads to a leaf size increase in various natural Arabidopsis accessions (Vanhaeren *et al.*, 2017), as well as the formation of bigger organs in *Brassica napus* (rapeseed), including leaves, seeds, and flowers (Wang *et al.*, 2017). Although some data on seed development is available (Khan *et al.*, 2021), functional characterization of these members of the DA1-pathway, in the context of leaf development, remains to be investigated in *Brassica* species beyond Arabidopsis. Several orthologs of members of the DA1 pathway have also been identified in *Oryza sativa* (rice), such as the DA2 ortholog GRAIN WIDTH AND WEIGHT 2 (GW2), which is a negative regulator of grain size in both rice and Arabidopsis (Song *et al.*, 2007; Xia *et al.*, 2013). Rice has four DA1 orthologs, including OsDA1 that has been shown to interact with OsUBP15, a positive regulator of grain size (Shi *et al.*, 2019). GW2 and OsUBP15 show antagonistic effects on grain size (Shi *et al.*, 2019). Interestingly, HOMOLOG OF DA1 ON RICE CHROMOSOME 3 (HDR3), another rice DA1 ortholog, was proposed as a positive regulator of organ size by interacting with and stabilizing GRAIN WEIGHT 6a (GW6a), suggesting a sub-functionalization among the different *DA1* genes in grain size control in rice (Gao *et al.*, 2021). In our evolutionary analysis, we only picked up two of these four orthologs, possibly due to using different reference genomes or a bit too stringent identification methods. Gene identifiers of all identified orthologs are listed in Table S1. Ten DA1/DAR1/DAR2 orthologs were identified in

Glycine max (soybean) (Figure 1B). Interestingly, overexpression of *DA1* family members from *Glycine soy* (wild soybean), a relative of soybean, in Arabidopsis had no effect on seed size, but enhanced salt tolerance (Zhao *et al.*, 2015), suggesting a putative sub-functionalization of these genes. *Zea mays* (maize) also contains orthologs of all core components (Figure 1B), however targeting of the DA1 pathway in maize only resulted in yield increases in specific maize genotypes (Xie *et al.*, 2018; Gong *et al.*, 2022). In *Triticum aestivum* (wheat) TaDA1 also acts in a common pathway with TaGW2, and disrupting TaDA1 function can increase grain size and weight, although overall grain yield and plant biomass remain unchanged (Liu *et al.*, 2020a; Mora-Ramirez *et al.*, 2021). Overall, these data indicate that whereas the DA1 module is likely to be at least partially conserved in many species, direct translatability from Arabidopsis into crops may be challenging because the DA1 pathway might be involved in controlling additional plant developmental processes.

PEAPOD PATHWAY

About 48% of pavement cells in the Arabidopsis leaf epidermis originate from asymmetric cell divisions of meristemoids during the formation of stomata (Geisler *et al.*, 2000). Among others, the PEAPOD (PPD) proteins PPD1 and PPD2, which belong to the TIFY protein family (Vanholme *et al.*, 2007; Bai *et al.*, 2011), restrict these meristemoid divisions (White, 2006; Gonzalez *et al.*, 2015). Accordingly, plants with reduced or abolished *PPD* expression produce enlarged, twisted, dome-shaped leaves, as well as enlarged seeds, flowers, and twisted petioles (White, 2006; Gonzalez *et al.*, 2015). PPD proteins interact with KINASE‐INDUCIBLE DOMAIN INTERACTING 8 (KIX8), KIX9 (Gonzalez *et al.*, 2015), and NOVEL INTERACTOR OF JAZ (NINJA), adaptor proteins recruiting the transcriptional co-repressor TOPLESS (TPL) to form a transcriptional repressor complex (Pauwels *et al.*, 2010; Baekelandt *et al.*, 2018) (Figure 2A). It is likely that the PPD/KIX/NINJA/TPL transcriptional repressor complex is guided to its target sequences by interacting with specific TFs (Pauwels *et al.*, 2010; Gonzalez *et al.*, 2015). Several targets of the PPD complex have been identified, including the *CYCD3* genes *CYCD3;2* and *CYCD3;3*, directly linking the PPD pathway with the cell cycle (Gonzalez *et al.*, 2015; Baekelandt *et al.*, 2018). Overexpression of *CYCD3;2* also results in the formation of dome-shaped leaves, though not increased in leaf area and lacking increased meristemoid cell division rates (Baekelandt *et al.*, 2018). Combined with the observation that the primary cell cycle arrest front in *ppd* and *ninja* leaves shows an altered shape, these findings indicate that the PPD module regulates both primary and meristemoid cell division during leaf development (Baekelandt *et al.*, 2018). To affect the expression of cell cycle genes, PPD proteins may also function with LIKE HETEROCHROMATIN PROTEIN 1 (LHP1) (Zhu *et al.*, 2020), which acts within the POLYCOMB REPRESSIVE COMPLEX 1 to identify and maintain a trimethylated lysine 27 state of HISTONE 3 (H3K27Me3) (Turck *et al.*, 2007; Zhang *et al.*, 2007; Exner *et al.*, 2009). LHP1 interacts with PPD2 in yeast, and *lhp1* mutants display a dwarfed phenotype with a reduced cell number and size. Several cell cycle-related genes, including *CYCD3;2*, *CYCD3;3*, *CYCA2;1*, *CDKB2;1* (*CYCLIN-DEPENDENT KINASE B2;1*)and *HMGA* (*HIGH MOBILITY GROUP A*), are upregulated in *ppd2* and *lhp1* mutants (Zhu *et al.*, 2020). Additionally, both PPD2 and LHP1 are enriched at *CYCD3;3* and *HMGA* promoter sites, and *35S::amippd* plants display reduced levels of tri-methylation of lysine 27 on histone 3 (H3K27me3), suggesting that PPD2 and LHP1 may function in concert during Polycomb-mediated gene repression (Zhu *et al.*, 2020).

The PPD complex is regulated by the F-box protein STERILE APETALA/SUPPRESSOR OF DA1 3 (SAP/SOD3), which targets the complex, most likely via the KIX proteins, for proteasomal degradation (Wang *et al.*, 2016; Li *et al.*, 2018). Accordingly, *SAP* overexpression lines produce a *ppd*-like phenotype, whereas *sap* mutants display small, flat leaves (Wang *et al.*, 2016; Li *et al.*, 2018). Not much is currently known about the transcriptional regulation of *PPD* genes, but a contribution of light signaling seems likely (Romanowski *et al.*, 2021; White, 2022).

The PPD pathway is largely conserved in several eudicot species as evidenced by altered organ sizes in PPD pathway mutants or overexpression lines in a variety of crop species such as *Solanum lycopersicum* (tomato) (Swinnen *et al.*, 2022), *Cucumis sativus* (cucumber) (Yang *et al.*, 2018), and several legume species (Ge *et al.*, 2016; Naito *et al.*, 2017; Kanazashi *et al.*, 2018; Li *et al.*, 2019; Nguyen *et al.*, 2020; Yin *et al.*, 2020; Barmukh *et al.*, 2022). In *Cicer arietinum* (chickpea), allelic variation of the *PPD2* ortholog *CaTIFY4B* is additionally associated with improved leaf growth and yield under water-deficit conditions (Barmukh *et al.*, 2022). The evolutionary conservation is further supported by a study expressing *PPD* orthologs of different species in *ppd* deletion (*Δppd*) Arabidopsis plants, showing that PPD orthologs from the lycophyte *Selaginella moellendorffii* (spikemoss), the gymnosperm *Picea abies* (Norway spruce) and the monocot *Musa acuminata* (banana) can at least partially complement the *Δppd* leaf phenotype (Cookson *et al.*, 2022). Although TFs recruited to the PPD complex during leaf development are currently unknown, PPD proteins interact during Arabidopsis seed development with MYC3 and MYC4, guiding the complex to the *GRF-INTERACTING FACTOR1/ANGUSTIFOLIA3* (*GIF1/AN3*) promoter to repress its expression (Liu *et al.*, 2020b). Another potential direct or genetic interactor could be WOX1, a TF that positively regulates lateral organ development in several species, including Arabidopsis, *Pisum sativum* (garden pea) and *Petunia × hybrida* (Petunia) (Vandenbussche *et al.*, 2009; Zhuang *et al.*, 2012). WOX1 orthologs LATHYROIDES (LATH) of pea and NARROW ORGANS 1 (NAO1) of *Lotus japonicus* interact with the respective KIX orthologs in yeast two-hybrid assays (Li *et al.*, 2019). Furthermore, *LATH* may genetically interact with the pea *PPD–KIX* module during leaf growth and its gene expression is upregulated in their respective single mutants (Li *et al.*, 2019). The *Medicago truncatula* (Medicago) SAP ortholog SMALL LEAF AND BUSHY 1/MINI ORGAN1 (SLB1/MIO1) is the so far only reported SAP ortholog capable of directly interacting with the PPD ortholog BIG SEEDS 1 (BS1), without requiring the KIX proteins (Yin *et al.*, 2020; Zhou *et al.*, 2021). Overall, these findings suggest that, whereas the core functions of the PPD module are conserved across dicot species (Figure 2B), specific functions may have evolved in individual species.

Curiously, *PPD* genes, as well as *KIX* and *SAP* genes, are absent from all studied *Poaceae* (monocot grasses) (Gonzalez *et al.*, 2015; Wang *et al.*, 2016; Zhu *et al.*, 2020) (Figure 2B). Key differences in grass leaf development, such as the absence of meristemoids and a linear arrangement of stomata, could explain the lack of PPD/KIX/SAP proteins during leaf development, whereas other proteins may fulfil their functions in other developmental contexts (Nelson and Dengler, 1997; Liu *et al.*, 2009b; Peterson *et al.*, 2010; Vatén and Bergmann, 2013; Nelissen *et al.*, 2016).

KLU PATHWAY

The duration of leaf, flower and seed cell division, as well as the plastochron (time between the initiation of new leaf primordia) are positively regulated by KLU/KLUH/CYP78A5, which together with CYP78A6-10 belongs to the CYP78A subfamily within the cytochrome P450 proteins (Anastasiou *et al.*, 2007; Adamski *et al.*, 2009; Eriksson *et al.*, 2010). *klu* loss-of-function mutants display a decreased growth as well as a shortened plastochron, meaning they form more leaves within a certain time frame (Anastasiou *et al.*, 2007; Wang *et al.*, 2008). *KLU* is expressed in the boundary domain between shoot apical meristem and leaf primordia, and is proposed to produce or degrade a mobile growth signal, allowing to modulate leaf growth in a cell non-autonomous manner (Anastasiou *et al.*, 2007; Eriksson *et al.*, 2010). However, although this mobile signal has previously been speculated to be related to fatty acid biosynthesis, KLU's mode of action remains elusive, as neither substrate nor product have been identified yet (Kajino *et al.*, 2022; Zhou *et al.*, 2022). KLU likely shares partial functional redundancy with CYP78A7, because *cyp78a7* loss-of-function mutants display no mutant phenotype compared with wild-type plants, whereas the *klu cyp78a7* double mutant is either embryo lethal or develops a small rosette with a further increased number of leaves and does not produce seeds (Wang *et al.*, 2008). Other members of the CYP78A subfamily have not been directly linked with leaf growth

so far. However, this likely results from specific expression patterns rather than distinct protein functionality, because expression of *CYP78A6* from the *KLU* promoter can complement the *klu* plastochron phenotype (Nobusawa *et al.*, 2021) and CYP78A6 and CYP78A9 are regulators of seed size (Fang *et al.*, 2012). Additionally, in *Camelina sativa* (Camelina), overexpression of *AtKLU* leads to moderate increases in organ size, whereas overexpression of *AtCYP78A6* and *AtCYP78A9* has more severe growth effects, showing that other *AtCYP78A* family members share similar functions (Hölzl and Dörmann, 2021). KLU and CYP78A7 may also act in a shared pathway with ALTERED MERISTEM PROGRAM1 (AMP1) and LIKE AMP1 (LAMP1) to control cell pluripotency and maintain undifferentiated cells capable to divide (Poretska *et al.*, 2020; Nobusawa *et al.*, 2021). However, whereas current data suggests that these four genes regulate the plastochron in a shared pathway, this is probably not the case for leaf size (Nobusawa *et al.*, 2021) (Figure 3A).

The expression of *KLU* is regulated, among others, via transcriptional repression by NGATHA-LIKE PROTEIN 2/SUPPRESSOR OF DA1-7 (NGAL2/SOD7) and DEVELOPMENT-RELATED PcG TARGET IN THE APEX (DPA4/NGAL3) (Zhang *et al.*, 2015) (Figure 3A). In agreement, the dominant-negative *sod7-1D* mutant displays a smaller seed area and weight and a reduced cotyledon area because of a lower cell number, although it is unclear whether reduced *KLU* expression is the reason for this phenotype (Zhang *et al.*, 2015). *KLU* transcript levels also seem to be regulated in response to strigolactones (SLs), because treatment with the SL analog GR24 enhances *KLU* transcript levels in wild-type plants and several SL signaling mutants display an altered *KLU* expression compared with wild-type plants (Cornet *et al.*, 2021). During SAM formation, *KLU* expression is also positively regulated by the TFs CUC1 and CUC2 (Aida *et al.*, 2020).

CYP78A orthologs are identified in all analyzed species, with *KLU* orthologs first appearing in the lycophyte *Selaginella moellendorffii*, although a one-to-one assignment of orthologs to differentiate between *KLU* and the other *CYP78As* would require a deeper analysis (Figure 3B). Interestingly, based on our analysis, the bryophytes only contain *CYP78A7* orthologs, which could place *CYP78A7* as the ancestral gene within its family. Phenotypic effects upon misregulation of the KLU pathway in other species are best-characterized in different cereals, including maize, rice and wheat (Miyoshi *et al.*, 2004; Mimura *et al.*, 2012; Mimura and Itoh, 2014; Sun *et al.*, 2017; Wang *et al.*, 2021b; Guo *et al.*, 2022b; Laureyns *et al.*, 2022; Zhou *et al.*, 2022). In maize, ectopic expression of the *KLU* ortholog *PLASTOCHRON1* (*PLA1*) results in fewer but bigger leaves, whereas the opposite is observed in *pla1* plants (Sun *et al.*, 2017). Like AtKLU, ZmPLA1 promotes the duration of cell division by repressing cell fate determination (Sun *et al.*, 2017). Accordingly, a transposon insertion *Zmpla1* mutant possesses a smaller leaf 4 cell division zone and shorter leaves (Sun *et al.*, 2017). As KNOTTED1 is capable to directly bind with the *ZmPLA1* promoter, the KNOTTED1-like homeobox (KNOX) pathway involved in organ patterning was proposed to regulate *ZmPLA1* expression (Bolduc *et al.*, 2012). Overexpression of *TaKLU* in wheat also results in a bigger leaf size and biomass due to an increased cell number (Zhou *et al.*, 2022). In rice, OsPLA1 additionally acts as a suppressor of bract outgrowth and is regulated at the transcriptional level by SQUAMOSA PROMOTER BINDING PROTEIN LIKE14 (SPL14) and NECK LEAF1 (NL1) (Wang *et al.*, 2021b), which themselves act as bract outgrowth repressors (Wang *et al.*, 2021b). The loss-of-function mutants *Osspl7 spl14 spl17* and *Osnl1* display leafy phenotypes during the reproductive stage (Wang *et al.*, 2021b). This might differ from Arabidopsis, where *SPL* genes are also involved in plastochron control albeit likely independently of KLU (Wang *et al.*, 2008).

GRF–GIF PATHWAY

Both the GROWTH REGULATING FACTOR (GRF) and GRF-INTERACTING FACTOR (GIF) families comprise several regulators of cell number determination in leaves (Kim and Kende, 2004; Lee *et al.*, 2009; Kim, 2019; Liebsch and Palatnik, 2020) (Figure 4A). The most prominent among the three Arabidopsis GIFs

is ANGUSTIFOLIA3/GIF1 (AN3/GIF1), because overexpression of *GIF1* results in enlarged leaves and in the upregulation of several cell cycle genes, including *CYCB1;1 (Vercruyssen et al., 2014)*. In agreement, *gif1* mutants display smaller and more narrow leaves (Kim and Kende, 2004; Horiguchi *et al.*, 2005). Furthermore, GIF1 also promotes the expression of *GRF5* and *GRF6 (Vercruyssen et al., 2014)*. Overexpression of *GIF2* and *GIF3* also leads to increased organ size, suggesting that all GIF proteins are positive regulators of organ size, including leaf growth (Lee *et al.*, 2009).

Several GRF proteins are positive regulators of growth. For instance, plants overexpressing *GRF1*, *GRF2,* or *GRF5* display enlarged leaves due to increased cell numbers, whereas *GRF5* downregulation leads to smaller and more narrow leaves containing fewer cells (Kim *et al.*, 2003; Kim and Kende, 2004; Horiguchi *et al.*, 2005; Kim and Lee, 2006; Vercruyssen *et al.*, 2015). GRF3 is also a positive regulator of leaf growth, because the expression of an allele resistant to *microRNA396* (*miR396*)-mediated degradation results in bigger plants organs (Beltramino *et al.*, 2018), whereas the *grf4-1* loss-of-function mutant shows slight decreases in leaf size but further enhances the *grf1 grf2 grf3* triple mutant phenotype (Kim and Lee, 2006). However, not all GRF proteins are positive regulators of leaf size. Whereas ectopic expression of *GRF7* results in no or only small increases in leaf size (Liang *et al.*, 2014), overexpression of *GRF9* leads to reduced leaf size and *grf9* mutants display an enlarged organ size because of enhanced cell proliferation (Omidbakhshfard *et al.*, 2018). This is achieved by activating the expression of *OBF-BINDING PROTEIN 3-RESPONSIVE GENE 3* (*ORG3/bHLH039*), a negative regulator of leaf growth. In agreement, *org3* mutants show an increased leaf size and *ORG3* overexpression causes a reduced leaf area (Omidbakhshfard *et al.*, 2018).

Expression of all *GRF* genes, except *GRF5* and *GRF6*, is controlled at the post-transcriptional level by *miR396A* (Liu *et al.*, 2009a; Rodriguez *et al.*, 2010; Debernardi *et al.*, 2014; Liebsch and Palatnik, 2020). *miR396A* expression follows a tip-to-base direction during leaf development, restricting *GRF* expression to the leaf base (Liu *et al.*, 2009a; Wang *et al.*, 2011). It has been proposed that this process is further fine-tuned by the production of two long non-coding natural antisense transcripts (lncNATs) transcribed from a region overlapping the *UGT73C6* gene, named $NAT1_{UGT73C6}$ and $NAT2_{UGT73C6}$, which may act as target mimics sequestering *miR396* (Meena *et al.*, 2023). In agreement, overexpression or downregulation of $NAT_{UGT73C6}$ results in bigger or smaller rosettes, respectively (Meena *et al.*, 2023). This is presumably because of a higher or lower abundance of GRFs, respectively. Intriguingly, *GRF6* is not a target of *miR396A*, suggesting a yet unidentified mechanism to be at play during the *miR396A*-mediated regulation of *GRF* transcripts because *GRF4*, *GRF6* and *GRF9* transcript levels are all increased in $NAT2_{UGT73C6}$-overexpressing lines (Meena *et al.*, 2023). Evolutionary studies have shown that the *GRF5* promoter is more conserved compared to the promotors of other *GRF* genes, suggesting a more evolutionarily conserved transcriptional regulatory mechanism, and it has been shown that AUXIN RESPONSE FACTOR 2 (ARF2) directly represses *GRF5* expression (Beltramino *et al.*, 2021). In accordance, *arf2* mutants display bigger leaves due to an increased cell number and size, of which the cell number component could be attributed to ectopic *GRF5* expression (Beltramino *et al.*, 2021). Additionally, the ORESARA15 (ORE15) pathway acts synergistically with the GRF–GIF pathway to promote leaf growth, and ORE15 directly promotes *GRF1* and *GRF4* expression (Kim *et al.*, 2018; Jun *et al.*, 2019). Accordingly, *ore15* loss-of-function mutants display smaller leaves due to a reduced leaf cell number (Jun *et al.*, 2019).

GIF and *GRF* genes are highly evolutionarily conserved (Kim, 2019; Fonini *et al.*, 2020; Meng *et al.*, 2022). Interestingly, *GRFs* have diversified much more than *GIFs* throughout evolution, often giving rise to ten or more *GRFs* in higher plants, whereas there are only about five identified *GIFs* per species (Figure 4B), possibly reflecting the higher sub-functionalization of *GRFs*. *GIF1* loss-of-function mutants in the moss *Physcomitrium patens* can be complemented by expression of *AtGIF1*, displaying the high

evolutionary conservation of GIF function across plant species (Kawade *et al.*, 2020). Numerous studies showed that both the function and regulation of the GRF–GIF module by *miR396* are largely conserved across species. For example, in cucumber, *CsGRF3* and *CsGRF5*, which are orthologs of *AtGRF1* and *AtGRF9* respectively, display opposing roles in leaf size control (Wang *et al.*, 2022). Whereas CsGRF3 promotes leaf growth, CsGRF5 restricts leaf growth, similar to what was shown for the Arabidopsis orthologs (Kim *et al.*, 2003; Omidbakhshfard *et al.*, 2018; Wang *et al.*, 2022). In poplar (*P. pseudo-simonii × P. nigra*), PpnGRF5-1 interacts with PpnGIFs and promotes leaf growth when overexpressed through repression of *PpnCYTOKININ OXIDASE/DEHYDROGENASE 1* (*PpnCKX1*), encoding an enzyme involved in cytokinin (CK) degradation (Wu *et al.*, 2021b). Similarly, the CK signaling component CK RESPONSE FACTOR 2 (CRF2) is situated downstream of GIF1 in Arabidopsis, potentially connecting the GRF–GIF module with the CK hormone pathway (Vercruyssen *et al.*, 2014). In monocots such as rice and maize, GIF and GRF proteins regulate leaf size (Nelissen *et al.*, 2015; Zhang *et al.*, 2018; Lu *et al.*, 2021). For instance, MAKIBA 3 (MKB3), the rice ortholog of AtGIF1, promotes leaf cell proliferation and its protein function is largely conserved between AtGIF1 and MKB3 (Shimano *et al.*, 2018). Both *gif1* and *mkb3* mutants produce smaller and more narrow leaves, slightly compensated by an increased cell area (Kim and Kende, 2004; Shimano *et al.*, 2018). Additionally, both proteins display cell-to-cell movement, albeit with species-specific movement patterns (Kawade *et al.*, 2013; Shimano *et al.*, 2018). Similarly, maize GIF1 is crucial for leaf growth and mutants display various developmental defects, including more narrow leaves and an overall dwarfed plant phenotype (Zhang *et al.*, 2018). Like in Arabidopsis, monocot GIF proteins work together with GRF proteins to control cell proliferation. For example, OsGRF1 and OsGIF1 co-regulate leaf growth in rice (Lu *et al.*, 2020), whereas ZmGRF10, a maize GRF that interacts with maize GIF proteins and lacks most of its transactivation domain, reduces leaf size and plant height when overexpressed (Wu *et al.*, 2014). The GRF–GIF module is also active in the monocot orchid *Phalaenopsis equestris,* where silencing of *PeqGRF5*, with *AtGRF1* and *AtGRF2* as closest Arabidopsis homologs, results in smaller leaves with more but smaller cells (Ma *et al.*, 2023). The cell proliferation-promoting properties of most GRF–GIF complexes are currently also being explored to improve plant regeneration by using chimeric GRF–GIF proteins, as shown for the TaGRF4-TaGIF1 chimera improving regeneration in different wheat, triticale and rice cultivars (Debernardi *et al.*, 2020).

SWI/SNF PATHWAY

The SWITCH/SUCROSE NON-FERMENTING (SWI/SNF) complex is one of several conserved chromatin remodeling complexes in plants that can alter chromatin accessibility. The SWI/SNF complex acts by gliding over and ejecting nucleosomes, thus changing DNA-histone interactions and activating or repressing transcription of target loci (Clapier and Cairns, 2009; Shang and He, 2022). The SWI/SNF complex is composed of multiple proteins (Figure 5A) (Thouly *et al.*, 2020; Guo *et al.*, 2022a; Shang and He, 2022). Generally, the complex is defined by its respective SWI2/SNF2-type ATPase, including either BRAHMA (BRM), SPLAYED (SYD) or MINUSCULE 1/CHROMATIN REMODELING 12 (MINU1/CHR12, hereafter MINU1) and MINU2/CHR23. The complex further incorporates core proteins present in all SWI/SNF complexes, as well as subunits specific to individual SWI/SNF complexes depending on the incorporated ATPase (Guo *et al.*, 2022a; Shang and He, 2022). SWI/SNF complexes regulate the expression of a plethora of genes and their mutants often display pleiotropic effects or are even lethal. As discussing the large number of subunits (Figure 5A) is out of scope of this review, Table 1 provides an overview of described leaf growth phenotypes for known subunits, including recently described novel putative subunits.

Reduced leaf size and increased leaf curvature are common features among many SWI/SNF complex mutants. For example, *BRM* is mainly expressed in young and dividing tissues and the *brm* loss-of-function mutant shows an overall reduced organ size, as well as downward curling of the leaves

(Farrona *et al.*, 2004; Hurtado *et al.*, 2006). Smaller, curled leaves are also observed in knock out *swi3c* mutants (Sarnowski *et al.*, 2005), whereas *SWI3C* overexpression leads to the formation of enlarged leaves (Vercruyssen *et al.*, 2014). Conversely, a *SWI3B* knockdown or a loss-of-function mutant of LEAF AND FLOWER RELATED (LFR), an interactor of SWI3B, show smaller, upward curling leaves (Wang *et al.*, 2009; Lin *et al.*, 2021). LFR and SWI3B co-target the *FILAMENTOUS FLOWER* (*FIL*) locus (Lin *et al.*, 2021). Reduced *FIL* expression in *lfr-2* mutants could be partially responsible for the leaf curling phenotype, because enhanced *FIL* expression can partially complement this phenotype (Lin *et al.*, 2021). LFR can also interact with other SWI/SNF subunits, such as SWI3A and SWI3D (Lin *et al.*, 2021; Guo *et al.*, 2022a), which is further supported by findings from rice, in which OsLFR can also interact with orthologs of Arabidopsis SWI/SNF subunits (Qi *et al.*, 2020).

SWI/SNF subunits also interact with other chromatin remodelers. For example, BRM interacts with RELATIVE OF EARLY FLOWERING 6 (REF6) (Li *et al.*, 2016a), a H3K27 demethylase involved in antagonizing Polycomb-mediated silencing (Yamaguchi, 2021) and whose mutant displays pleiotropic effects, including shortened leaf blades and petioles due to impaired cell elongation (Yu *et al.*, 2008). In fact, although SWI/SNF complexes are most often implied in transcriptional activation, both BRM and SYD have been shown to regulate the chromatin of target loci both in cooperative or antagonistic means to the Polycomb repressor complexes (Wu *et al.*, 2012; Yang *et al.*, 2015; Xu *et al.*, 2016a; Shu *et al.*, 2021; Yang *et al.*, 2022). For example, SWI3B interacts with HISTONE DEACETYLASE 6 (HDA6) to mediate repression of certain transposons (Yang *et al.*, 2020). HDA6 mutants display leaves with moderately enhanced curling and serration but leaf size was not quantified and appears to be similar to the wild type (Hung *et al.*, 2023). Polycomb silencing itself is also a crucial regulator of plant development, because loss-of-function mutants in core subunits show severe phenotypes, such as a greatly reduced leaf blade area in *curly flower-25* (*clf*) (Kim *et al.*, 1998). Besides proteins, long non-coding RNAs have also been implicated in the interaction with SWI/SNF complexes by acting as scaffolds to form super protein complexes at target loci (Jampala *et al.*, 2021).

Although subunits of the SWI/SNF complexes are largely conserved across plant species (Figure 5B, Figure S1), information about the functional characterization of SWI/SNF subunits in other species during leaf growth is currently relatively scarse. Tomato contains four SWI3-like proteins and overexpression of tomato *SlSWI3C* in Arabidopsis results in increased rosette and leaf areas, whereas overexpression of *SlSWI3A*, *SlSWI3B* and *SlSWI3D* has no significant effects on leaf growth (Zhao *et al.*, 2019). In the monocots rice and maize, SWI/SNF complexes are also conserved (Besbrugge *et al.*, 2018; Guo *et al.*, 2022a). In fact, many subunits of SWI/SNF complexes are conserved in many other eukaryotes outside of the plant kingdom. Nonetheless, some of the uncharacterized putative SWI/SNF interactors identified through pulldown experiments with SWI/SNF subunits do not have homologs in other eukaryotes, suggesting that plant lineage-specific SWI/SNF subunits may also have arisen during evolution (Hernández-García *et al.*, 2022).

GA/DELLA PATHWAY

Gibberellins (GAs) are a class of plant hormones and overexpression or knock-out of GA biosynthesis or signaling genes can have strong effects on plant organ growth and development (Achard *et al.*, 2009). For example, plants overexpressing *GIBBERELLIN 20-OXIDASE 1* (*GA20ox1*) display bigger leaves containing more and larger cells. These effects result from elevated GA levels because GA20ox1 is one of the several rate-limiting enzymes within the GA biosynthetic pathway (Coles *et al.*, 1999; Gonzalez *et al.*, 2010). Similarly, dwarfed phenotypes are observed when GA biosynthesis or signaling is inhibited, for example in the *ga1-3* mutant, containing a loss-of-function allele of *ARABIDOPSIS THALIANA ENT-COPALYL DIPHOSPHATE SYNTHETASE 1* (*CPS1*), encoding another GA biosynthetic enzyme (Sun *et al.*, 1992). The same can also be observed for other GA biosynthetic enzymes such as

the GA3ox family, where loss of GA3ox1 or GA3ox2 function results in mild rosette area decreases that are enhanced in higher-order mutants (Mitchum *et al.*, 2006; Hu *et al.*, 2008). However, *ga3ox3* and *ga3ox4* mutations do not further decrease leaf size when stacked with *ga3ox1* or *ga3ox2* (Hu *et al.*, 2008).

Key players of GA signaling are the DELLA proteins (Xue *et al.*, 2022) (Figure 6A). The Arabidopsis genome encodes five DELLA proteins: GA INSENSITIVE (GAI), REPRESSOR OF *gai1-3* (RGA), RGA-LIKE 1 (RGL1), RGL2 and RGL3, which repress the expression of GA-responsive genes in the absence of GA, including the aforementioned *GA3ox1*, *GA20ox1* and *GA20ox2* (Sun and Gubler, 2004; de Lucas *et al.*, 2008; Claeys *et al.*, 2014; Xue *et al.*, 2022). Upon perception of GA by the GA receptors GIBBERELLIN-INSENSITIVE DWARF 1a (GID1a), GID1b and GID1c, the receptor binds with DELLA proteins (Hirano *et al.*, 2008) Subsequent recruitment of the F-box protein SLEEPY 1 (SLY1) results in the proteasomal degradation of the DELLA proteins and expression of GA-responsive genes (McGinnis *et al.*, 2003; Dill *et al.*, 2004). In agreement, GA signaling mutants, like the GA-insensitive *gid1* or *sly1*, in which DELLA proteins are stabilized, display a dwarfed phenotype (Dill *et al.*, 2004; Fu *et al.*, 2004; Griffiths *et al.*, 2006). Conversely, the quadruple DELLA mutant *gai-t6 rga-t2 rgl1-1 rgl2-1* shows enhanced growth due to a constitutive GA signaling (Achard *et al.*, 2009).

Due to their central role in plant development, DELLA proteins are subject to a complex network of regulations (Blanco-Touriñán *et al.*, 2020b; Qianyu *et al.*, 2021). DELLA proteins bind to and modify the transcriptional repressive activity of SPL9, influencing axillary meristem initiation (Zhang *et al.*, 2020). Moreover, when ectopically expressing *SPL9* and *SPL13*, plants form bigger and elongated leaves, likely due to the enhanced repression of their target genes *BLADE ON PETIOLE 1* (*BOP1*) and *BOP2* (Hu *et al.*, 2023). *BOP1* and *BOP2* are involved in leaf patterning, and loss-of-function double mutants display elongated leaf blades and delayed petiole development, whereas ectopic expression of *BOP1* results in smaller plants with smaller leaves (Hepworth *et al.*, 2005; Norberg *et al.*, 2005). DELLA proteins also interact with HISTONE ACETYLASE 1 (HAT1), inhibiting HAT1's repressive transcriptional ability during cotyledon expansion (Tan *et al.*, 2021). Accordingly, ectopic expression and downregulation of *HAT1* result in smaller and bigger cotyledons, respectively (Tan *et al.*, 2021). Whether this is also the case for true leaves, is to our knowledge not reported. Other interaction partners include GAI-ASSOCIATED FACTOR 1 (GAF1)/INDETERMINATE DOMAIN 2 (IDD2), with the double *idd1 idd2* mutant showing a semi-dwarf plant phenotype (Fukazawa *et al.*, 2021), and ELONGATED HYPOCOTYL 5 (HY5), of which a loss-of-function *hy5* mutation results in bigger cotyledons and first leaves (Sibout *et al.*, 2006; Huang *et al.*, 2022).

Post-translational modifications are a common mechanism to modulate DELLA activity and stability. CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) is an E3 ubiquitin ligase that ubiquitinates DELLA proteins in response to shade or warmth, marking them for proteasomal degradation in a GA-independent manner (Blanco-Touriñán *et al.*, 2020a; Frerigmann *et al.*, 2021). Non-lethal, light-grown *cop1* mutants display an overall dwarfed plant phenotype with small rosette leaves (Deng and Quail, 1992). Similarly, under long-day conditions FLAVIN-BINDING, KELCH REPEAT, F BOX 1 (FKF1) targets DELLA proteins for degradation (Yan *et al.*, 2020) and the T-DNA insertion line *fkf1-t* produces longer leaf blades and an overall higher rosette fresh weight compared to wild-type plants (Yuan *et al.*, 2019). Besides ubiquitination, other post-transcriptional modifications are also involved in regulating DELLA function and stability. By *O*-fucosylating RGA, SPINDLY (SPY) is capable of enhancing DELLA binding activity to its numerous binding partners, thus promoting DELLA activity (Silverstone *et al.*, 2007; Zentella *et al.*, 2017). Accordingly, *spy* mutants display pleiotropic phenotypes, including elongated stems, erect and pale green leaves and an overall reduced rosette leaf number, somewhat similar to repeatedly GA-treated plants (Jacobsen and Olszewski, 1993). Although the SPY paralog SECRET AGENT

(SEC) adds O-β-N-acetylglucosamine to RGA, resulting in a conformational change and abolishing the inhibitory activity of RGA (Zentella *et al.*, 2016), the T-DNA insertion lines *sec-1* and *sec-2* do not show changes in leaf size compared to the wild type (Hartweck *et al.*, 2006). Moreover, phosphorylation may stabilize DELLA proteins (Qin *et al.*, 2014a; Wang *et al.*, 2014), whereas SUMOylation allows DELLA proteins to bind to and sequester GID1 independently of GA, resulting in the accumulation of non-SUMOylated DELLA proteins (Conti *et al.*, 2014). SUMOylation also affects DELLA stability, and ectopic expression of a mutated *RGA* lacking the SUMOylation site results in higher protein accumulation and an overall slightly reduced plant growth compared to ectopically expressed wild-type *RGA* in a *ga1-5* background (Conti *et al.*, 2014).

In many other plant species, DELLA and GA signaling proteins are largely conserved (Figure 6B) and act as important growth regulators. Already before the emergence of canonical GA signaling in vascular plants, DELLA proteins played a crucial role in plant development as seen in the liverwort *Marchantia polymorpha*, in which overexpression of *MpDELLA* leads to reduced plant growth (Hernández-García *et al.*, 2021). Support for the conservation of interactions in the GA/DELLA pathway is also found in many other species such as tomato, in which SlBES1.8 represses the production of two GA-inactivating enzymes to increase GA levels and control leaf morphology (Su *et al.*, 2022). This process is counteracted by the single DELLA protein in tomato, PROCERA (PRO), that interacts with SlBES1.8 to inhibit its transcriptional repressor capacity (Su *et al.*, 2022). Ectopic expression of *SlBES1.8* results in a decreased leaf complexity, whereas a disruption of the DNA-binding domain of *PRO* leads to an elongated plant phenotype (Bassel *et al.*, 2008). In fact, GA signaling components overall seem to not have diversified very much, because the number of orthologs of *DELLAs*, but also of *GID1* and *SLY1*, are relatively low in all of our analyzed species. Other examples of conservation are the characterization of various IDD–DELLA complexes in *Prunus persica* (peach), creating a feedback loop controlling GA biosynthesis (Jiang *et al.*, 2022), and that several peach varieties are dwarfed due to a missense mutation in the *PpGID1c* gene (Cheng *et al.*, 2019). The role of GA signaling has also been studied extensively in cereals such as rice and wheat, where it led to the "Green Revolution" by generating high-yielding, semi-dwarf cultivars (Gao and Chu, 2020; Lu *et al.*, 2021; Phokas and Coates, 2021; Ptošková *et al.*, 2022). Additionally, a potentially novel module of GA signaling involving Os*NITROGEN-MEDIATED TILLER GROWTH RESPONSE 5* (OsNGR5) and OsGRF4 that regulate nitrogen use efficiency, and therefore also plant growth, might be the next step to further improve current crop varieties (Wu *et al.*, 2020). The absence of GID1 orthologs in Norway spruce in our analysis might be explained by the fact that *P. abies* contains a different type of GID1 receptor compared to the types found in angiosperms (Yoshida *et al.*, 2018).

THE CELL CYCLE MODULE – A HUB FOR LEAF GROWTH CONTROL

To control cell division, all growth regulatory pathways feed back to the cell cycle in one way or another, turning it into a central convergence point (Figure 7). Cell division is marked by the separation of a cell into two daughter cells, co-occurring with the distribution of the duplicated DNA over both cells. The cell cycle consists of four major phases: genetic material is synthetized or duplicated during the S-phase whereas mitosis, the division of chromosomes over the two emerging daughter cells, takes place during the M-phase. Alternatively, DNA duplication without mitosis may occur, referred to as endoreduplication and resulting in the formation of polyploid cells (Inzé and De Veylder, 2006). S-phase and M-phase are separated by two gap phases, G_1 and G_2, which act as checkpoints to prepare a cell for the next step in the cell cycle (Figure7).

During the cell cycle, complexes of CYCs and CDKs regulate the progression through the different cell cycle phases (Inzé and De Veylder, 2006). Functional specificity is dependent on the constitution of these complexes, incorporating different types of CYCs (CYCAs, CYCBs and CYCDs) and A- and B-type

CDK proteins (CDKAs and CDKBs) (Vandepoele *et al.*, 2002). *cdka1;1* mutants are embryo lethal or may develop into severely dwarfed plants if they complete embryogenesis (Nowack *et al.*, 2012). CYC–CDK complexes are regulated both at the transcriptional and post-translational level. Three E2F proteins form complexes with DIMERISATION PROTEINs (DPs) to control the expression of genes crucial for G_1-to-S transition and S-phase progression. Depending on their composition, these complexes act as transcriptional activators (E2Fa/DP and E2Fb/DP) or repressors (E2Fc/DP) and are inhibited by RETINOBLASTOMA-RELATED (RBR) proteins (Magyar *et al.*, 2000; Kosugi and Ohashi, 2002; Desvoyes *et al.*, 2006; Yao *et al.*, 2018). RBR proteins in turn are phosphorylated by CYCD–CDKA;1 complexes and subsequently degraded to promote G_1-to-S transition (Huntley *et al.*, 1998; Nakagami *et al.*, 1999; del Pozo *et al.*, 2006; Boruc *et al.*, 2010). Loss-of-function alleles of *E2Fb* result in a slightly larger first true leaf pair due to increased leaf cell number (Őszi *et al.*, 2020), whereas ectopic expression of *E2Fa* leads to enlarged cotyledons, also because of enhanced cell proliferation (De Veylder *et al.*, 2002). However, co-overexpression of *E2Fa* with its partner *DP* results in severely dwarfed seedlings due to an even more increased cell division and reduced cell differentiation (De Veylder *et al.*, 2002), suggesting that the level of perturbance and following compensation define the difference between positive and negative growth effects. Plants deficient in E2Fc display a lowered sensitivity to UV-B-mediated leaf growth inhibition because E2Fc acts as a GIF1 modrepressor of cell division after DNA damage, suggesting that E2Fc acts as a negative regulator of leaf growth under certain stress conditions (Gómez *et al.*, 2019).

KIP-RELATED PROTEIN/INTERACTOR OF CDKs (KRP/ICK), SIAMESE (SIM) and SIM RELATED (SMR) proteins interact with CYC–CDK complexes to inhibit their function (Walker *et al.*, 2000; Churchman *et al.*, 2006; Van Leene *et al.*, 2010). Higher-order *KRP* mutants, such as the triple *krp4 krp6 krp7* mutant, display enlarged, elongated and downward-curling leaves due to enhanced cell proliferation (Cheng *et al.*, 2013). Accordingly, *KRP* overexpression results in smaller leaves due to a decreased cell number, somewhat compensated by an increase in cell expansion (De Veylder *et al.*, 2001; De Veylder *et al.*, 2011). *SIM*-overexpressing plants also display a reduced leaf size, whereas *sim and smr* mutants have clustered and multi-cellular trichomes but do not show obvious changes in leaf area (Walker *et al.*, 2000; Churchman *et al.*, 2006; Kumar *et al.*, 2015). However, in the first leaves of Arabidopsis *smr1/smr2/smr13* triple mutants, the size of palisade cells is decreased, suggesting functional redundancy resulting in an altered cell size in higher-order mutants (Yamada *et al.*, 2022).

CYC–CDK complexes are also subject to proteasomal degradation mediated by SKP 1/CULLIN 1/F-BOX PROTEIN (SCF) and the anaphase-promoting complex/cyclosome (APC/C) (Van Leene *et al.*, 2010; Heyman and De Veylder, 2012). Loss-of-function or ectopic expression of APC/C components results in bigger and smaller leaf areas, respectively (Willemsen *et al.*, 1998; Marrocco *et al.*, 2009; Eloy *et al.*, 2011; Heyman and De Veylder, 2012). Whereas strong overexpression of the APC/C activators *CELL CYCLE SWITCH PROTEIN 52A/B* (*CCS52A/B*) and *CELL DIVISION CYCLE 20* (*CDC20*) leads to a reduced leaf size due to the formation of fewer cells, mild overexpressing lines produce bigger leaves due to an increased cell division (Fülöp *et al.*, 2005; Eloy *et al.*, 2011; Kevei *et al.*, 2011; Breuer *et al.*, 2012; Baloban *et al.*, 2013). Mitotic cyclins like CYCA2 proteins are also targeted by SAMBA for degradation via the APC/C (Eloy *et al.*, 2012). Conversely, *samba* plants display enlarged leaves, but also an enlarged SAM and leaf primordia (Eloy *et al.*, 2012). In this case, increased leaf size results at least partially from an increase in the number of initial founder cells. Accordingly, loss of CYCA2s results in mild to strong decreases in organ size accompanied by a reduction in cell number and an increase in cell size and endoreduplication (Vanneste *et al.*, 2011).

Additionally, the ectopic expression of several F-box proteins degrading cell cycle regulators alters leaf size. For example, F-BOX-LIKE 17 (FBL17) can interact and likely degrade KRPs, such as KRP2 and KRP7, and *fbl17* mutants show a decreased cell number and thus reduced leaf size (Gusti *et al.*, 2009; Noir *et*

al., 2015). In contrast, reduced levels of F-BOX PROTEIN 92 (FBX92) result in the formation of bigger leaves due to an enhanced cell proliferation, although interestingly both positive and negative cell cycle components are upregulated upon downregulation of *FBX92* (Baute *et al.*, 2017). In summary, the cell cycle is subject to a panoply of regulatory mechanisms that communicate with the various pathways orchestrating growth.

CELL EXPANSION MODULE

In addition to cell division, cell expansion greatly contributes to final leaf size. The transition from cell proliferation to cell expansion is thought to be mediated in part by decreased CK signaling. Expression of *ARABIDOPSIS RESPONSE REGULATOR 6* (*ARR16*) is promoted by a TCP4–BRM complex and likely plays a role in this transition (Efroni *et al.*, 2013). Additionally, TCP4 can activate *miR396b* to negatively regulate GRF-mediated promotion of cell proliferation (Schommer *et al.*, 2014). In turn, TCP4 is controlled by *miR319* and ectopic expression of *TCP4* or of *miR319*-resistant TCP4 results in smaller leaves (Palatnik *et al.*, 2003; Schommer *et al.*, 2014). A main regulator of cell expansion is auxin, which induces the acidification of the apoplast by importing H^+-ions via ATPases (Cosgrove, 2000, 2005). Acidification of the apoplast activates cell wall-associated EXPANSIN proteins (EXPs), which subsequently loosen the cell wall (Cosgrove, 2000, 2005). For example, overexpression of *EXP10* results in the formation of enlarged leaves and elongated petioles containing larger cells, whereas downregulation of *EXP10* results in smaller organs containing smaller cells (Cosgrove, 2015). Besides EXP proteins, also other cell wall-modifying enzymes, such as XYLOGLUCAN ENDOTRANSGLUCOSEYLASE/HYDROLASEs (XTHs) and PECTIN METHYLESTERASEs (PMEs), and reactive oxygen species are implicated in cell expansion (Cosgrove, 2015). The *UBP14* mutant allele *elongated hypocotyl under high-temperature* (*ehl*) displays an increase in organ size due to an increased cell area, unlike the previously described *UBP14* allele *da3*, which affects both cell proliferation and expansion (Xu *et al.*, 2016b; David *et al.*, 2021). *ehl* plants also show higher auxin levels and an altered plastochron, linking cell expansion with auxin signaling and suggesting that at least in the case of UBP14, regulatory functions in cell division and expansion can be separated (David *et al.*, 2021).

A second group of genes involved in regulating cell expansion are the *SMALL AUXIN UP RNA* (*SAUR*) genes. SAUR proteins are thought to promote apoplast acidification by inhibiting 2C PROTEIN PHOSPHATASE proteins (PP2Cs), which are negative regulators of ATPase activity (Spartz *et al.*, 2014). However, different *SAUR* genes result in different phenotypes when misexpressed. For example, overexpression of *SAUR53* or stabilization of *SAUR19* results in the production of longer and bigger cells, respectively, and accordingly enlarged organs (Spartz *et al.*, 2012; Spartz *et al.*, 2014; Kathare *et al.*, 2018). On the other hand, *saur36* displays larger cells and leaves, suggesting SAUR36 to be a negative regulator of cell expansion (Hou *et al.*, 2013). Expression of the *Vitis vinifera* (grape) gene *VvSAUR41* in Arabidopsis also promotes cell expansion, suggesting that *SAUR* gene function is likely at least partially conserved across species (Li *et al.*, 2021).

Additionally, several other genes control cell expansion in leaves, although the interconnections with other modules are often still largely unknown. Overexpression and downregulation of *CYP78A6/EOD3*, a close relative of *KLU*, result in increased and decreased organ sizes due to larger and smaller cells, respectively (Fang *et al.*, 2012). KUODA 1 (KUA1) is a MYB-like TF involved in cell wall relaxation, and thus promoting cell growth (Lu *et al.*, 2014). HOMEOBOX PROTEIN 12 (HB12) and HB33 are also positive regulators of leaf growth by increasing cell expansion rates (Hong *et al.*, 2011; Hur *et al.*, 2015; Ferela *et al.*, 2023). HB12 promotes the expression of *EXPA*, which is also linked with increases in cell area (Hur *et al.*, 2015). In turn, TCP13 represses *HB12* and *TCP13* overexpression or downregulation of *TCP13*, *TCP5* and *TCP17* results in the production of smaller and bigger leaves, respectively, due to alterations in cell area (Hur *et al.*, 2019). Although it was initially described that enlarged leaves in

GRF1- and *GRF2*-overexpressor lines mainly result from an increased cell expansion (Kim *et al.*, 2003), this is likely not the case (Kim and Kende, 2004; Kim and Lee, 2006; Lee *et al.*, 2022).

THE GROWTH REGULATORY PATHWAYS ARE HIGHLY INTERCONNECTED

To ensure tight regulation of leaf growth, the different growth-modulating pathways need to work in concert with each other, as well as with the cell cycle and cell expansion modules and other growth-regulating factors, such as plant hormones and environmental stimuli. This is most apparent in the case of the SWI/SNF module, which regulates the expression of thousands of genes across the Arabidopsis genome (Shu *et al.*, 2021; Yang *et al.*, 2022). For example, *brm-1* plants show changed levels of several GA biosynthesis and signaling genes, including a decreased expression of the GA oxidases *GA3ox1, GA3ox2* and *GA2ox1* and an increased expression of *GA20ox1*, *GA20ox2*, *GID1a* and *GID1b* (Archacki *et al.*, 2013). The SWI/SNF subunit SWI3B also interacts with ERECTA (ER), ERECTA-LIKE 1 (ERL1) and ERL2, and the *er erl1 erl2* triple mutant is severely dwarfed with small leaves, whereas single and double mutants display milder effects (Sarnowska *et al.*, 2023). ER, ERL1 and ERL2 are involved in the transcriptional regulation of genes involved in GA biosynthesis (Sarnowska *et al.*, 2023). Moreover, SWI/SNF and GA/DELLA pathways are interconnected at the protein level, because the DELLA proteins RGA and RGL1 interact with the SWI/SNF subunit SWI3B, and RGL2 and RGL3 can interact with SWI3C (Sarnowska *et al.*, 2013; Sarnowska *et al.*, 2023). Additionally, SWI3C interacts with SPY, a known regulator of DELLA activity (Sarnowska *et al.*, 2013). Furthermore, SPY interacts with the DA1 targets TCP14 and TCP15, also shown to be transcriptionally repressed by DELLA proteins (Steiner *et al.*, 2012; Davière *et al.*, 2014; Resentini *et al.*, 2015). During seed development, DA1 also seems to act downstream of ER, although it remains elusive whether this is also the case in leaves (Wu *et al.*, 2022). And BRM-containing SWI/SNF complexes might act antagonistically to the PPD proteins, because the PPD2 interactor LHP1 is a Polycomb subunit and some overlap between LHP1 and BRAHMA target genes exists (Bezhani *et al.*, 2007).

SWI/SNF complexes do not directly bind DNA, but associate with TFs to bind with their target loci. For example, during leaf growth, GIF1 interacts with several SWI/SNF subunits, including BRM, SYD, and SWP73B, and can recruit the SWI/SNF complex to target loci of its GRF-binding partners (Vercruyssen *et al.*, 2014). Also in maize, many SWI/SNF subunits were identified as putative interactors of ZmGIF1, suggesting that the SWI/SNF–GIF1 connection is conserved across species (Nelissen *et al.*, 2015). *OsGRF1* expression is increased by GA signaling (van der Knaap *et al.*, 2000) and in Arabidopsis, *GRF5* and also *KLU* might be situated downstream of DELLA proteins, because their expression levels decrease upon expression of an inducible dominant version of *GAI* (Claeys *et al.*, 2014).

The PPD and GIF–GRF pathways are likely to intersect, because *AtGIF1* expression is repressed by the PPD complex during seed development (Liu *et al.*, 2020b). The increased expression of *GIF1* orthologs in young soybean and Medicago leaves of *ppd* mutants suggests that similar mechanisms could be present in Arabidopsis, possibly linking the PPD and GIF1–GRF pathways during leaf development (Ge *et al.*, 2016). Similarly, studies on legumes, such as garden pea, soy bean and chick pea, suggest that in leaves the expression of *GRFs* is also regulated by the PPD pathway (Ge *et al.*, 2016; Li *et al.*, 2019; Barmukh *et al.*, 2022). Furthermore, both the KLU and PPD pathway may also be interlinked with the DA1 pathway, because both contain proteins that were initially identified as SUPRESSOR of DA1 (SOD), namely NGAL2 and SAP, respectively (Zhang *et al.*, 2015; Ge *et al.*, 2016). Alternatively, the different pathways might be able to compensate for each other to achieve a certain, optimal leaf size. The different cell proliferation-regulating pathways are not only highly interconnected with each other but also all converge at the cell cycle. Both the DA1 and the PPD pathways regulate the expression of *CYC* genes (Gonzalez *et al.*, 2015; Peng *et al.*, 2015; Baekelandt *et al.*, 2018). Whereas degradation of TCP14/15/22 via the DA1 pathway results in an increased expression of *CYCA3;2* and *RBR* (Peng *et al.*,

2015), the PPD complex negatively affects the expression of *CYCD3;2* and *CYCD3;3* (Gonzalez *et al.*, 2015; Baekelandt *et al.*, 2018). Strong ectopic expression of *CYCD3;2* leads to plants with a propeller-shaped rosette and more narrow, dome-shaped leaves, whereas strong ectopic expression of *CYCD3;3* results in overall dwarfed plants as a result of excessive cell proliferation (Baekelandt *et al.*, 2018). Plants with reduced *RBR* expression levels are also somewhat reminiscent of *ppd* mutants, because they display a propeller-like phenotype (Dorca-Fornell *et al.*, 2013). GRFs also control the gene expression of many cell cycle proteins, because, for example, *CYCB1;1* and the MYB3R-encoding gene *KNOLLE* (*KN*) are among their targets (Lauber *et al.*, 1997; Touihri *et al.*, 2011; Debernardi *et al.*, 2014; Vercruyssen *et al.*, 2014). KLU also affects cell proliferation but the exact mechanism remains to be discovered. What is known, is that KLU acts cell-non-autonomously by generating a mobile growth factor distinct from the classical plant hormones (Anastasiou *et al.*, 2007). DELLA proteins promote KRP and SMR activity by acting as transcriptional regulators and inducing the expression of several cell cycle inhibitors, including *KRP2*, *SIM*, *SMR1* and *SMR2* (Achard *et al.*, 2009). Additionally, KRP5 might recruit SWI/SNF complexes to modulate target gene expression, because it can interact with SWP73B (Van Leene *et al.*, 2010; Jégu *et al.*, 2013), showing that all discussed growth regulatory pathways are involved in cell cycle control (Figure 7).

The links of the presented growth regulatory modules with cell expansion are less explored, but probably just as important. For example, high GRF activity correlates with an increased expression of several Zinc-Finger Homeodomain (ZF-HD) family members, and GRF3 activates the expression of *HB33* (Ferela *et al.*, 2023). A moderate increase in *HB33* expression results in enlarged leaves due to an enhanced cell size and number, whereas strong overexpression lines display smaller leaves with a reduced cell size (Ferela *et al.*, 2023). The related protein HB12 not only promotes the expression of *EXPA10* genes but also APC/C components, linking it with the cell cycle and endoreduplication (Hur *et al.*, 2015). GRF-mediated regulation of cell expansion is likely conserved across species, as overexpression of poplar *PpnGRF5-1* leads to increased transcript levels of several *EXP* genes, suggesting that cell expansion is also affected (Wu *et al.*, 2021b). Cell proliferation needs to be in tune with cell expansion to reach the optimal final leaf size, and compensatory mechanisms can often be observed when cell division is impaired (Horiguchi and Tsukaya, 2011). For example, the decrease in cell division in *gif1* and triple *cycd3* mutants is partially compensated by an increase in cell expansion, partially counterbalancing the reduction in leaf size (Horiguchi *et al.*, 2005; Dewitte *et al.*, 2007). Conversely, enhanced cell division under ectopic expression of, for instance, *E2Fa*, is counteracted by a reduction in cell expansion, resulting in an overall only moderate leaf size increase (De Veylder *et al.*, 2002). An extreme case is the *er* allele, which displays an almost halved epidermal cell area phenotype, which is largely compensated by an almost doubled cell number, not showing any significant difference in final leaf size (Tisné *et al.*, 2011). However, studying compensation in determinate organs such as leaves or petals is complicated as it is achievable via different means or a combination thereof rather than a singular mechanism (Ferjani *et al.*, 2007; Randall *et al.*, 2015b; Tabeta *et al.*, 2022). These mechanisms include, for example, an altered cell expansion rate or cell expansion duration and can be regulated in cell-autonomous and cell-non-autonomous manners (Ferjani *et al.*, 2007; Kawade *et al.*, 2010). However, to understand why some mutant phenotypes are compensated whereas others are not, more knowledge of when which compensatory mechanisms come into effect and how an ideal target leaf size is determined, is required.

Plant hormones are crucial players in orchestrating plant development and impinge on all discussed growth regulatory pathways covered by this review. Although plant hormones act on a panoply of developmental processes and may affect them in different ways depending on the specific biological context, they can generally be classified into growth-promoting and growth-inhibiting hormones with auxin, CKs, GAs, BRs and strigolactones as rather positive and jasmonates, salicylic acid, ethylene and

abscisic acid as rather negative regulators of leaf growth (Perrot-Rechenmann, 2010; Zhiponova *et al.*, 2013; Huang *et al.*, 2017; Waters *et al.*, 2017; Dubois *et al.*, 2018b; Chen *et al.*, 2020; Wu *et al.*, 2021a; Li *et al.*, 2022; Ritonga *et al.*, 2023). As giving a complete overview of their interplay lies outside the scope of this review, only selected examples highlighting the dense interconnectedness will be given. For example, BRs regulate the expression of GA biosynthetic genes, such as *GA20ox1*, via the transcriptional regulator BES1 (Unterholzner *et al.*, 2015). A BES1 homolog in tomato, SlBES1.8, also regulates leaf development in a GA-dependent manner (Su *et al.*, 2022). Additionally, DELLA proteins also interact with the BR pathway by interacting with the TF BRASSINAZOLE RESISTANT 1 (BZR1), and BZR1 abundance is regulated by DELLA activity (Li *et al.*, 2012). Furthermore, BZR1 and RGA antagonize each other by attenuating their mutual transcriptional activity (Li *et al.*, 2012). Moreover, the BR receptor kinase pair BRASSINOSTEROID INSENSITIVE 1 (BRI1) and BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) can phosphorylate DA1, reducing its peptidase activity and thus stabilizing DA1 targets, placing DA1 also downstream of BR signaling (Dong *et al.*, 2020). Strong *BRI1* loss-of-function alleles result in generally dwarfed plants with reduced organ sizes (Noguchi *et al.*, 1999). Additionally, BRI1 abundance itself is modulated by UBP12 and UBP13, and UBP13 can directly interact with and deubiquitinate BRI1, leading to its stabilization (Luo *et al.*, 2022). This marks a second, indirect way of how UBP12 and UBP13 may affect DA1 functionality.

Plant hormones also connect cell proliferation and cell expansion. Ethylene is a negative regulator of both processes (Dubois *et al.*, 2018b). Plants with enhanced ethylene production or signaling display dwarfed phenotypes, including smaller leaves (Dubois *et al.*, 2018b). The expression of *ORGAN SIZE-RELATED* (*OSR*) family members is induced by ethylene signaling and these proteins in turn negatively regulate ethylene sensitivity (Rai *et al.*, 2015; Shi *et al.*, 2015). Members of the OSR family also control leaf size, although via different mechanisms. AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE (ARGOS), founding member of the OSR family, positively regulates leaf growth by promoting *AINTEGUMENTA* (*ANT*) and *CYCD3;1* expression, thus prolonging the cell division phase (Hu *et al.*, 2003). In contrast, OSR2 and ARGOS-LIKE (ARL) likely mainly act through promoting cell expansion, and overexpression lines result in an increased plant size (Hu *et al.*, 2006; Qin *et al.*, 2014b). Finally, OSR1 impinges on both processes (Feng *et al.*, 2011). Whereas the exact underlying molecular mechanism is still unclear, it is likely conserved across species, because overexpression of either *ZmARGOS1* or *ZmARGOS8* leads to a reduced ethylene sensitivity in both Arabidopsis and maize plants (Shi *et al.*, 2015). Ethylene has been proposed to promote cell cycle exit and cell differentiation via several mechanisms (reviewed in Dubois *et al.* (2018b)), which function via inhibition of positive cell cycle regulators, such as CYCLINs (Street *et al.*, 2015), or by promoting the expression or stabilization of negative regulators, such as *KRP1* (Street *et al.*, 2015), type II *TCPs* (Marsch-Martinez *et al.*, 2006), *SMR1* (Dubois *et al.*, 2018a) and *DELLAs* (Dubois *et al.*, 2013). Similarly, leaf cell expansion is mainly negatively regulated by ethylene, likely also via DELLA proteins (reviewed in Dubois *et al.* (2018b)), as well as via the regulation of *EXP* gene expression (Marsch-Martinez *et al.*, 2006; Feng *et al.*, 2015).

Similarly, CKs link cell division and cell expansion by regulating components of both modules (Wu *et al.*, 2021a). CKs promote leaf growth by positively regulating the expression of several cell cycle genes, including previously discussed *CYCD3s* (Dewitte *et al.*, 2007) and *CDKs* (Zhang *et al.*, 2005). Additionally, CKs also promote the expression of *ANT*, at least in roots (Randall *et al.*, 2015a). Cell division is ANT-dependent and *ANT*-overexpressing plants display enhanced growth, whereas *ant* plants are reduced in size (Mizukami and Fischer, 2000). Furthermore, ANT signaling has been implicated to converge at a common target with GIF1 signaling, resulting in two parallel upstream regulatory pathways of cell proliferation (Jun *et al.*, 2019). Downstream of CKs are also the CK-promoted ARABIDOPSIS RESPONSE REGULATORS (ARRs), further divided into type A and type B ARRs, exhibiting negative and positive effects on CK signaling, respectively (To *et al.*, 2004; Mason *et al.*, 2005; Argyros *et al.*, 2008). ARR2

activates *CCS52A1*, whereas reduced *CCS52A1* expression is observed when CK receptors are mutated (Lammens *et al.*, 2008; Takahashi *et al.*, 2013). CCS52A1 promotes endocycle entry and *ccs52a1* loss-of-function mutants display reduced endoreduplication levels and a reduced cell expansion (Lammens *et al.*, 2008; Larson-Rabin *et al.*, 2009). Cell size is also affected by CYTOKININ-RESPONSIVE GROWTH REGULATOR (CKG) in an endoreduplication-independent manner and loss-of-function *ckg* mutants display smaller cotyledons, whereas increased expression levels result in bigger cotyledons (Park *et al.*, 2021). Additionally, CKs have been shown to affect cell wall-loosening processes during cell expansion by regulating *EXP* gene expression (Pacifici *et al.*, 2018; Samalova *et al.*, 2020) and by promoting the accumulation of soluble carbohydrates (Skalák *et al.*, 2019), which in turn leads to changed turgor pressure within the cell and facilitates cell wall loosening (Cosgrove, 2016).

Leaf growth also always needs to take place in coordination with external factors. Among others, light signaling impinges on virtually all growth regulatory pathways via PHYTOCHROME INTERACTING FACTOR (PIF) and CRY proteins. For example, PIF4 is likely to regulate the expression of *PPD1* and *PPD2*, which in turn repress the expression of *SUPPRESSOR OF phyA-105* (*SPA1*) (White, 2022). Whereas loss of function of SPA1 does not or only moderately alter leaf size, it significantly enhances the dwarfed *spa3 spa4* double mutant phenotype, demonstrating its importance for leaf growth (Fittinghoff *et al.*, 2006). SPA1 acts together with COP1 to degrade HY5 (Saijo *et al.*, 2003), possibly linking the PPD and DELLA modules this way. Besides light, PIF4 also plays a pivotal role in repressing cell division in response to elevated temperatures by promoting *KRP1* expression in a TCP4-dependent manner (Saini *et al.*, 2022). Moreover, light exposure results in a decreased expression of *BRM* in young seedlings and BRM interacts with PIF1 to counteract its function (Zhang *et al.*, 2017), whereas SWP73B antagonizes PIF4 to repress seedling growth during photomorphogenesis (Jégu *et al.*, 2017). DELLA proteins can mediate the degradation of several PIF proteins to coordinate GA and light signaling during hypocotyl elongation, although this might be a more general mechanism during plant growth (Li *et al.*, 2016b). PIF7 can supersede GIF1 at its target loci and may also affect the expression of several *GRF* genes and *GIF1* itself under end of day far red (EODFR) light (Hussain *et al.*, 2022). Accordingly, the *pif7-1* mutant allele displays enhanced epidermal cell numbers but not an overall increased leaf 3 blade area under EODFR light conditions compared to the wild type (Hussain *et al.*, 2022). Additionally, EODFR light promotes the expression of *NGAL2* and the *DA1* paralogs *DAR5* and *DAR7* (Romanowski *et al.*, 2021). In *Marchantia polymorpha*, MpDELLA can interact with MpPIF, suggesting an evolutionarily conserved role of this complex in response to stress conditions (Hernández-García *et al.*, 2021). Blue light is also involved in growth regulation, as interactions between DELLA proteins and GID1 with CRY1 modulate not only photomorphogenesis but also inhibit GA signaling, because CRY1 protects DELLAs from GID1- and SLY1-mediated degradation (Yan *et al.*, 2021). The same mechanism has been described in wheat, in which TaCRY1a interacts with TaGID1 and Reduced Height-1 (TaRht/TaDELLA) and competitively inhibits the TaGID1–TaRht interaction (Yan *et al.*, 2021). CRY2 is a target of UBP12 and UBP13 for ubiquitination and subsequent degradation, possibly linking also the DA1 pathway with blue light signaling (Lindbäck *et al.*, 2022).

Overall, these few examples illustrate that growth-regulating pathways do not function on their own but are embedded in a highly complex system. Although vital for ultimately understanding and validating gene function, the studies of single genes or mutant phenotypes provide puzzle pieces rather than a global perspective on comprehending the larger picture of leaf development. To capture system-wide dynamics and gain a more complete understanding of these regulatory networks, the need for multi-omics approaches is rising (Skirycz and Fernie, 2022; Depuydt *et al.*, 2023). For example, to identify putative novel regulators of Arabidopsis leaf development, untargeted metabolomics and proteomics have been applied, showing that the both proteome and metabolome undergo big changes when transitioning from the cell division to the cell expansion phase (Omidbakhshfard *et al.*, 2021). A

combination of transcriptomics and metabolomics was used to shed new light on the underlying mechanisms of KLU activity, showcasing roles in leaf longevity and drought tolerance as well as interactions with the CK signaling cascade (Jiang *et al.*, 2021). This development goes hand in hand with advancing computational approaches which allow to analyze these datasets as they grow in size and complexity. Methods such as MINI-EX (Motif-Informed Network Inference based on single-cell EXpression data) and MINI-AC (Motif-Informed Network Inference based on Accessible Chromatin) allow to construct gene regulatory networks and predict regulatory relationships between TFs and target genes in several plant species from single cell transcriptomics and Assay for Transposase-Accessible Chromatin using sequencing (ATACseq) data, respectively, coupled to TF binding motif information (Ferrari *et al.*, 2022; Manosalva Pérez *et al.*, 2023). And the use of cross-species approaches such as comparative transcriptomics and cross-species networks can aid in answering evolutionary questions, such as the identification of differential *BOP* ortholog regulation in tomato and related *Solanum* species as a contributor to their distinct leaf complexity phenotypes (Ichihashi *et al.*, 2014) or the prediction of evolutionarily conserved putative novel growth regulators (Curci *et al.*, 2022).

CONCLUDING REMARKS

Growth regulatory pathways form an intricate and complex network. Although some growth regulatory mechanisms underlying leaf size and shape determination are conserved across species, some clear differences are also observed both on the molecular and phenotypic level (Nelissen *et al.*, 2016). Transferring knowledge from model species to crops has been a challenge, because conserved genes may take up novel functions, additional molecular players enter regulatory networks, or certain genes have been duplicated or lost in certain plant lineages. To successfully modify crops to tackle future societal and environmental challenges, it will thus be necessary to model and anticipate network effects rather than single mutant phenotypes. Since evolutionarily conserved gene networks are more likely to be functionally conserved than individual genes (Curci *et al.*, 2022), the functional characterization of genes combined with network analysis-based approaches could form the foundation for a more successful transfer of knowledge from one species to another. Traditional mutant studies, exploitation of genetic diversity of different plant ecotypes and cultivars as well as examination of the discussed regulatory modules in phenotypically distinct non-model species can be applied to detangle regulatory relationships and determine levels of pathway plasticity. Multiple target genome editing approaches like the maize gene discovery pipeline BREEDIT (Lorenzo *et al.*, 2023) can be employed to create multi-order mutants and simultaneously study several growth-related genes, whereas novel techniques such as single-cell sequencing (Liu *et al.*, 2021; Lopez-Anido *et al.*, 2021; Wang *et al.*, 2021c; Tenorio Berrío *et al.*, 2022) and spatial transcriptomics (Laureyns *et al.*, 2022) allow to study gene expression of many genes within a leaf simultaneously and at an unprecedented cellular resolution in a variety of species. However, focusing solely on genetics and transcriptomics might be shortsighted as the need for multi-omics approaches to obtain a broader understanding of biological processes becomes apparent (Skirycz and Fernie, 2022; Depuydt *et al.*, 2023). Although considerable progress on comprehending organ size determination in plants has been made, our understanding is far from complete. A combination of aforementioned strategies will further increase our knowledge and fill the gaps in our current understanding of the intricate regulation of leaf size control.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest associated with this work.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Methods. Evolutionary conservation analysis and ortholog identification.

Orthologous evolutionary relationships were retrieved in an automatic and pair-wise manner (between *Arabidopsis thaliana* and the target species) from various instances within the PLAZA platform: Dicots 5.0 (*Amborella trichopoda*, *Anthoceros agrestis*, *Arabidopsis thaliana*, *Glycine max*, *Marchantia polymorpha*, *Physcomitrium patens*, *Populus trichocarpa*, *Selaginella moellendorffii, Solanum lycopersicum*), Monocots 5.0 (*Musa acuminata*, *Oryza sativa*, *Zea mays*), Dicots 4.5 (*Picea abies*), and Basal 1.0 (*Ceratopteris richardii*). Orthologous relationships were determined using the PLAZA Integrative Orthology toolkit, limited to the TROG (Tree-Based Orthologous Groups), BHIF (Best-Hit and Inparalogs Families), and ORTHO (OrthoClusters) methods. A minimum of two supporting methods was required for the positive identification of an orthologous relationship. All orthologous data was subsequently mapped to the custom phylogenetic tree containing the species used in the evolutionary study. Due to the presence of multiple many-to-many orthologous relationships within families, a separate count of unique genes per species per family was also determined, in order to remove the overestimation of the total number of orthologs per family. A manual pass was performed to try and resolve the many-to-many orthologous relationships, the results of which were used in the final computational delineation of the orthologous relationships.
The orthology counts were used in automatically generated PhyloXML files, which were used in conjunction with a customized version of PhyD3 (Kreft *et al.*, 2017) to generate the basis of the SVG figures used in the publication.

Figure S1. Evolutionary conservation of all putative SWI/SNF subunits.

Table S1. Gene identifiers of input genes and identified orthologs of evolutionary analysis.

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Figures

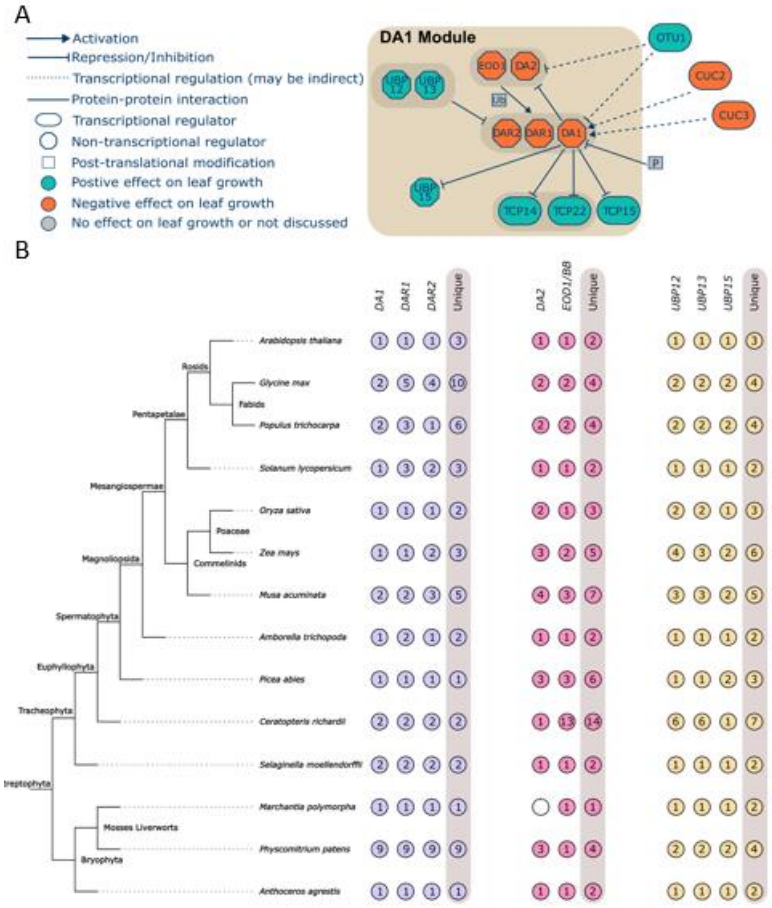

Figure 1. Genetic network and evolutionary conservation of the DA1 pathway

(A) Overview of the core members of the DA1 growth regulatory pathway. Transcriptional regulators are displayed in ovals, other proteins as octagons. Colors denote their described effect on leaf growth: teal – positive; orange – negative. Relationships among proteins are represented by lines and arrows. An arrow indicates activation, a T-shaped junction inhibition/repression of the target. A solid line indicates interaction between two proteins, a dashed line (indirect) transcriptional regulation.

(B) Evolutionary conservation of selected genes of the DA1 module. Number of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Different colors represent different gene families. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. "Unique" presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: BB (BIG BROTHER); CUC (CUP-SHAPED COTYLEDON); DAR (DA1-RELATED); EOD1 (ENHANCER OF DA1); OTU1 (OTUBAIN-LIKE CYSTEINE PROTEASE 1); P (Phosphorylation) TCP (TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL NUCLEAR ANTIGEN FACTOR); Ub (Ubiquitination); UBP (UBIQUITIN SPECIFIC PROTEASE)

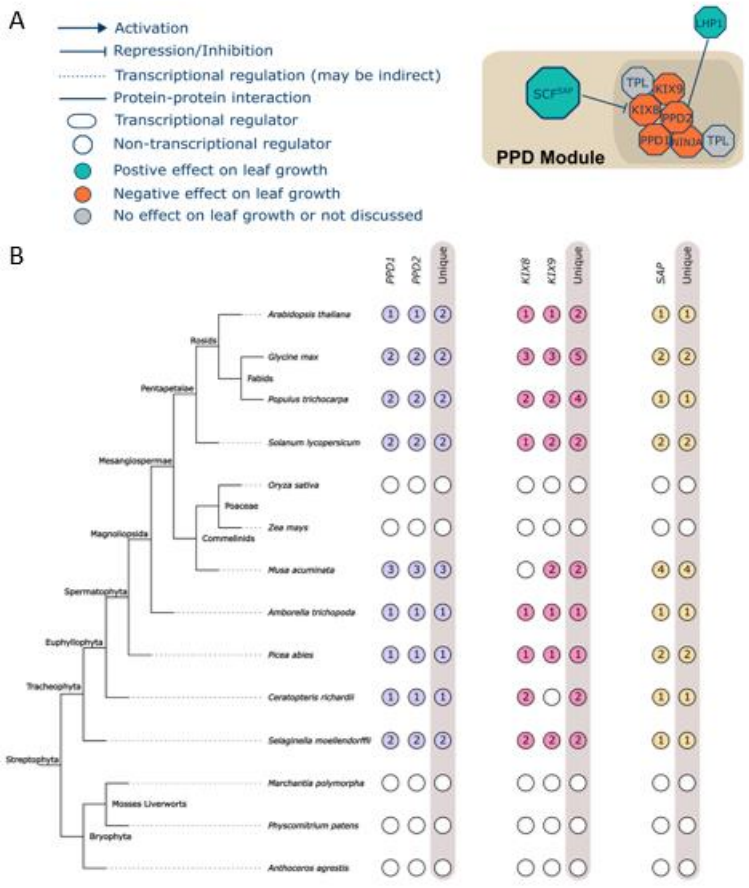

Figure 2. Genetic network and evolutionary conservation of the PEAPOD pathway

(A) Overview of the core members of the PEAPOD growth regulatory pathway. Transcriptional regulators are displayed in ovals, other proteins as octagons. Colors denote their described effect on leaf growth: teal – positive; orange – negative; grey – neutral, not described or not discussed. Relationships among proteins are represented by lines and arrows. A T-shaped junction indicates inhibition/repression of the target. A solid line indicates interaction between two proteins.

(B) Evolutionary conservation of selected genes of the PEAPOD module. Number of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Different colors represent different gene families. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. "Unique" presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: KIX (KINASE-INDUCIBLE DOMAIN INTERACTING); LHP1 (LIKE HETEROCHROMATIN PROTEIN 1); NINJA (NOVEL INTERACTOR OF JAZ); PPD (PEAPOD); SAP (STERILE APETALA); SCF (SKP 1/CULLIN 1/F-BOX PROTEIN); TPL (TOPLESS)

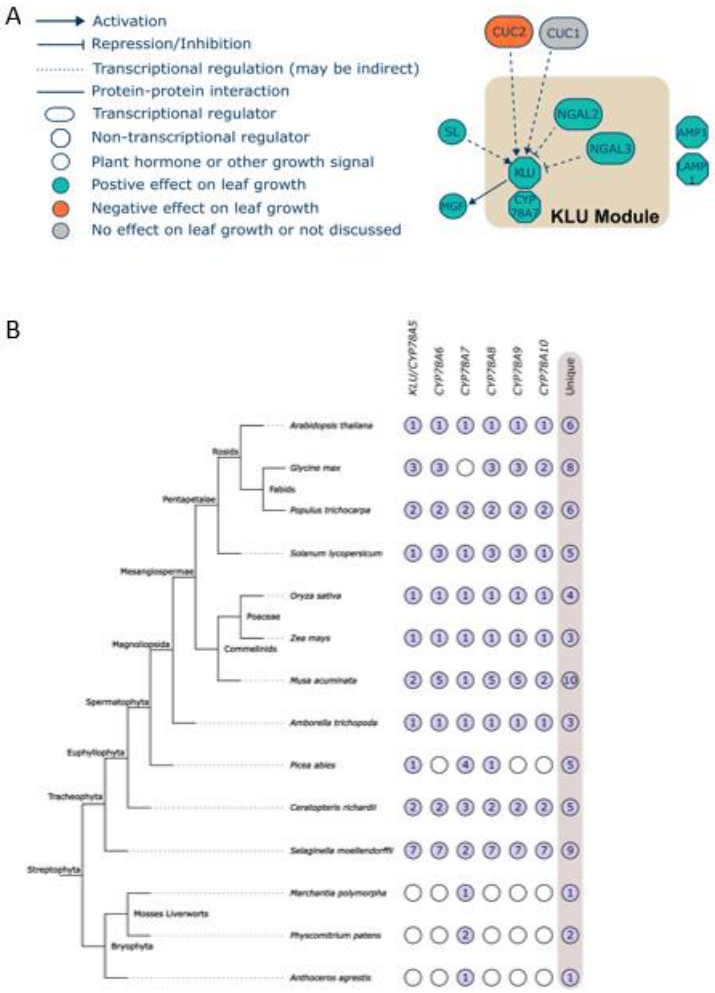

Figure 3. Genetic network and evolutionary conservation of the KLU pathway

(A) Overview of the core members of the KLU growth regulatory pathway. Transcriptional regulators are displayed in ovals, other proteins as octagons. Small circles depict plant hormones or other unidentified plant growth regulators. denote their described effect on leaf growth: teal – positive; orange – negative; grey – neutral, not described or not discussed. Relationships among proteins are represented by lines and arrows. An arrow indicates activation, a T-shaped junction inhibition/repression of the target. A solid line indicates interaction between two proteins, a dashed line (indirect) transcriptional regulation.

(B) Evolutionary conservation of selected genes of the KLU module. Number of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. “Unique” presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: AMP1 (ALTERED MERISTEM PROGRAM 1); CUC (CUP-SHAPED COTYLEDON); CYP78A (CYTOCHROME P450, FAMILY 78, SUBFAMILY A); LAMP1 (LIKE AMP1); MGF (mobile growth factor); NGAL (NGATHA-LIKE PROTEIN); SL (strigolactones)

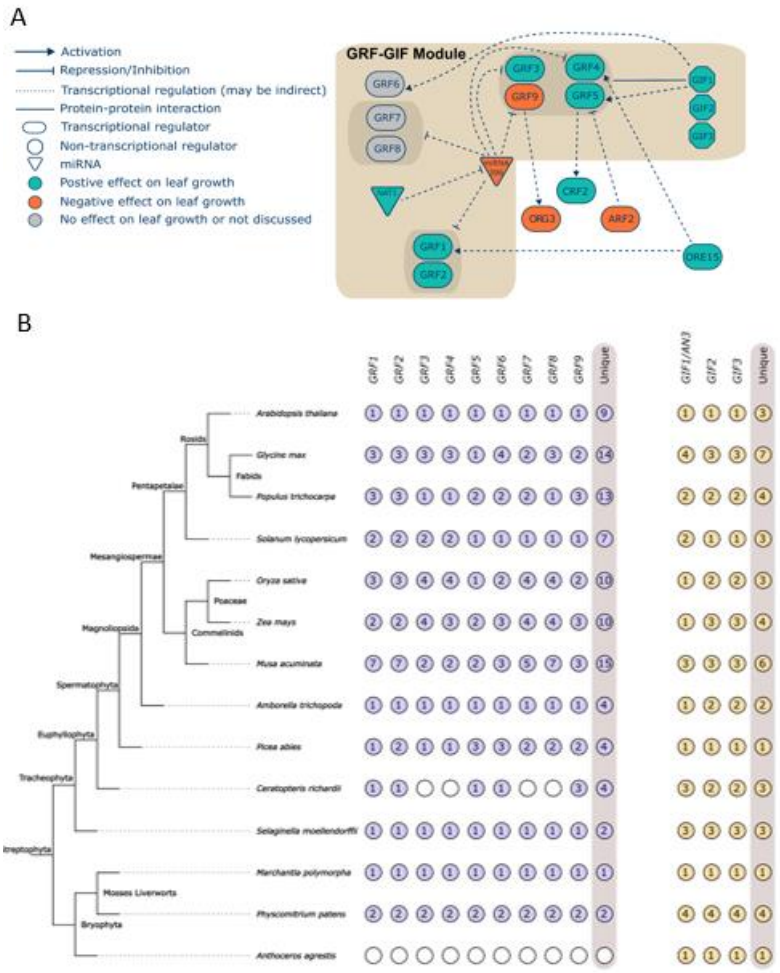

Figure 4. Genetic network and evolutionary conservation of the GRF–GIF pathway

(A) Overview of the core members of the GRF–GIF growth regulatory pathway. Transcriptional regulators are displayed in ovals, other proteins as octagons. Triangles are miRNAs. Colors denote their described effect on leaf growth: teal – positive; orange – negative; grey – neutral, not described or not discussed. Relationships among proteins are represented by lines and arrows. An arrow indicates activation, a T-shaped junction inhibition/repression of the target. A solid line indicates interaction between two proteins, a dashed line (indirect) transcriptional regulation.

(B) Evolutionary conservation of selected genes of the GRF–GIF module. Number of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Different colors represent different gene families. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. "Unique" presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: ARF2 (AUXIN RESPONSE FACTOR 2); CRF2 (CK RESPONSE FACTOR 2); GIF (GRF-INTERACTING FACTOR); GRF (GROWTH REGULATING FACTOR); miR396 (microRNA 396); NAT (natural antisense long noncoding RNA); ORE15 (ORESARA15); ORG3 (OBF-BINDING PROTEIN 3-RESPONSIVE GENE 3)

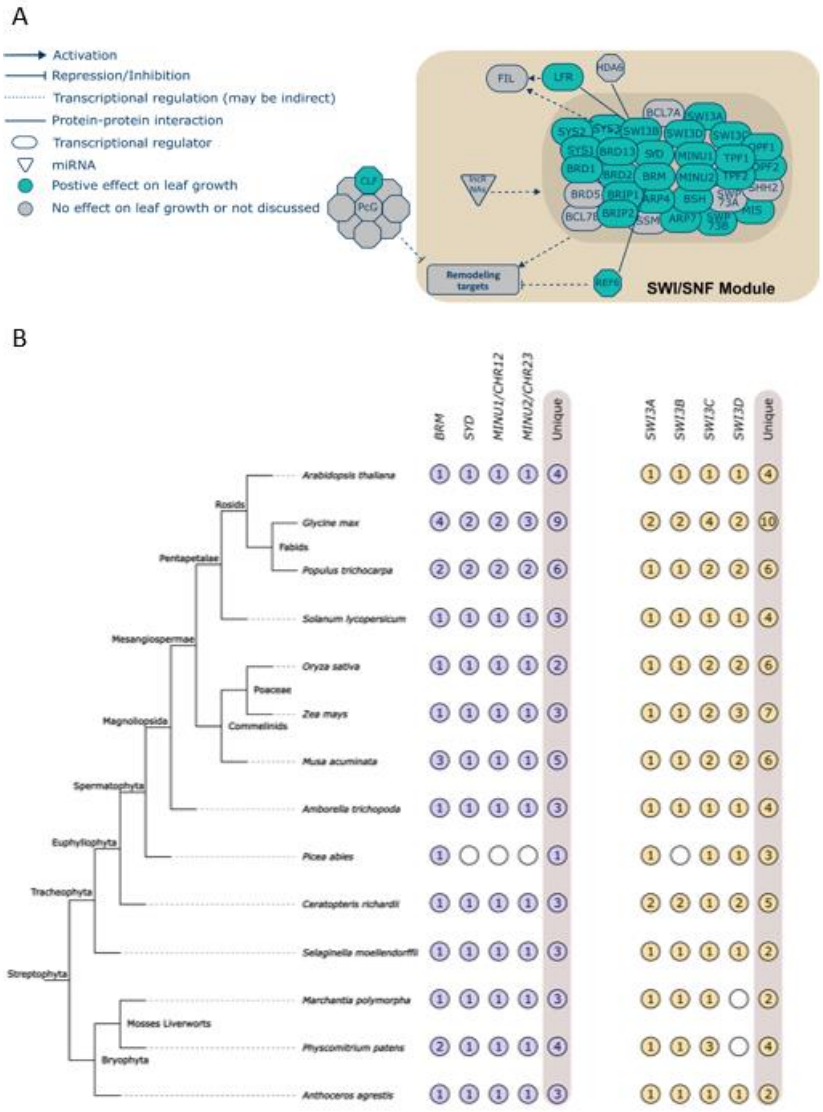

Figure 5. Genetic network and evolutionary conservation of the SWI/SNF pathway

(A) Overview of the core members of the SWI/SNF growth regulatory pathway. For simplicity, all SWI/SNF subunits are shown within the same complex. Transcriptional regulators are displayed in ovals, other proteins as octagons. Triangles are miRNAs. Colors denote their described effect on leaf growth: teal – positive; grey – neutral, not described or not discussed. Relationships among proteins are represented by lines and arrows. An arrow indicates activation, a T-shaped junction inhibition/repression of the target. A solid line indicates interaction between two proteins, a dashed line (indirect) transcriptional regulation.

(B) Evolutionary conservation of selected genes of the SWI/SNF module. Number of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Different colors represent different gene families. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. "Unique" presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: ARP (ACTIN RELATED PROTEIN); BCL7A (B-cell CLL/lymphoma-DOMAIN HOMOLOG); BRD (BROMODOMAIN-CONTAINING PROTEIN); BRIP (BRAHMA-INTERACTING PROTEIN); BRM (BRAHMA); BSH (BUSHY); CLF (CURLY FLOWER); FIL (FILAMENTOUS FLOWER);

HDA6 (HISTONE DEACETYLASE 6); LFR (LEAF AND FLOWER RELATED); lncRNAs (long non-coding RNAs); MINU (MINUSCULE); MIS (MINU-INTERACTING SUBUNIT); OPF (ONE PHD FINGERS); PcG (POLYCOMB-group proteins); REF6 (RELATIVE OF EARLY FLOWERING 6); SHH2 (SAWADEE HOMEODOMAIN HOMOLOG 2); SSM (SMALL SUBUNIT OF MINU1/2-ASSOCIATED SWI/SNF COMPLEX); SWI3 (SWITCH/SUCROSE NONFERMENTING 3); SWP73 (SWI/SNF ASSOCIATED PROTEINS 73); SYD (SPLAYED); SYS (SYD-ASSOCIATED SWI/SNF COMPLEX SUBUNIT); TPF (TRIPLE PHD FINGERS)

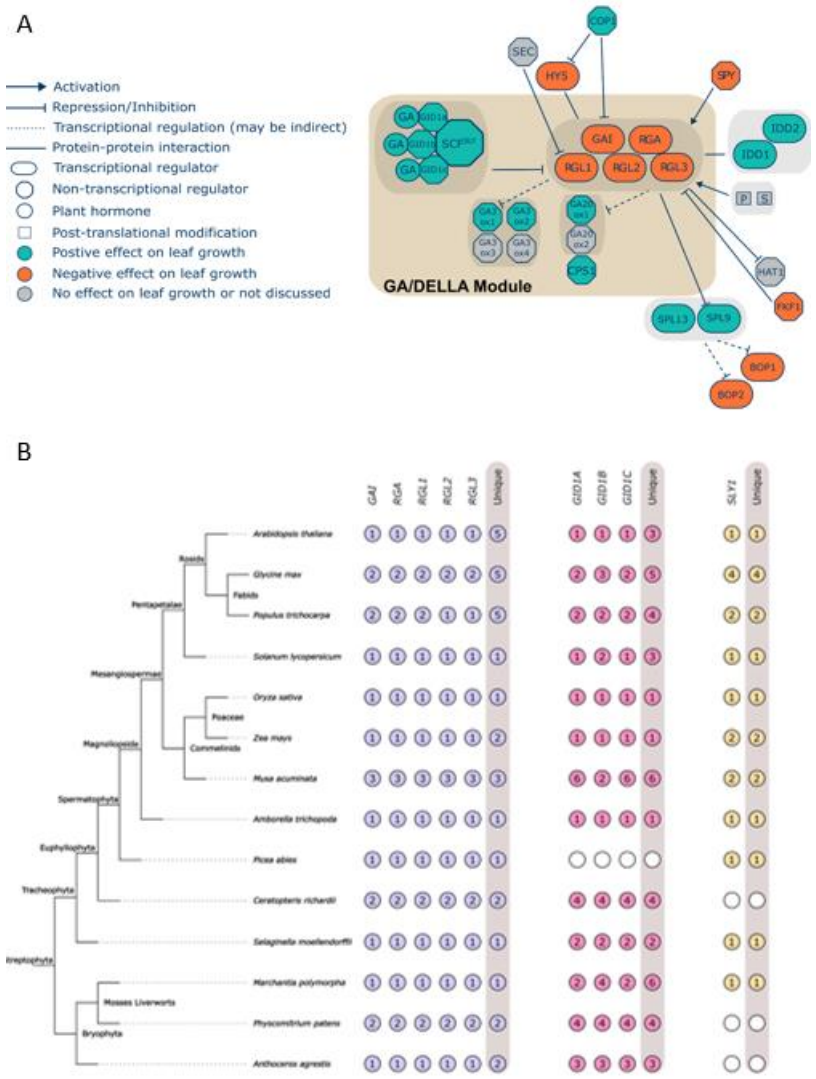

Figure 6. Genetic network and evolutionary conservation of the GA/DELLA pathway

(A) Overview of the core members of the GA/DELLA growth regulatory pathway. Transcriptional regulators are displayed in ovals, other proteins as octagons. Small circles depict plant hormones. Squares denote post-translational modifications. Colors denote their described effect on leaf growth: teal – positive; orange – negative; grey – neutral, not described or not discussed. Relationships among proteins are represented by lines and arrows. An arrow indicates activation, a T-shaped junction inhibition/repression of the target. A solid line indicates interaction between two proteins, a dashed line (indirect) transcriptional regulation.

(B) Evolutionary conservation of selected genes of the GA/DELLA module. Number of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Different colors represent different gene families. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. "Unique" presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: BOP (BLADE ON PETIOLE); COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1); CPS1 (ARABIDOPSIS THALIANA ENT-COPALYL DIPHOSPHATE SYNTHETASE 1); FKF1 (FLAVIN-BINDING, KELCH REPEAT, F BOX 1); GA (gibberellins); GA20ox (GIBERELLIN 20-OXIDASE); GA3ox (GIBERELLIN 3-OXIDASE); GAI (GA INSENSITIVE); GID1 (GIBBERELLIN-INSENSITIVE

DWARF 1); HAT1 (HISTONE ACETYLASE 1); HY5 (ELONGATED HYPOCOTYL 5); IDD (INDETERMINATE DOMAIN); P (Phosphorylation); RGA (REPRESSOR OF gai1-3); RGL (RGA-LIKE); S (SUMOylation); SCF (SKP 1/CULLIN 1/F-BOX PROTEIN); SEC (SECRET AGENT); SLY 1 (SLEEPY 1); SPY (SPINDLY); SPL (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE)

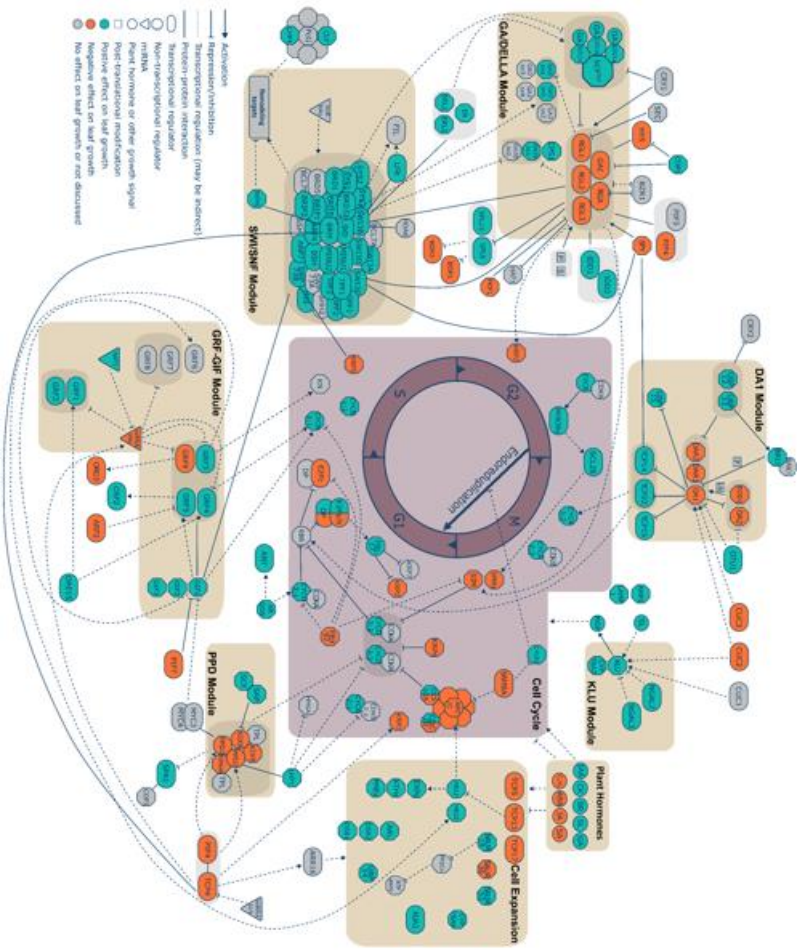

Figure 7. Overview of the discussed growth regulatory pathways and their connections with each other and with the cell cycle machinery and cell expansion module

Transcriptional regulators are displayed in ovals, other proteins as octagons. Small circles depict plant hormones or other unidentified plant growth regulators. Triangles are miRNAs. Squares denote post-translational modifications. Colors denote their described effect on leaf growth: teal – positive; orange – negative; gray – neutral, not described or not discussed. Relationships among proteins are represented by lines and arrows. An arrow indicates activation, a T-shaped junction inhibition/repression of the target. A solid line indicates interaction between two proteins, a dashed line (indirect) transcriptional regulation.

Abbreviations: ABA (abscisic acid); AMP1 (ALTERED MERISTEM PROGRAM 1); ANT (AINTEGUMENTA); APC/C (anaphase-promoting complex/cyclosome); ARF2 (AUXIN RESPONSE FACTOR 2); ARGOS (AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE); ARL (ARGOS-LIKE); ARP (ACTIN RELATED PROTEIN); ARR (ARABIDOPSIS RESPONSE REGULATOR); ATPase (Adenosine 5'-TriPhosphatase); BAK1 (BRI1-ASSOCIATED RECEPTOR KINASE 1); BCL7 (B-cell CLL/lymphoma-DOMAIN HOMOLOG); BOP (BLADE ON PETIOLE); BR (brassinsoteroids); BRD (BROMODOMAIN-CONTAINING PROTEIN); BRI1 (BRASSINOSTEROID INSENSITIVE 1); BRIP (BRAHMA-INTERACTING PROTEIN); BRM (BRAHMA); BSH (BUSHY); BZR1 (BRASSINAZOLE-RESISTANT 1); C_2H_4 (ethylene); CCS52 (CELL CYCLE SWITCH PROTEIN 52); CDC20 (CELL DIVISION CYCLE 20); CDK (CYCLIN-DEPENDENT KINASE); CK (cytokinins); CLF (CURLY FLOWER); COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1); CPS1 (ARABIDOPSIS THALIANA ENT-COPALYL DIPHOSPHATE SYNTHETASE 1); CRF2 (CK RESPONSE FACTOR 2); CRY (CRYPTOCHROME); CUC (CUP-SHAPED

COTYLEDON); CYC (CYCLIN); CYP78A (CYTOCHROME P450, FAMILY 78, SUBFAMILY A); DAR (DA1-RELATED); DP (DIMERIZATION PARTNER); E2F (E2F TRANSCRIPTION FACTOR); EOD1 (ENHANCER OF DA1); ER (ERECTA); ERL (ERECTA-LIKE); EXP (EXPANSIN); FBL17 (F-BOX-LIKE 17); FBX (F-BOX PROTEIN 92); FIL (FILAMENTOUS FLOWER); FKF1 (FLAVIN-BINDING, KELCH REPEAT, F BOX 1); GA (gibberellins); GA20ox (GIBERELLIN 20-OXIDASE); GA2ox (GIBERELLIN 2-OXIDASE); GA3ox (GIBERELLIN 3-OXIDASE); GAI1 (GA INSENSITIVE); GID1 (GIBBERELLIN-INSENSITIVE DWARF 1); GIF (GRF-INTERACTING FACTOR); GRF (GROWTH REGULATING FACTOR); HAT1 (HISTONE ACETYLASE 1); HB (HOMEOBOX PROTEIN); HDA6 (HISTONE DEACETYLASE 6); HMGA (HIGH MOBILITY GROUP A); HY5 (ELONGATED HYPOCOTYL 5); IAA (indole-3-acetic acid/auxin); IDD (INDETERMINATE DOMAIN); JA (jasmonic acid); KIX (KINASE-INDUCIBLE DOMAIN INTERACTING); KN (KNOLLE); KRP (KIP-RELATED PROTEIN); KUA1 (KUODA 1); LAMP1 (LIKE AMP1); LFR (LEAF AND FLOWER RELATED); LHP1 (LIKE HETEROCHROMATIN PROTEIN 1); lncRNAs (long non-coding RNAs); MGF (mobile growth factor); MINU (MINUSCULE); miRNA (microRNA); MIS (MINU-INTERACTING SUBUNIT); MYB3Rs (THREE REPEAT MYB DOMAIN PROTEINs); MYC (MYELOCYTOMATOSIS); NAT (natural antisense transcript); NGAL (NGATHA-LIKE PROTEIN); NINJA (NOVEL INTERACTOR OF JAZ); OPF (ONE PHD FINGERS); ORE15 (ORESARA15); ORG3 (OBF-BINDING PROTEIN 3-RESPONSIVE GENE 3); OSR (ORGAN SIZE-RELATED); OTU1 (OTUBAIN-LIKE CYSTEINE PROTEASE 1); P (phosphorylation); PcG (POLYCOMB-group proteins); PIF (PHYTOCHROME INTERACTING FACTOR); PME (PECTIN METHYLESTERASE); PP2C (2C PROTEIN PHOSPHATASE); PPD (PEAPOD); RBR (RETINOBLASTOMA-RELATED); REF6 (RELATIVE OF EARLY FLOWERING 6); RGA (REPRESSOR OF gai1-3); RGL (RGA-LIKE); S (SUMOylation); SA (salicylic acid); SAP (STERILE APETALA); SAUR (SMALL AUXIN UP RNA); SCF (SKP 1/CULLIN 1/F-BOX PROTEIN); SCL (SCARECROW-LIKE); SEC (SECRET AGENT); SHH2 (SAWADEE HOMEODOMAIN HOMOLOG 2); SIM (SIAMESE); SL (strigolactones); SLY 1 (SLEEPY 1); SMR (SIM RELATED); SPA1 (SUPPRESSOR OF phyA-105); SPL (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE); SPY (SPINDLY); SSM (SMALL SUBUNIT OF MINU1/2-ASSOCIATED SWI/SNF COMPLEX); SWI3 (SWITCH/SUCROSE NONFERMENTING 3); SWP73 (SWI/SNF ASSOCIATED PROTEINS 73); SYD (SPLAYED); SYS (SYD-ASSOCIATED SWI/SNF COMPLEX SUBUNIT); TCP (TEOSINTE BRANCHED 1/CYCLOIDEA/PROLIFERATING CELL NUCLEAR ANTIGEN FACTOR); TPF (TRIPLE PHD FINGERS); TPL (TOPLESS); Ub (ubiquitination); UBP (UBIQUITIN SPECIFIC PROTEASE); XTH (XYLOGLUCAN ENDOTRANSGLUCOSEYLASE/HYDROLASE)

Table 1. Reported leaf growth phenotypes of loss-of-function mutants of SWI/SNF subunits.

Gene	Leaf phenotype	Reference
BRM	KD/LoF: dwarfed growth, smaller, curled leaves	(Farrona *et al.*, 2004; Hurtado *et al.*, 2006)
SYD	LoF: dwarfed growth, smaller, curled leaves	(Wagner and Meyerowitz, 2002)
MINU1/CHR12	Single LoF: WT-like; double LoF: lethal; double KD: dwarfed and delayed growth, smaller leaves	(Sang *et al.*, 2012)
MINU2/CHR23		
SWP73A	LoF: leaves WT-like	(Sacharowski *et al.*, 2015)
SWP73B	KD: dwarfed and delayed growth, smaller and curling leaves	(Sacharowski *et al.*, 2015)
SWI3A	KO: lethal	(Sarnowski *et al.*, 2005)
SWI3B	KO: lethal	(Sarnowski *et al.*, 2005)
SWI3C	KO: dwarfed growth, smaller and curling leaves	(Sarnowski *et al.*, 2005)
SWI3D	KO: dwarfed growth, smaller and curing leaves	(Sarnowski *et al.*, 2005)
BSH	KD: dwarfed growth	(Brzeski *et al.*, 1999)
ARP4	KD: dwarfed growth, smaller and fewer leaves	(Kandasamy *et al.*, 2005a)
ARP7	KO: lethal; KD: dwarfed growth, smaller leaves	(Kandasamy *et al.*, 2005b)
BCL7A/BDH1	*bcl7a*: WT-like; *bcl7b*: curling of some older leaves; double LoF: curling leaves	(Stachula *et al.*, 2023)
BCL7B/BDH2		
BRIP1	Single LoF: WT-like; double LoF: curling leaves	(Yu *et al.*, 2020)
BRIP2		
BRD1	Single/double LoF: WT-like; triple LoF: curling, slightly smaller leaves	(Jarończyk *et al.*, 2021; Yu *et al.*, 2021)
BRD2		
BRD13		
BRD5	/	/
SYS1	Triple LoF: reduced growth, smaller and curled leaves	(Guo *et al.*, 2022a)
SYS2		
SYS3		
PMS1A/OPF1	Double LoF: dwarfed growth, smaller curled leaves	(Guo *et al.*, 2022a)
PMS1B/OPF2		
PMS2A/TPF2	Single LoF: WT-like; double LoF: dwarfed growth, smaller leaves	(Diego-Martin *et al.*, 2022)
PMS2B/TPF1		
LFR	LoF: smaller, upward-curled leaves	(Lin *et al.*, 2021)

Gene	Leaf phenotype	Reference
SHH2	/	/
SSM	/	/
MIS	LoF: lethal; KD: reduced growth, smaller, narrower leaves	(Jin *et al.*, 2023)

Reduced growth refers to overall plant size. Abbreviations: KD: knock-down; KO: knock-out; LoF: loss-of-function allele; WT: wild type; /: to our knowledge no leaf phenotype has been described; ARP (ACTIN RELATED PROTEIN); BCL7 (B-cell CLL/lymphoma-DOMAIN HOMOLOG); BRD (BROMODOMAIN-CONTAINING PROTEIN); BRIP (BRAHMA-INTERACTING PROTEIN); BRM (BRAHMA); BSH (BUSHY); LFR (LEAF AND FLOWER RELATED); MINU (MINUSCULE); OPF (ONE PHD FINGERS); PMS (PHD DOMAIN-CONTAINING MAS SUBUNIT); SHH2 (SAWADEE HOMEODOMAIN HOMOLOG 2); SSM (SMALL SUBUNIT OF MINU1/2-ASSOCIATED SWI/SNF COMPLEX); SWI3 (SWITCH/SUCROSE NONFERMENTING 3); SWP73 (SWI/SNF ASSOCIATED PROTEINS 73); SYD (SPLAYED); SYS (SYD-ASSOCIATED SWI/SNF COMPLEX SUBUNIT); TPF (TRIPLE PHD FINGERS)

Supplementary Table legend and Figure

Table S1. Gene identifiers of input genes and identified orthologs of evolutionary analysis.

Orthologs of specific genes were identified via PLAZA 5.0 (Van Bel *et al.*, 2022)# *Due to alternative splicing events, *OsGID2* could not be identified as an ortholog of *AtSLY1*; this was manually corrected.

Abbreviations: ARP (ACTIN RELATED PROTEIN); BB (BIG BROTHER); BCL7 (B-cell CLL/lymphoma-DOMAIN HOMOLOG); BRD (BROMODOMAIN-CONTAINING PROTEIN); BRIP (BRAHMA-INTERACTING PROTEIN); BRM (BRAHMA); BSH (BUSHY); CYP78A (CYTOCHROME P450, FAMILY 78, SUBFAMILY A); DAR (DA1-RELATED); EOD (ENHANCER OF DA1); GAI (GA INSENSITIVE); GID1 (GIBBERELLIN-INSENSITIVE DWARF 1); GIF (GRF-INTERACTING FACTOR); GRF (GROWTH REGULATING FACTOR); KIX (KINASE-INDUCIBLE DOMAIN INTERACTING); LFR (LEAF AND FLOWER RELATED); MINU (MINUSCULE); MIS (MINU-INTERACTING SUBUNIT); OPF (ONE PHD FINGERS); PMS (PHD DOMAIN-CONTAINING MAS SUBUNIT); PPD (PEAPOD); RGA1 (REPRESSOR OF gai1-3); RGL (RGA-LIKE); SAP (STERILE APETALA); SHH2 (SAWADEE HOMEODOMAIN HOMOLOG 2); SLY 1 (SLEEPY 1); SSM (SMALL SUBUNIT OF MINU1/2-ASSOCIATED SWI/SNF COMPLEX); SWI3 (SWITCH/SUCROSE NONFERMENTING 3); SWP73 (SWI/SNF ASSOCIATED PROTEINS 73); SYD (SPLAYED); SYS (SYD-ASSOCIATED SWI/SNF COMPLEX SUBUNIT); TPF (TRIPLE PHD FINGERS); UBP (UBIQUITIN SPECIFIC PROTEASE)

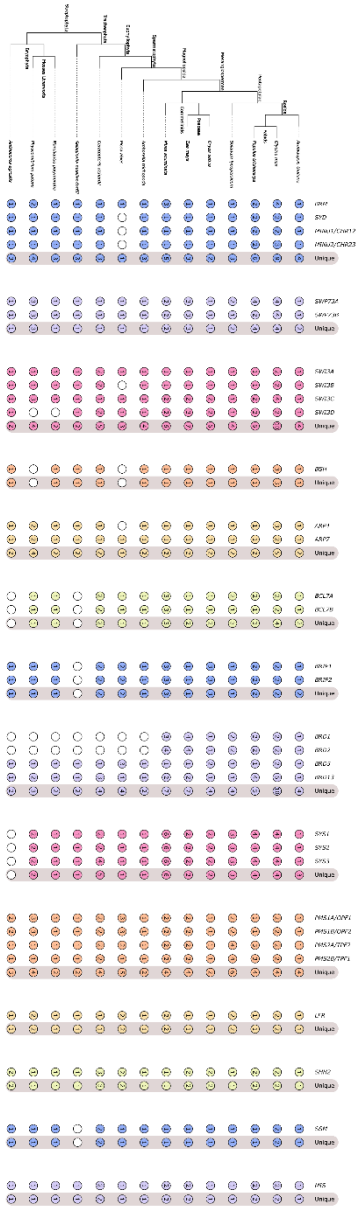

Figure S1: Evolutionary conservation of all putative SWI/SNF subunits.

Evolutionary conservation of selected genes of the SWI/SNF module. Numbers of orthologs of *Arabidopsis thaliana* genes in selected species are presented per gene within the colored circles. Empty circles denote that no ortholog was detected. Different colors represent different gene families. Closely related Arabidopsis genes may lead to the identification of identical orthologs in other species. "Unique" presents the number of unique orthologs identified per group and species. Table S1 lists gene identifiers of all input sequences and identified orthologs.

Abbreviations: ARP (ACTIN RELATED PROTEIN); BCL7 (B-cell CLL/lymphoma-DOMAIN HOMOLOG); BRD (BROMODOMAIN-CONTAINING PROTEIN); BRIP (BRAHMA-INTERACTING PROTEIN); BRM (BRAHMA); BSH (BUSHY); LFR (LEAF AND FLOWER RELATED); MINU (MINUSCULE); OPF (ONE PHD FINGERS); PMS (PHD DOMAIN-CONTAINING MAS SUBUNIT); SHH2 (SAWADEE HOMEODOMAIN HOMOLOG 2); SSM (SMALL SUBUNIT OF MINU1/2-ASSOCIATED SWI/SNF COMPLEX); SWI3 (SWITCH/SUCROSE NONFERMENTING 3); SWP73 (SWI/SNF ASSOCIATED PROTEINS 73); SYD (SPLAYED); SYS (SYD-ASSOCIATED SWI/SNF COMPLEX SUBUNIT); TPF (TRIPLE PHD FINGERS)