Leaf growth in dicots and monocots: so different yet so alike
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In plants, most organs grow post-embryonically through cell division and cell expansion. The coordination of these two growth processes is generally considered to be different between dicots and monocots. In dicot plants, such as the model plant Arabidopsis, leaf growth is most often described as being temporally regulated with cell division ceasing earlier at the tip and continuing longer at the base of the leaf. Conversely, in monocot leaves, the organization of the growth processes is rather viewed as spatially regulated with dividing cells at the base of the leaf, followed by expanding cells and finally mature cells at the tip. As our understanding of the leaf growth processes in the two major classes of flowering plants expands, it becomes increasingly clear that the regulation of the growth processes is to a great extent conserved between dicots and monocots. In this review, we highlight how the temporal and spatial organization of cell division and cell expansion takes place in both dicot and monocot leaves. We also show that there are similarities in the molecular wiring that coordinates these two processes during leaf development.

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Introduction
The systematic classification of species based on the similarities in overall morphology by the British naturalist John Ray first divided flowering plants into two categories, dicots and monocots (Historia Plantarum (The history of Plants), 1686). One characteristic of that classification, that holds true in modern taxonomy, is the shape of the leaf. Monocot leaves are typically narrow and elongated with parallel veins, while dicot leaves are usually more rounded-shaped with reticulate veins [1]. In line with this, it was long thought that the organization of the growth processes could also be used to make the classification. Plant organ growth is governed by the integration of cell division, providing new cells, and cell expansion, a process that greatly increases the cellular volume once cells have ceased to divide. In the last decade, the study of the contribution of cell division and cell expansion to growth and final leaf size in both dicots and monocots, often referred to as kinematic analysis [2], has provided a vast amount of data allowing to identify differences and similarities existing between species. Here, we compare the cellular and molecular basis of leaf growth in dicots and monocots and show that as for seed size (Na Li and Yunhai Li, COPB, this issue), there are many parallels between these two major groups of plants.

Being at the right place at the right time
At the initial stage of leaf growth, immediately after the outgrowth of the leaf primordium from the shoot apical meristem, all cells in the leaf are dividing. As time progresses, cells at the tip of the leaf cease to divide and start expanding, while the cells at the base are still dividing. This was observed for dicots [3*] and monocots [4*], indicating that the temporal regulation of leaf growth is very similar. In Arabidopsis, the transition between cell division and cell expansion can be visualized by the mitotic pCYCLINB1;1::DB-CYCLINB1;1::GUS marker [3] and is called the cell cycle arrest front. As this cell cycle arrest front gradually moves from the tip to the base of the leaf over time, the coordination of the growth processes is considered to be temporal [6–8] and as such, at a given point in time, the growth processes are linearly organized in the Arabidopsis leaf, a situation that is very reminiscent of the linear organization of cell division and cell expansion in monocot leaves. Indeed, the typical view on the growth processes in monocot leaves is that of a linear organization with dividing cells at the base, followed by expanding cells and finally mature cells at the tip when the leaf elongation rate is maximal [4*,9,10]. This means that both spatial and temporal regulatory components are present during leaf growth in dicot and monocot leaves, but that the proportions at which they occur, and eventually contribute to final leaf size, might differ (Figure 1).

The spatial and temporal processes regulating growth were shown to be independent both in dicots and monocots. A detailed phenotypic analysis of maize leaf growth of B73xH99 recombinant inbred lines showed that the leaf
In addition to the very similar spatial and temporal organization of the growth processes in dicots and monocots, there are also parallels in how the coordination between cell division and cell expansion influences the growth rate. In *Arabidopsis*, a kinematic analysis of the first two leaves, as well as higher order leaves, showed that the leaf size is increasing exponentially until immediately after the cell division rate declines [6,7]. Also in maize leaves, the decline in LER is preceded by a decrease in cell production [13]. These data suggest that mere cell expansion is unable to sustain maximal growth, and that cell division is an important driver of exponential growth. This effect of cell division on final leaf size is striking, especially since only a very small portion of all the cells in the leaf are actively dividing. When the cell cycle arrest front first appears, the division zone in the *Arabidopsis* leaf still comprises about 75% of the total leaf size, but in later stages, the division zone makes up for a relative small fraction of the total leaf size [5,7,14]. However, when the position of the cell cycle arrest front was monitored relative to the base of the leaf, it became clear that the size of the division zone remains constant for few days and then starts to decline [7,14]. Also in monocot leaves, the size of the division zone remains maximal and constant for some days of steady-state growth prior to the decline in growth rate [4*].

**Many molecular growth mechanisms are highly conserved between dicots and monocots**

Interestingly, more and more studies also report similarities in the molecular regulation of leaf growth, because similar genes have been found to control organ size in dicots and monocots (Table 1). These conserved regulators belong to distinct functional classes affecting transcription, translation, protein abundance, hormone signaling and cell wall loosening, underlining that diverse biological routes converge on the two major processes of cell division and cell expansion to regulate organ growth.

**Transcriptional regulation**

In both dicots and monocots, members of the plantspecific transcription factor family GROWTH-REGULATING FACTOR (GRF) have an important role in the regulation of leaf size [15–20,21**,**22*]. In both *Arabidopsis* and maize, GRFs interact with ANGUSTIFOLIA3/GRF-INTERACTING FACTOR1 (AN3/GIF1), a transcriptional co-activator protein, and the composition of the SWI/SNF chromatin remodeling complex associated with AN3 is remarkably conserved between the two species [21**,**23]. Also the interaction of GRFs and transcription factors of the KNOX family is conserved in both monocot and dicot plants [22*]. Another plant-specific transcriptional regulator, member of the INDETERMINATE DOMAIN (IDD) protein family, BROAD LEAF1 (BLF1), limits leaf width by restricting cell proliferation during primordia growth in barley [24].
Arabidopsis, IDD14, IDD15, and IDD16 are closely related to BLF1 and the triple mutant idd14 idd15 idd16 produces leaves with a reduced length-to-width ratio similar to the blf1 mutant in barley [25]. In Arabidopsis, these proteins regulate morphogenesis by modulating auxin accumulation [25].

Protein synthesis and degradation
Also several genes involved in the regulation of protein synthesis and degradation have a conserved role in organ growth control. Human EBP1 is a dsRNA-binding protein that associates with ribosome biogenesis factors and is probably involved in protein translation through the regulation of rRNA processing and ribosome assembly [26]. In Arabidopsis and potato, EBP1 overexpression results in the formation of larger leaves due to an increase of both cell number and cell size [27], whereas in maize, high expression of EBP1 enlarges organ size. The functional conservation is also manifested in the observation that ectopic expression of Zea mays EBP1 in Arabidopsis produces larger organs [28]. Arabidopsis plants overexpressing a dominant-negative form of the ubiquitin receptor DAI, putatively involved in protein abundance regulation, produce larger organs, leaves and seeds, containing more cells [29]. Similarly, in maize, overexpression of the mutant form of DAI leads to the formation of larger seeds [30]. In Arabidopsis, DAI1 works in synergy with two ubiquitin E3 ligase proteins, BIG BROTHER (BB) [29] and DA2 [31], that also regulate organ growth. Interestingly, Arabidopsis DA2 shares significant similarity with the rice GRAIN WIDTH AND WEIGHT2 (GW2), a quantitative trait locus for grain width and weight [32]. When GW2 is down-regulated, rice plants produce larger grains, whereas GW2-overexpressing rice plants produce smaller grains and in wheat and maize, the expression of GW2 is negatively correlated with grain size [33,34], suggesting a role of GW2 as a negative regulator of growth also in monocots.

Hormone signaling
Changes in hormone metabolism and/or signaling can affect growth and several hormone-related mechanisms act similarly in dicots and monocots. In Arabidopsis, maize or rice, ectopic expression of GA20-oxidase, a rate-limiting enzyme in the gibberellin biosynthesis pathway, leads to the formation of larger leaves [9,18,35]. In Arabidopsis, ARGOS expression is induced by auxin [36] and ethylene [37] and increased levels of ARGOS lead to the formation of larger leaves containing more cells [36,37]. In maize, overexpression of the Zea mays ARGOS1 (ZAR1) enhances leaf, stalk and ear size, and grain yield by an increased cell number and promotes drought-stress tolerance [38]. In Arabidopsis, ectopic expression of ZAR1 affects ethylene perception or the early stages of ethylene signaling somewhere between an ethylene receptor and the serine/threonine-protein kinase CONSTITUTIVE TRIPLE RESPONSE1 [39]. In addition, overexpression of another member of the maize ARGOS family, ARGOS8, in maize has also been shown to lead to increased grain yield under both drought stress and well-watered conditions in the field [39]. There is also ample evidence that brassinosteroids (BRs) play a pivotal role in growth control [40]. Overexpression of BRASSINOSTEROID INSENSITIVE 1 (BRI1), encoding the BR receptor, in Arabidopsis increases organ size [18,41], whereas in maize down-regulation of BRI1 reduces growth [42]. In addition, treatment of rice plantlets with 24-epibrassinolide, a synthetic BR, leads to an increase in plant growth rate, seed fresh and dry weight, root size and root dry weight [43].

Other signaling pathways
In Arabidopsis, KLUH, encoding the cytochrome P450 CYP78A5, was proposed to produce an unknown growth-promoting signal different from the classical phytohormones, Overexpression of KLUH leads to the formation of larger leaves and flowers probably through the increased production of this signal [44]. In rice, a likely ortholog of KLUH, PLASTOCHRON1, is involved in the regulation of the rate of leaf initiation and the termination of vegetative growth [45].

Cell wall extension
In Arabidopsis, increased levels of EXPANSIN10, a gene that encodes an enzyme facilitating cell wall loosening,
result in an enhanced leaf size due to an increased cell size [46]. In rice, constitutive expression of OsEXP4 or OsEXP4A leads to the production of taller plants with more leaves and an enlarged leaf size due to an increased cell size [47]. In maize, decreased expression of the Zea mays ZmEXPB6 is correlated with salt-mediated leaf growth reduction and exogenous application of ZmEXPB6 can restore leaf growth in these conditions [48].

Conclusions and perspectives

Whereas the tiny Arabidopsis leaf limits the sampling of tissues enriched for dividing or expanding cells to study growth over time [7], the linear organization of the large monocot leaves enables to obtain sufficient material to analyze specific aspects of leaf development [9]. However, monocot leaves are already growing while they are still hidden and covered by older leaves, making it harder to standardize the time points of sampling. We are currently at an era in which technological advances make it more and more possible to sample a limited amount of cells while maintaining a tissue context [49] or to non-destructively image hidden plant organs [50], enabling us to study more easily all aspects of plant growth in both dicots and monocots. Furthermore, the observation that similar cellular and molecular pathways govern leaf growth in dicots and monocots has important consequences for translational research and underlines a strategy in which each system maximally contributes to the understanding of growth. The ability to switch between model systems, depending on the experimental feasibility and biological question, will greatly enhance progress in understanding leaf growth.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest


This review provides a comprehensive overview of the five cellular mechanisms driving leaf growth in Arabidopsis known to date.


This paper describes the time course of grass leaf length and the contribution of cell division and cell expansion from the primordial stage to maturity.


Detailed analysis of leaf growth parameters in 103 RIL lines and transcriptome analysis of dividing cells at the leaf basis of all lines demonstrated that two independent mechanisms contribute to final leaf size, maximal growth rate and the duration of growth.

12. Baute J, Herman D, Coppens F, De Block J, Slabbinck B, • Dell’Acqua M, Pe ME, Maere S, Nelissen H, Inzé D: Combined large-scale phenotyping and transcriptome data integration from the two diverse populations allowed to identify a set of 226 genes that are robustly associated with diverse leaf traits.


Not only the composition of the SWI/SNF complex associated with AN3 but also the function of the GRFs in leaf growth, as well as the regulation of the GRFs through miR396, is conserved between dicots and monocots.


This work demonstrates conserved interactions between the GRF and KNOX families of transcription factors in both monocot and dicot plants.


Cloning of GW2, a QTL for grain width and weight, that encodes a RING-type protein with E3 ubiquitin ligase activity. Loss of GW2 function increases seed yield by increased cell proliferation.


This article show that overexpression of ARGOS positively affects plant growth and stress tolerance in Arabidopsis and maize by interfering with early ethylene signaling.


