forests

Review

The Formation of Shapes: Interplay of Genes during Leaf Development Processes

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Abstract: Leaf shape, as one of the clearest manifestations of plant morphology, shows considerable variation owing to genetics and the environment. Leaf initiation occurs in the peripheral zone of the SAM and goes through the three overlapping phases of leaf primordium initiation, leaf dorsiventral development, and leaf marginal meristem establishment. Transcription factors, such as *KNOX*, WOX, and *CUC*; hormone-regulating genes, such as *GA2ox*, *GA20ox*, and *PIN1*; and miRNAs such as *miR164/165* are tightly involved in leaf shaping through the generation of intricate cooperative networks in different temporal phases and specific tissue zones. Here, we briefly discuss the critical interplay occurring between certain genes and the pivotal role these play in the leaf developmental network and phytohormone regulation, including *AS1/AS2–KNOX–GA20ox*–GA, *miR164–NAM/CUC–PIN1*–auxin, and *CUC–BAS1/CYP734A*–BR, and we attempt to summarize several basic insights into the mechanisms of leaf shape regulation.

Keywords: leaf shape; regulatory interplay; transcription factors; phytohormone

Citation: Ma, J.; Li, H. The Formation of Shapes: Interplay of Genes during Leaf Development Processes. *Forests* **2022**, *13*, 1726. https://doi.org/10.3390/f13101726

Academic Editors: Marilena Idžojtić and Igor Poljak

Received: 15 August 2022
Accepted: 17 October 2022
Published: 20 October 2022

1. Introduction

Leaf morphology is a notable part of plant morphology exhibiting tremendous diversity for most plants [1]. As we know, the leaf has profound significance for photosynthesis, respiration, and photoperception [2]. As a solar panel, the leaf has to capture solar energy, which is required for photosynthesis to maintain growth and development [3]. Leaf shape has a relevant impact on the efficiency of light capture and heat dissipation and can reflect how plants have adapted to their climates [4,5]. For instance, *Serratula tinctoria* L. (Asteraceae) has vigorous vertical growth under limited light conditions and develops extensively lobed leaves due to shading from its competitors [6]. Moreover, a leaf's hydraulic resistance is negatively correlated with its lobes, since deep lobes may promote water balance in dry atmospheres, as shown in *Quercus* L. (Fagaceae) [7]. Generally, leaf shape and size are essential factors that partially govern angiosperm growth [8]. Leaf shape can be manipulated by genetic and environmental factors. For example, North American lake cress (*Rorippa aquatica* (Eaton) E.J.Palmer et Steyerm., of the family Brassicaceae), is a typical example of heterophylly in which leaves with a variety of shapes and sizes grow on the same plant, bearing simple leaves on land but pinnately divided leaves in submerged conditions [9]. Indeed, this heterophylly is altered by the induction of the *KNOX*–GA module [10]. Essentially, *KNOX* and BELL are two types of TALE TF that control meristem formation and maintenance, organ morphogenesis, organ position, and several aspects of the reproductive phase [11]. Members of the class 1 *KNOX* family (*KNOXI*), in particular, are critical in the maintenance of the shoot apical meristem and contribute to leaf dissection and complex morphology through hormone regulation [12–23]. In the Brassicaceae family, the RCO homeodomain protein plays a pivotal role in determining leaf complexity [13,24]. In *C. hirsuta* (*Cardamine hirsuta* L., family Brassicaceae), RCO goes through gene duplication and neofunctionalization, increasing leaf complexity, but this is evolutionarily lost in *A. thaliana* (*Arabidopsis thaliana* (L.) Heynh., family Brassicaceae), resulting in simple leaf morphology [24].

Leaf initiation begins with a group of cells around the flank of the SAM, which is the growth region in plants found within the tips of the shoots. At the beginning of leaf initiation in the SAM, the TALE TFs play remarkable roles in SAM maintenance and serve as the pluripotent regulators of the corresponding gene network. This group includes the *GA20ox*, *GA2ox*, and *PIN1* hormonal regulators [23,25–27]. Furthermore, several TF, such as *AS1* and CUC1-3, are involved in leaf development. As a model plant, *Arabidopsis* Heynh. has been well-studied in the field of leaf development. In the regulatory interplay occurring upstream of *KNOX*, *AS1*, a MYB TF, and *AS2* belonging to the LOB family interact with LHP1 to repress *KNOX* genes in *Arabidopsis* [28]. *AS1* also combines with auxin activities to regulate *KNAT1/BP*, a prominent *KNOXI* gene, promoting leaf development [29]. Furthermore, *CUC* genes act as key factors in the gene network involved in the development of the leaf margin. *KNOXI* genes can coordinate with *CUC* genes and hormonal regulatory genes to balance cell differentiation and proliferation, facilitating leaf lobes in *Arabidopsis* [12,30]. Along with leaf emergence, the *CUC* genes are critical regulators that cooperate in these genetic interplays, including interactions with hormonal factors such as the PIN protein, transcriptional factors such as *KNOX*, and microRNA such as *miRNA164a*. These regulators act to promote sinus formation at the leaf margin [31]. It has been reported that inactivating the *CUC3* gene partially suppresses serrations at the leaf margin in *A. thaliana* [16,32].

There are many factors that play indispensable roles in different phases of leaf development, which is profoundly controlled by these factors in determining the final shape. Even though many works have referred to leaf development and morphogenesis in retrospect, a comprehensive understanding of the mechanisms of leaf shaping is lacking, and further work in this regard is required. Here, we concisely review a few studies of leaf development and discuss these regulations with the main focus on the roles of genes, such as *KNOX* and *CUC*, from leaf initiation to the development of the entire leaf, referring to model networks of regulation.

2. Leaf Initiation and Morphogenesis

2.1. Where Does Leaf Initiation Occur?

In seed plants, the SAM is the basic unit of plant development incorporating the leaves, stem, and shoot, and regulatory mechanisms also occur within this dynamic structure [33]. The SAM has the dual function of maintaining an active stem cell population while concurrently generating new organs [34]. The organs form as primordia on the meristem flanks, whereas the self-renewing stem cell reservoir at the apex replenishes the cells that depart from the meristem into primordia including leaf primordia.

2.2. How Is a Leaf Shaped?

The early events of leaf initiation are similar across angiosperms [35]. Once leaf initiation begins from the SAM, it continuously progresses through three overlapping phases: leaf primordium initiation, the establishment of dorsiventrality, and the development of a marginal meristem [2,33]. These events generally lead a group of cells to form an entire leaf [2,33,36]. Additionally, there are three axes of growth in the establishment of a leaf: adaxial–abaxial, proximal–distal, and medial–lateral [37–39]. The leaf expands along these three axes and undergoes determinate growth, during which time the basic shape and potential size of the leaf are determined, and the organogenesis of the lateral appendages occurs [37,38,40]. The leaf's final shape depends on the cooperation of two growth modes, namely a conserved organ-wide growth mode that reflects differentiation and a local, directional mode involving the patterning of growth foci along with the leaf margin [22].

3. Molecular Regulation of Leaf Development

In spite of growing on the same individual plant, there are no two completely identical leaves, mainly because of the impacts of external factors from the environment and the internal factors from the plant's genetics.

3.1. Regulation in Early Developmental Events: Leaf Initiation and Development

Prior to leaf emergence, there are interplays between a broad number of genes within the SAM through interactions and collaborations and established networks of leaf development. Previous studies have suggested that cell cycling associated with leaf morphogenesis patterns of cell proliferation and differentiation occurs concurrently during leaf development [41,42]. Leaf initiation from the SAM involves a balance between cell proliferation and the generation of primordia. These processes are regulated by a great number of genes, such as the *KNOX* genes [35,43,44]. SAM maintenance and leaf development require a balance between pluripotent and differentiated cells, and there are multitudinous genes involved in meristem regulatory activity [37].

3.1.1. Regulation of *KNOX*

*KNOXI*s are expressed during the early leaf developmental events in the SAM and are essential for SAM formation and maintenance [45]. *STM*, a *KNOXI* gene, is locally downregulated during leaf primordia development [46–48]. The mutations of *stm* and the loss of function of *KNOX* lead to a failure to form the undifferentiated cells of the shoot meristem during embryonic development [49,50]. The ectopic expression of *KNAT1* induces all leaves to become lobed [51]. Additionally, the ectopic expression of the rice *OSH*, a *KNOXI* gene, interferes with the development of leaf blades and maintains leaves in less differentiated states [52]. In fact, *KNOX* genes were first found in maize, and they can be classified into two subclasses based on sequence similarity within the homeodomain, intron locations, expression pattern, and phylogenetic analysis [53–56]. On the one hand, *KNOXI* genes, including *KNAT1/BP*, *KNAT2*, *KNAT6,* and *STM* in *Arabidopsis*, are characteristically expressed in the meristem and stem, but their expression is downregulated in the leaf primordia of most simple leaf species [57]. On the other hand, previous studies have shown that in plant organs, there is a more widespread expression of class 2 *KNOX (KNOXII)* genes than of *KNOXI* genes, which indicates that they might have different functions [53,58,59]. Conversely, *KNOXI* genes can be expressed in the leaf primordia of dissected leaf plants, which implies that they may be involved in leaf diversity. Even if the *KNOXII* genes are barely involved in leaf shape regulation, they are extremely important for the regulation of other processes, which is a critical point when considering the classification of *KNOXI* and *KNOXII* genes. For example, *KNOX4*, a member of the *KNOXII* class, controls physical dormancy by regulating seed-coat cuticle development in *Medicago truncatula* Gaertn. (Fabaceae) [60]. Moreover, the *KNOXII* members *KNAT3* and *KNAT7* can work cooperatively to influence secondary cell wall deposition [61].

3.1.2. The Upstream Regulation of *KNOX*

The *KNOX* genes can be mediated by several genes, including *AS1*, *AS2*, *BOP1*, and *BOP2* genes in the meristem (Figure 1b). Previous studies have shown that *as1* mutations lead to marginal outgrowths or lobes at blades in *Arabidopsis* [62–65]. In fact, the leaf phenotype of the *as2* mutant is similar to that of the *as1* mutant in that *KNOX* genes are aberrantly expressed [63,64,66,67]. In addition to phenotypic similarities between *as1*/*as2* and *KNOX* over- or aberrant expressors, genetic analysis has demonstrated *KNOX*-mediated *as1*/*as2* phenotypes [67]. *AS1* has been identified as negatively mediating the *KNOXI* genes *KNAT1* and *KNAT2,* whereas STM negatively represses *AS1* [62]. Moreover, *AS1* and *AS2* complexes can facilitate the generation of H3K27me3 modifications in the chromatin regions of *KNAT1* and *KNAT2* to facilitate direct interaction with LHP1 (Figure 1b) [28]. The complex can bind to the regulatory motifs CWGTTD and KMKTTGAHW, which are present at two sites in the promoters of *KNOX* targets immediately upstream and surrounding an enhancer region required for expression in developing leaves [68]. The complex is required for stable *KNOX* gene silencing and can lead to the formation of a stable repressive chromatin state that blocks enhancer activity throughout leaf development. In addition, it is critical that *BOP1* and *BOP2*, both encoding an organ-specific BTB–POZ domain protein, can mediate leaf morphogenesis and patterning by directly activating *AS2* transcription and generating conditions for *KNOX* repression at the leaf base [69–71].

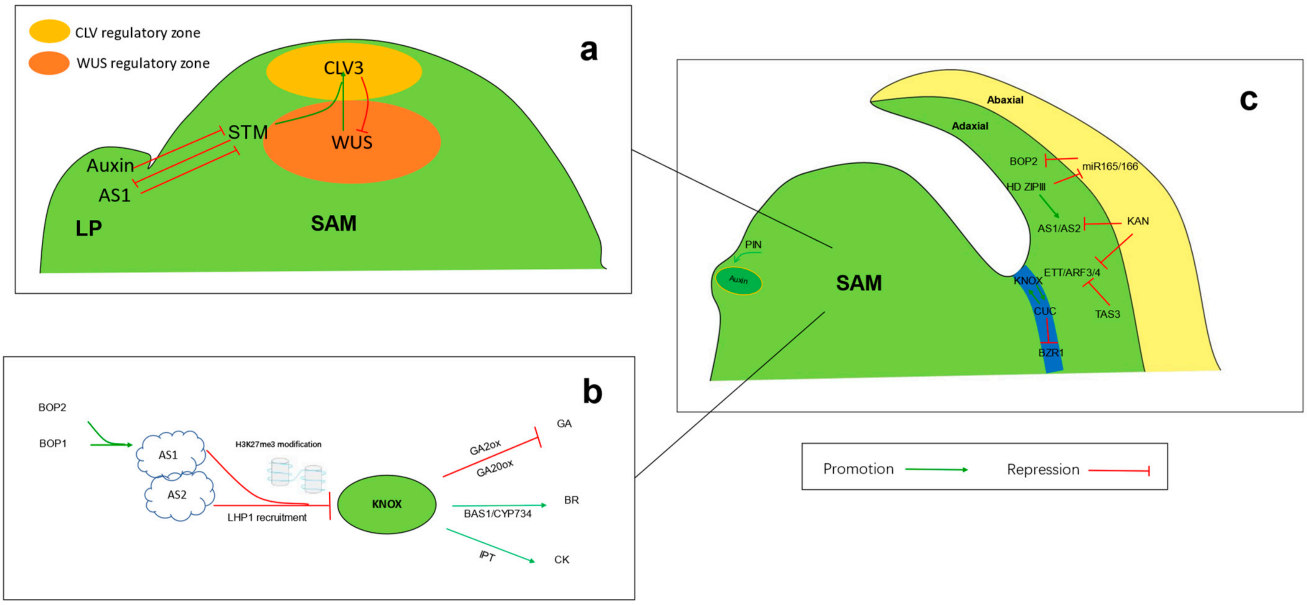

Figure 1. Interplay between genes in the shoot apical meristem (SAM) and leaf primordium (LP): (**a**) the regulation of SAM maintenance and organogenesis; (**b**) the genetic regulatory networks of *KNOXI*; (**c**) the genetics interplay related to ad–ab polarity leaf establishment.

3.1.3. Gibberellin Regulation by *KNOX*

Gibberellin regulation by *KNOX* takes the form of the net repression of the active GA level to maintain SAM activity [72] (Figure 1b). *GA20ox* and *GA2ox* are two key genes involved in GA biosynthesis regulated by *KNOX* proteins. Genetic studies have shown that *KNOXI* proteins can bind to TGAC sequences, especially including specific cis regulators in vitro, and four specific cis-regulatory elements recognized by *KNOX* proteins have been identified as having the TGAC sequence. In tobacco, *NTH15* is mainly expressed in the leaf primordia and young leaves, and its protein strongly binds to GTGAC, a 5 bp dyad symmetric sequence in the first intron of *Ntc12*, which encodes the GA 20-oxidase enzyme and leads to decreased GA biosynthesis [73–75]. In the potato, *StBEL5* and *POTH1* interact with TALE proteins in binding to the *ga20ox1* promoter through two TGAC cores [76]. Previous research has also indicated that the *KNOX* protein can bind to an intron of *ga2ox1* through a cis-regulatory element containing two TGAC motifs in maize [77].

3.1.4. Cytokinin Regulation by *KNOX*

CK biosynthesis is required alongside *KNOX* activity. *KNOX* proteins maintain SAM function, establishing a zone with increased CK and depressed GA activity for meristem maintenance (Figure 1b) [27]. In rice, *KNOX* proteins decrease GA biosynthesis while elevating CK biosynthesis through *OsIPT2* and *OsIPT3*, two CK biosynthesis genes that maintain the high-CK and resulting low-GA context needed for meristem formation and maintenance [78].

3.1.5. Brassinosteroid Regulation by *CUC*

BRs are a class of steroid hormones that are essential for differentiation in plants [79–81]. In BR-hypersensitive mutants, organ fusion occurs [82]. BRs are involved in organ boundary formation and are regulated by organ boundary identity genes. *BZR1*, a BR-activated nuclear protein, directly represses *CUC*, the organ boundary identity gene (Figure 1c). In rice, *CYP734A2*, *CYP734A4*, and *CYP734A6*, which encode BR catabolism enzymes, are upregulated through *OSH1* gene induction, whereas *OSH1* loss of function mutants have boundary defects in leaves and in SAM, which leads to a BR-overproduction phenotype [82–85].

3.1.6. Auxin Transported by PIN

The auxin phytohormone is one of the most crucial factors regulating plant organ formation, especially leaf development. Generally, auxin is transported by PIN1-dependent efflux; however, it must act together with *AS1* to repress *BP* expression to promote leaf development and outgrowth at the flanks of the SAM [29,86]. Furthermore, leaf initiation can generate auxin, and it can be depleted from the proximity region via the PIN auxin efflux transporter, thereby inhibiting additional leaf primordium initiation at the SAM periphery [86–88] (Figure 1b). The auxin is transported back to the meristem under epidermal PIN1 polarity to stimulate the leaf and the leaf primordium to produce auxin [48,86,88]. Recently, it was reported that a WOX–auxin regulatory module determines the formation of leaf shape by coordinating growth along the proximodistal and mediolateral leaf axes [89].

3.1.7. Interplay between *KNOX* and *CUC*

The *CUC* genes encoding NAC TFs contribute to organ boundary formation, especially between lateral organs and the SAM [90]. The double mutant of *cuc1* and *cuc2* exhibits cotyledon fusion on both sides and has an obvious lack of SAM defects. Similarly, *stm* mutants also display a loss of SAM phenotype but show weak cotyledon fusion. The *CUC/STM* regulatory pathway is critical for the establishment of the boundary between the cotyledons and for the initiation of the SAM [91]. *CUC1* was shown to be regulated by *KNOX* binding sites in its promoter [30]. *CUC* genes are required for *STM* expression and are involved in SAM formation and processes at the shoot organ boundary (Figure 1b) [46,90,92,93].

3.1.8. Regulation of Other Genes in the SAM

The *CLV–WUS* feedback signaling interaction maintains the pluripotency of stem cells and coordinates their cell proliferation and differentiation in the SAM (Figure 1a) [94]. The *WUS* gene encodes a transcription factor with a homeobox domain and is expressed in the stem-end meristem tissue. When *WUS* protein translation is completed, it will gradually migrate to the upper three layers of cells in the central region and directly bind to the 1080 bp upstream of the CLV gene promoter to activate the expression of the *CLV3* gene, and CLV can move back to the organizing center to inhibit *WUS* expression [95,96]. Furthermore, *KNOX*s, especially STM, act as indispensable regulators in the SAM. The main function of STM is to inhibit cell differentiation and maintain the undifferentiated state of some cells in the SAM. *CLV* gene expression regulation is also influenced by STM and *WUSWUS* [97]. STM is required to suppress differentiation throughout the meristem dome, and these two processes sustain the maintenance and formation of the SAM. STM has converse functions to CLV, and undifferentiated cells of the shoot meristem fail to form in *stm* mutants. Overall, CLV and STM play relevant but opposing roles in the regulation of cell division or cell differentiation in meristems [50].

To maintain SAM function, *KNOX* genes serve as versatile factors regulating downstream genes, especially the plant phytohormonal regulatory factors [10,23,27,72–74,76,77,85,86,98]. The interplays between genes are maintained in early leaf primordium development along the adaxial–abaxial axis (Figure 1a).

3.2. Axial Polar Growth Regulation

3.2.1. Adaxial–Abaxial Establishment Regulation

If the primordia lose adaxial–abaxial development, they will produce a terete or stick-like leaf organ but barely shape an entire lamina. Leaving the SAM behind, as noted above, the primordia develop along three axes. Indeed, leaf adaxial fate is determined by the activity of a few gene products including PHV, PHB, and REV of HD-ZIP III [99,100]. The *miR165/166*, which acts in the abaxial domain of the leaf primordium, can target *HD-ZIP III* mRNAs [101]. Conversely, *HD-ZIP III* genes interact with *HD-ZIP II* genes to repress *miR165/166* [102,103]. In addition, *AS2* is directly repressed in the adaxial region by KANADI (KAN), a nuclear-localized protein in the GARP [104,105] (Figure 1c).

Additionally, *BOP2* is indispensable for *AS2* activation, specifically in the proximal, adaxial zone of the leaf [69,71].

Additionally, leaf abaxial fate is controlled by KAN, which governs the abaxial fate together with the YABBY (YAB) TF and ETT/ARF3-ARF4 [86,99,104,106–108]. The mutations of *ETT/ARF3-ARF4* have been found to alleviate ectopic KAN activity [109]. Three *ARF* genes, *ARF2*, *ETT*, and *ARF4*, have been identified as targets by the trans-acting siRNA (ta-siRNAs/TAS)3 (Figure 1c) [108,110,111]. Moreover, *HD-ZIP III* and *KANADI* mutants exhibit complementary phenotypes in *A. thaliana* [99].

3.2.2. Leaf Blade Formation

Leaf size is largely contingent on the plant species but varies, to a certain extent, due to environmental factors [112–115]. It has been reported that leaf size is partially mediated by overlapping pathways involving *AS2*, *CIN* encoding *TCP* TF, and hormone dynamics. There are two classes of adverse function factors in charge of the switch balance between cell expansion and cell proliferation: class II *TCP*, which negatively regulates leaf growth, and the *GRF*, whose overexpression often results in a larger leaf size [116,117]. The size of the proliferative region at the leaf base seems to be enlarged, and mutants with a loss of function of *CIN* have a concave distal boundary, such that cells at the leaf margin still proliferate, whereas cells in the center are already inhibited from proliferation [118,119]. Furthermore, *ARP* (*AS1*/RS2/PHAN), a MYB domain TF, is named by the *AS1* of *Arabidopsis*, the RS2 of maize, and the PHAN of *Antirrhinum* L., three homologous proteins. *ARP* and *AS2* also can manipulate the development of a symmetrical polarity of lamina expansion [62,120–123]. *AS1*/*AS2* may directly inhibit *KNOXI* gene expression to enhance leaf primordia initiation at the SAM flank [124]. Furthermore, *AS1*/*AS2* promotes leaf development by regulating the dorsoventral axis of leaf primordia initiation of organ formation [125].

3.3. *Patterning Determination: Leaf Complexity*

Leaf morphology can be classified as simple or dissected, whereas different types of leaves may recruit different factors and undergo different pathways in generating the final leaf shape. In *C. hirsuta*, a dissected leaf species, *ChBP* is repressed by the *miR164A/ChCUC* module and *ChAS1*, but this interaction never occurs in *A. thaliana*, a simple leaf species [12]. *KNOX* activity is under the control of different cis-regulatory factors in leaf primordia development, which induce leaflet formation [126]. The cis-regulatory factors of *KNOX* have significant roles in determining leaf complexity [127]. Additionally, the HBs, which contain a conserved 60 amino acid motif TF, contribute substantially to controlling leaf complexity. As mentioned above, *KNOXI* genes are expressed in the primordia of dissected leaves but are downregulated in the primordia of simple leaves, which indicates that different pathways are regulated by *KNOXI* genes in simple and dissected leaves. *A. thaliana*, which has simple leaves, and *C. hirsuta,* which has dissected leaves, are classic examples used in the study of simple dissected leaf diversity. In *C. hirsuta*, *KNOX* proteins are indispensable in the leaf, as they delay cellular differentiation, resulting in the development of dissected leaves, whereas in *A. thaliana*, they are excluded from leaves, leading to the generation of simple leaves [127]. In addition to the *KNOX*, *RCO*, encoding the homeodomain protein, has also been specifically identified as being involved in leaf complexity, and its patterns of expression enhance *C. hirsuta* leaf complexity by repressing growth at the flanks as well as leaflet formation [13]. However, *STM/BP-like* genes are uncoupled from *PHAN* in *M. truncatula*. Moreover, *KNOX*I and SGL1, which is an LFY ortholog, regulate parallel pathways of leaf development in *M. truncatula* [124].

3.4. *The Elaboration of the Edge: Leaf Margins*

Whether a leaf shape is simple or dissected, the leaf margin can be characterized as entire (smoothed), serrated, or lobed [33]. Members of the *NAM*/*CUC* family, which encode large evolutionarily conserved NAC proteins, are also involved in organ initiation and delimitation [90,128,129]. Notably, a collaborative group of *CUC* genes has been explored in different species with lobed and dissected leaves: *Aquilegia caerulea* E.James (Ranunculaceae), *C. hirsuta*, *Pisum sativum* L. (Fabaceae), *Solanum lycopersicum* L. (Solanaceae), and *S. tuberosum* L. [130]. The formation of the leaf margin mediated by a small gene regulatory network including *miR164* and *CUC/NAM* genes and auxin activity components establishes a *miR164*–*CUC/NAM*–PIN–auxin module, which has been demonstrated to play a role in leaf serration [12,32,130,131]. Recent genetic studies resulted in the revelation of an elegant module in elucidating the mechanism underlying the development regulation of leaf shape, which includes two loops at the leaf margin [131]. The first loop requires PIN1 auxin efflux transporters to capture potential auxins with self-organizing patterns in diverse developmental contexts. The other loop depends on *CUC2,* which facilitates the *PIN1*-dependent generation of auxin maxima activity. For instance, the serration development is driven by interspersed active peaks of growth-promoting auxin and *CUC2* [131]. The coordination between *CUC2* and *miR164a* determines the extent of serration. The mutations of the *miR164a* gene enhance serration at the leaf margin, and the overexpression of *miR164* promotes the smoothness of the leaf margin in *A. thaliana*. It is certain that deep serrations are extensively governed by interaction with *miR164*-resistant *CUC2* [132]. While *CUC2* interacts early with *miR164* at the commencement of tooth development, *CUC3* is prone to sustaining serrated tooth outgrowth (Figure 2). The *CUC3* gene functions in partially suppressing leaf serration [16]. However, as long as *CUC2* is uniformly expressed along the leaf margin instead of discretely expressed at the teeth, a smooth leaf margin will be generated, replacing the serrated margin of the leaf. At the dissected leaf margin, *NAM/CUC* genes establish a boundary domain that delimits leaflets and has a dual role in locally promoting leaflet separation [130]. Furthermore, the *KNOXI* proteins facilitate leaflet initiation in dissected leaf plants, and the actions of *KNOX* proteins depend on the ability of the PIN1 auxin efflux transporter to organize auxin [133]. *KNOX* activity inhibits cellular differentiation, leading to the production of dissected leaves in *C. hirsuta* [127]. Additionally, the ectopic expression of *KNOX* in leaves can perturb PIN1-dependent local gradients, thereby influencing auxin activity and resulting in leaf lobe or leaflet outgrowth promotion (Figure 2) [29].

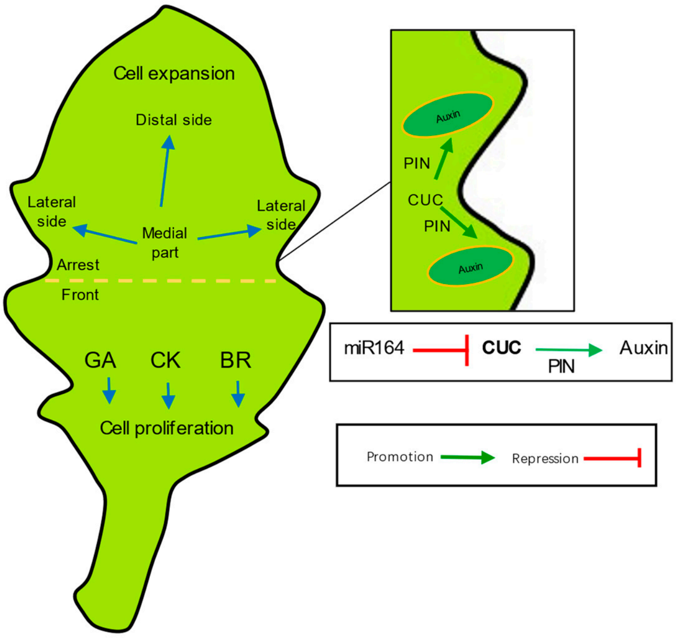

Figure 2. Interplay of genes in determining leaf polarity and margin. The serrations at the leaf margin are contingent on the regulatory interplay of *miR164*–*CUC*–*PIN*–auxin. *CUC* genes facilitate the *PIN*-dependent generation of auxin maxima activity at the leaf margin. Conversely, *miR164* represses the *CUC* gene, promoting smooth margin development.

4. Further Perspectives and Conclusions

Leaf shape is one of the most valuable traits for studying plants. Despite important studies having been conducted on a few model plants, there are still many plant species with possibly different leaf shape regulatory mechanisms that have played significant roles in plant evolution and, therefore, require further research. Furthermore, some genetic networks are still not yet fully elucidated, i.e., the precise domains in which genes impact their target genes and the regulatory balance in developmental phases have not been determined.

Here, we briefly summarized the leaf formation process to present the genes involved in leaf shaping and describe their roles throughout dynamic and overlapping phases. In each special phase, we attempted to concentrate on several core genes as the key players in that specific phase. For example, the *KNOXI* genes serve as a pivotal component contributing to the coordination of up/downstream genes in the SAM. Indeed, the genetics of leaf morphology shaping processes comprise enormous networks, and we concisely presented the details of the interplay between a few genetic elements associated with leaf shaping processes, such as *NAM/CUC–mi164a–PIN1*–auxin, *KNOX–GA20ox/GA2ox*–GA, and *KNOX–BAS1/CYP734A*–BR.

Author Contributions: Conceptualization, J.M. and H.L.; writing—original draft preparation, J.M.; writing—review and editing, J.M. and H.L.; supervision, H.L. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China (grant number 31770718).

Acknowledgments: We are thankful for funding from the National Natural Science Foundation of China (31770718) and three anonymous reviewers for inspiring comments on the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

ARF	AUXIN RESPONSE FACTOR
ARP	AS1/RS2/PHAN
AS1	ASYMMETRIC LEAVES1
BLH	BEL1-like homeobox
BOP1	BLADE ON PETIOLE1
BP	BREVIPEDICELLUS
BRs	Brassinosteroids
BZR1	Brassinazole-resistant 1
CIN	CINCINNATA
CK	Cytokinin
CLV	CLAVATA
CUC	CUP-SHAPED COTYLEDON
CYP734	Cytochrome P450 family 734
ETT	ETTIN
GA20ox	GIBBERELLIN 20 OXIDASE
GA2ox	GIBBERELLIN 2 OXIDASE
GARP	GLUTAMIC ACID-RICH PROTEIN
GRF	GROWTH REGULATING FACTOR
H3K27me3	histone H3 lysine 27 trimethylation
HD-ZIP	Homeodomain leucine zipper
KAN	KANADI
KNAT	KNOTTED-like HOMEOBOX Arabidopsis thaliana
KNOX	KNOTTED-like HOMEOBOX
LHP1	LIKE HETEROCHROMATIN PROTEIN 1
LOB	LATERAL ORGAN BOUNDARIES
miRNA	microRNA

NTH15	Nicotiana tabacum homeobox15
OSH	Oryza sativa homeobox
OsIPT	Oryza sativa isopentenyl transferases
PHAN	PHANTASTICA
PHB	PHABULOSA
PHV	PHAVOLUTA
PIN1	PIN-FORMED1
POTH1	potato homeobox1
RCO	REDUCED COMPLEXITY
REV	REVOLUTA
RS2	ROUGH SHEATH2
SAM	shoot apical meristem
SGL1	SINGLE LEAFLET1
StBEL5	Solanum tuberosom BEL5
STM	SHOOT MERISTEMLESS
TALE	three-amino-acid-loop-extension
TF	transcription factor
WOX	WUSCHEL-like HOMEOBOX

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