Review Article

Leaf angle: a target of genetic improvement in cereal crops tailored for high-density planting

Yingying Cao1, Zhuojun Zhong1, Haiyang Wang1,2,* and Rongxin Shen1,*

1State Key Laboratory for Conservation and Utilization of Subtropical Agro-Bioresources, South China Agricultural University, Guangzhou, China
2Guangdong Laboratory for Lingnan Modern Agriculture, Guangzhou, China

Summary
High-density planting is an effective measure for increasing crop yield per unit land area. Leaf angle (LA) is a key trait of plant architecture and a target for genetic improvement of crops. Upright leaves allow better light capture in canopy under high-density planting, thus enhancing photosynthesis efficiency, ventilation and stress resistance, and ultimately higher grain yield. Here, we summarized the latest progress on the cellular and molecular mechanisms regulating LA formation in rice and maize. We suggest several standing out questions for future studies and then propose some promising strategies to manipulate LA for breeding of cereal crops tailored for high-density planting.

Introduction
Global food production is predicted to increase at least 100%–110% to be enough to feed the projected 10 billion people by 2050 (Tilman et al., 2011; UN World Population Prospects, 2020). To meet this demand, annual cereal production will need to rise to about 3 billion tons from 2.79 billion in 2021 (FAO statistical databases, 2021). Therefore, new breeding technologies are urgently needed to boost crop yields. Growing evidence has shown that increasing planting density is an effective strategy to increase crop yield per unit area. For instance, the average plant density of maize in the Central Corn Belt of the United States has increased from ~30 000 plants per hectare in the 1930s to ~80 000 plants per hectare now, which contributed critically to the continuous yield increase in the past century (Duvick, 2005; Ma et al., 2014; Wang et al., 2020a). Therefore, identification of LA regulatory genes and elucidation of their functional mechanisms could provide promising targets and strategies for breeding elite cultivars tailored for high-density planting.

In this review, we summarize the latest progress on elucidating the molecular mechanisms regulating LA formation in cereal crops (mainly rice and maize). We also highlight some open questions for future in-depth LA studies. Finally, we propose some promising strategies to boost dense planting breeding through genetic modifications of LA and plant architecture in crops.

Cytological dynamics of LA development
The size of LA in grasses is largely determined by a structure called ligule (also called as lamina joint in rice) within leaf, which links the blade and sheath. The ligular region consists of an outgrowing ligule and a pair of wedge-like auricles, and bends the blade away from the vertical stem to form LA (Figure 1). Below, we use maize as the example to describe the cellular landscape of ligular development. As in other cereal crops, maize leaf is initiated through recruiting the founder cells at the flank of a shoot apical meristem. By the plastochron2 (P2) stage, the proximal–distal,
Medial-lateral and adaxial-abaxial polarities have been sequentially defined, then a genetic programme initiates LA formation at the base of a developing leaf. Cytologically, LA formation can be broadly divided into three main sequential stages (Figure 1b): (i) the establishment of the blade-sheath boundary (BSB) zone that separates the future leaf blade and leaf sheath, (ii) the formation of a small cell band called the preligule band (PLB) within the boundary region and (iii) the development of ligule and auricle within the ligular region due to distinct cell division and expansion patterns (Sylvester et al., 1990). At the boundary zone formation stage, the cells giving rise to blade and sheath are indistinguishable, and the ligular structure per se is invisible (Becraft et al., 1990; Sylvester et al., 1990) (Figure 1b, left). The ligular region becomes first visible at the P5-P6 stages when a group of epidermal cells undergo rapid longitudinal and transverse anticlinal division, forming a PLB harbouring small cells (Figure 1b, middle). Later, at the P7 stage, a ligule emerges from the small cells at the base of preligule that divide periclinally and produce a ligular ridge in the adaxial side of the blade. After ligule initiation, a thin wedge of small cells behind the ligule begins to divide and enlarge and subsequently develops into the auricle structure to bend the blade (Figure 1b, right; Figure 2a,b). Transverse section analysis revealed that the maize ligular region and the rice lamina joint are mainly composed of vascular bundles, sclerenchyma cells and parenchyma cells (Figure 2c,d). Interestingly, the rice contains several aerenchymas within the lamina joint, while the maize contains a large number of colourless cells (also called ‘clear cells’) instead (Figure 2c,d). It is believed that the size of auricle, the mechanical strength of the midrib (which is mainly determined by sclerenchyma cells) and the ratio of adaxial to abaxial surfaces of the ligular region or lamina joint are largely responsible for the size of LA. In general, increasing the ligular region becomes larger and enhances the proliferation and expansion of parenchyma cells in the adaxial side of the region enlarges LA (Figure 2) (Cao et al., 2020; Chen et al., 2018; Kong et al., 2017; Ning et al., 2011; Sun et al., 2015; Tian et al., 2019; Zhao et al., 2010).

**Molecular regulation of LA formation**

During the past 30 years, genetic-, molecular- and microdissection-based transcriptomic analyses have identified a few dozen genes and several classes of plant hormones that regulate the formation of ligule and auricle (Figures 3 and 4; Table 1 and Table S1). Below, we briefly summarize the molecular mechanisms regulating the three developmental stages of LA.

**Regulation of the proximal–distal boundary between leaf blade and sheath**

The initiation of ligular region marks the formation of a boundary between the leaf sheath and blade, and is key to the formation of the leaf proximal–distal axis and LA. Physiological and genetic studies have documented evidence for a role of auxin, brassinosteroids (BRs) and cytokinin (CK) in BSB formation. For example, applying inhibitors of polar transport of auxin in maize seedlings severely disrupts the formation of BSB (Tsiantis et al., 1999). Similarly, perturbation of BR synthesis or signalling transduction results in disrupted BSB, smaller ligule and abnormal auricle (Kir et al., 2015; Makarevitch et al., 2012). Furthermore, a semi-dominant Hairy Sheath Frayed1 (ZmHsf1, encoding a CK receptor) mutant produces an abnormal outgrowth at the distal blade margin that resembles a leaf-like structure carrying auricle/ligule and sheath, indicating a role of CK in regulating BSB formation (Muszynski et al., 2020).

In addition, a series of studies revealed a conserved role of KN1-LIKE HOMEOBOX (KNOX) genes in BSB establishment in monocots and dicots, as ectopic expression in the gain-of-function mutants such as Knotted1 (KN1), Gnarley1 (KNOX4), Liguleless3 (LG3) and Liguleless4 (LG4) causes formation of ectopic BSBs in maize (Fowler and Freeling, 1996; Moreno 1999; Muehlbauer et al., 1999; Ramirez et al., 2009; Smith et al., 1992; Strable and Nelissen, 2021). It has been proposed that KNOX protein accumulated at the base of the leaf primordium might mediate efflux auxin from the base and boundary to maintain distal auxin distribution, possibly through direct regulation of...
PIN1s (Bolduc et al., 2012; Johnston et al., 2014). In addition, KNOX genes might promote CK accumulation at the base of leaf primordium possibly through activating CK synthesis; then, CK signalling could be transduced by Hsf1 (see above) to promote sheath development (Muszynski et al., 2020; Sakamoto et al., 2006). These analyses collectively suggest that KNOX proteins function to maintain a distal auxin maxima and a proximal CKs level that is crucial for the BSB establishment. Besides, KNOX genes may also regulate a group of typical boundary genes to further define the BSB. For instance, it was reported that KN1 might directly regulate the expression of the maize homologs of Arabidopsis boundary gene Blade-On-Petiole (ZmBOPs) at the proximal leaf primordium to define BSB (Bolduc et al., 2012; Johnston et al., 2014). Consistent with this notion, the leaves of Osbop1/2/3 triple mutant exhibit blade- but not sheath-characteristics, with the disruption of BSB and malformation of...

Figure 2 Morphology and cytology of the ligular region in rice and maize. (a) Morphology of the lamia joints of rice leaf with large (left) and small (right) leaf angle (LA). (b) Morphology of the ligular regions of maize leaf with large (left) and small (right) LA. (c) Schematic models of the cross-sections for the lamia joints of rice leaf with large (left) and small (right) LA. (d) Schematic models of the cross-sections for the ligular regions of maize leaf with large (left) and small (right) LA. The schematic models are drawn based on the cross-sections of the maize ligular region and the rice lamia joints stained with Fasga (Méchin et al., 2005), in which the sclerenchyma cells are shown in red, while parenchyma cells and colourless cells are shown in blue. The colourless cells (also called ‘clear cells’) are a group of cells intervening the abaxial vascular bundle and the adaxial sclerenchyma cells within the maize ligular region (Strable et al., 2017). The auricles are highlighted with red dashed circles in (a) and (b). Ad, adaxial; Ab, abaxial; Sc, sclerenchyma; Vb, vascular bundle; Pc, parenchyma; Cc, colourless cells; Ac, arenchyma.

Figure 3 Models for blade–sheath boundary and preligule band formation. (a) A model for blade–sheath boundary (BSB) patterning. KNOX protein is accumulated at the base of the leaf primordium and might maintain distal auxin distribution through regulating PIN1s. KNOX protein might also promote CK accumulation at the proximal leaf primordium through activating CKs synthesis, and the CK signal could be further transduced by Hsf1. An intertwined regulatory network involving KONXs, BOPs, RS2 and LOB proteins likely operate in specifying BSB formation. (b) A model for preligule band formation. ZmLGN might phosphorylate and reorient ZmPIN1s to mediate transmission of auxin from midrib to the leaf margins. Two potential transcriptional modules (LG2-LG1 and TCPs-LG1) in regulating PLB formation are also shown.
ligule and auricle (Toriba et al., 2019). Similarly, a barley BOP homolog Uniculme4 (HvCUL4) also plays a role in ligule/auricle development (Tavakol et al., 2015). Interestingly, BOP genes may also regulate the expression of KNOX genes through a conserved feedback mechanism. In Arabidopsis, BOP proteins activate the Lateral Organ Boundary (LOB) transcription factors, and LOB in turn form a trimeric complex with Jagged Lateral Organs (JLO, LBD transcription factor) and Asymmetric Leaves1 (AS1, MYB transcription factor) to represses KNOX expression at the boundary (Ikezaki et al., 2010; Rast and Simon, 2012). Similarly, the maize AS1 homolog Rough sheath2 (RS2) and the LOB factor Indeterminate Gametophyte1 (IG1) are co-expressed with ZmBOPs and inhibit the expression of KNOX genes (Evans, 2007; Schneeberger et al., 1998). These findings collectively indicate BSD formation entails an intertwined regulatory network of KONX genes, BOP genes and phytohormones, yet much remains to be elucidated regarding their detailed regulatory relationship (Figure 3a).

### Regulation of PLB formation

The PLB produces small cells within the BSB region that undergo distinct division patterns, and ultimately give rise to ligule and auricle. It has been proposed that a signal originated from the midrib that transmits to the leaf margins triggers PLB formation (Becraft and Freeling, 1991). Limited evidence suggests that auxin might be the signal per se or plays a role in transmitting the preligule signal to guide PLB formation (Figure 3b). Interestingly, the semi-dominant Lgn-R maize mutant develops ligular patches next to midrib instead of a continuous ligule and displays diffuse blade–sheath boundaries with a discontinuous expression pattern for the auxin efflux transporter ZmPIN1a across the ligular region, in contrast with continuous expression pattern of ZmPIN1a in the wide type plant, suggesting that polar auxin transport plays a critical role in PLB formation (Moon et al., 2013). Further study showed that ZmLGN encodes a serine–threonine kinase and that it functions upstream of ZmLG1, hinting a possibility that ZmLGN might be involved in regulation of the phosphorylation status of ZmPIN1a, and subsequently influence transmission of auxin from midrib to the leaf margins (Figure 3b). However, further studies are required to validate this possibility.

Molecular genetic studies have also identified several transcription factors regulating PLB formation. Null mutants of maize Liguleless2 (ZmLG2, which encodes a bZIP/DOG domain transcription factor) often lack or have incorrectly positioned ligule and auricles, and the BSB is diffuse (Walsh et al., 1998), whereas mutants of Liguleless1 (LG1, which encodes a SQUAMOSA Promoter-Binding domain protein) in maize, rice, barley and wheat all have an evident BSB, but lack ligule and auricle, suggesting that LG1 does not affect BSB formation, but is essential for PLB formation and outgrowth of ligule and auricle (Becraft et al., 1990; Lee et al., 2007; Moreno et al., 1997; Rossini et al., 2006; Sylvester et al., 1990; Yu, 2019). Interestingly, mosaic analysis indicated that the maize lg2-R phenotype is cell non-autonomous, whereas the lg1-R phenotype is cell autonomous. Spatiotemporal expression analysis further suggested that ZmLG2 likely plays an early role prior to ZmLG1 in specifying the formation of both BSB and PLB within the young leaf primordia (Walsh et al., 1998). Consistently, studies of the phenotypes of OsLG2/2L and OsLG1 knockout lines, together

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**Figure 4** Model depicting the extensive cross-talks between the signalling pathways of BRs, Auxin, GA and SL in regulating leaf angle. Positive regulators which enlarge the size of leaf angle (LA) are shown in black, and the negative ones are shown in red. Black arrows indicate positive regulation, while black lines ended with perpendicular bars represent suppressive regulation. The dotted arrows and lines indicate undetermined relationships.
Table 1: Identified QTLs associated with leaf angle in maize and rice

| Species       | Parents                        | Pop.          | Chromosomes (no. of QTLs) | PVE range          | Candidate genes (maize and rice)                              | Reference         |
|---------------|--------------------------------|---------------|---------------------------|--------------------|---------------------------------------------------------------|-------------------|
| Zea mays      | B73, Mo17                       | RILs          | 1, (2), (2), (1), (1),   | 2%–28%            | ZmDWF4, ZmYABBY15                                             | Mickelson et al. (2002) |
|               |                                |               | 6, (1), 1, (1)           |                    |                                                               |                   |
| Zea mays      | Ye478, Dan340                   | F2,3          | 2, (2), (2), (1), (1),   | 2%–11%            |                                                               |                   |
|               |                                |               | 5, (1)                   |                    |                                                               |                   |
| Zea mays      | Yu82, Shen137                   | F2,3          | 1, (1), (1), (1), (1),  | 7%–20%            |                                                               |                   |
|               |                                |               | 5, (1), (1)              |                    |                                                               |                   |
| Zea mays      | NAM                            | RILs          | 1, (5), (3), (3), (3),  | 0.5%–2%           |                                                               |                   |
|               |                                |               | 6, (1), 7, (3), 8, (3), |                    |                                                               |                   |
|               |                                |               | 9, (2), 10, (2)          |                    |                                                               |                   |
| Zea mays      | Yu82, Yu87-1                    | F2,3          | 1, (1), (1), (1), (1),  | 7.34%–8.43%       | ZmDWF4, ZmLG1, ZmTAC1, ZmLG2, ZmLCIC, ZmYABBY15               | Ku et al. (2012)  |
|               |                                |               | 8, (1)                   |                    |                                                               |                   |
| Zea mays      | Ye478, Dan340                   | F2,3          | 1, (1), (1), (1), (1),  | 10.4%–16.4%       |                                                               |                   |
|               |                                |               | 5, (1)                   |                    |                                                               |                   |
| Zea mays      | Yu82, D132                      | F2,3          | 1, (4), (2), (2), (1),  | 6%–85%            | ZmDWF4, ZmLG1, ZmTAC1, ZmLG2, ZmLCIC, ZmYABBY15               | Ku et al. (2012)  |
|               |                                |               | 8, (1)                   |                    |                                                               |                   |
| Zea mays      | Ye478, Ro8                      | F2,3          | 1, (4), (2), (2), (1),  | 7.54%–17.17%      |                                                               |                   |
|               |                                |               | 5, (1)                   |                    |                                                               |                   |
| Zea mays      | Yu82, D683                      | RILs          | 1, (1), (1), (1), (1),  | 8.41%–12.11%      |                                                               |                   |
|               |                                |               | 4, (1), (1), (1), (1),  |                    |                                                               |                   |
|               |                                |               | 6, (1), 7, (3), 10, (1) |                    |                                                               |                   |
| Zea mays      | Yu82, D683                      | RILs          | 1, (1), (1), (1), (1),  | 3.61%–20.62%      | ZmGT1, ZmDWARF4, ZmPHB1, ZmLCR, ZmTB1, ZmKNI-D1, ZmLG1, ZmTAC1, ZmLCIC, ZmYABBY15 | Shi et al. (2017) |
Manipulating leaf angle for high density planting in crops

Table 1 Continued

| Species             | Parents  | Poped | Chromosomes (no. of QTLs) | PVE range | Candidate genes (maize and rice) | Reference          |
|---------------------|----------|-------|---------------------------|-----------|---------------------------------|-------------------|
| Oryza sativa        | 529 O. sativa accessions | Inbred | 1(1), 3(2), 6(1), 7(1), 8(1), 11(1), 12(1) | 0.2%–26.5% | OsbHLH174, OsbHLH173, OsbHLH153 | Dong et al. (2018) |
| Oryza sativa        | Cheongcheong, Nagdong | DH     | 4(1), 11(3) | 9%–51% | Osbsk2 | Ham et al. (2019) |
| Oryza sativa        | Takanari, Koshihikari | BILS, NILs | 1(2), 2(2), 4(1), 5(1), 9(1) | 13.3%–23.4% | OsbHLH174, OsbHLH173, OsbHLH153 | San et al. (2021) |

Pop., population; PVE, percentage of variation; F$_{2.3}$, F$_{2}$-derived F$_{3}$; CSSL, chromosome segment substitution line; RILs, recombinant inbred lines; DH, double haploid.

with their spatiotemporal expression patterns also indicated that OsLG2 and OsLG2L might function earlier than OsLG1 in lamina joint position determination and lamina joint formation (Wang et al., 2021). Moreover, transcriptomic analyses showed that enrichment of auxin signalling output-related processes, including altered expression of SAURs, AUX/IAA family of genes and ARF genes, suggesting that OsLG2/LG2L and OsLG1 likely act to regulate lamina joint development and thus LA size through regulating auxin signalling (Wang et al., 2021). In line with this notion, a recent study showed that TaSPL8, the ortholog of LG1 in wheat, regulates LA size via directly inducing the expression of TaSPL6 (Liu et al., 2019). Moreover, it was shown that expression of 2miLG1 is promoted by ectopically expressed Wavy Auricle in Blade (ZmWAB1), which encodes a Teosinte Brachched1, Cyclodea, PCF (TCP) transcription factor normally expressed in maize tassels (Hay and Hake, 2004; Lewis et al., 2014). Therefore, it was speculated that other TCP factors expressed in the ligule boundary region might trigger LG1 expression to induce ligule formation (Lewis et al., 2014). These findings suggest two potential transcriptional modules (LG2-LG1 and TCPs-LG1) regulating PLB formation, but the detailed regulatory relationship between them awaits further studies (Figure 3b).

Regulation of ligule and auricle formation

Leaf angle is a quantitative trait controlled by multiple genetic loci. Recent molecular genetic studies have identified dozens of QTLs and genes affecting LA in maize and rice (Figure 4; Table 1). Notably, most of the genes identified so far either encode transcriptional regulators or signalling components of various phytohormones. In particular, ample evidence indicates that BRs play a central role in regulating LA formation, while several other hormones, including auxin, gibberellins (GAs), strigolactones (SLs) and ethylene, also contribute to LA formation, likely through cross-talking with BR signalling. Below, we briefly summarize the signalling pathways of various hormones regulating LA formation.

BR regulation of LA formation

Numerous studies documented a positive role of BR in regulating LA formation (Figure 4; Table S1) (Li et al., 2020b; Luo et al., 2016). BR regulation of LA probably has been best studied in rice. Rice mutants deficient in BR biosynthesis (such as Osbrd1, Osbrd2, Osrd2, Osrd4 and Osrd11), BR perception (such as Osbr1) or signalling (OsbrZ1-RNAI, Osbsk2a, etc.) all display more erect leaves (Bai et al., 2007; Hong et al., 2003, 2005; Li et al., 2009; Mori et al., 2002; Nakamura et al., 2006; Sakamoto et al., 2006; Tanabe et al., 2005; Yamamuro et al., 2000; Zhang et al., 2016). It has been shown that OsbZ1 acts as a central transcriptional regulator in the OsBR1-mediated BR signalling pathway to mediate various BR responses, including LA (Figure 4). For example, OsBZR1 represses the transcription of OsDLT (encoding a GRAS transcription factor, a positive regulator of LA) and OsLC1 (encoding a CCHC-type zinc-finger transcription factor, a negative regulator of LA) to positively regulate LA (Tong et al., 2012). In turn, OsDLT promotes the expression of OsB2R1. Moreover, OsLC1 could repress the expression of OsIL1 (encoding an HLH protein) but activate OsSH1 (encoding a bHLH protein that binds IL1), and these two transcription factors jointly regulate the elongation of the adaxial cells in the lamina joint and LA size in rice via HLH/bHLH antagonism (Zhang et al., 2009, 2012). In the contrary, OsGSK2, a negative regulator of BR signalling in rice, can phosphorylate OsBZR1, DLT, OsLC1, OsRLA1, OsSFP3 and qSW5/GW5 (a plasma membrane-localized calmodulin-binding protein) and consequently regulate their protein accumulation, thus modulating BR responses and reducing LA (Liu et al., 2017; Qiao et al., 2017; Tong et al., 2012; Xiao et al., 2020; Zhang et al., 2012). Interestingly, a recent study showed that when BR signalling is attenuated, BIN2 (a GSK3-like kinase) is activated, which inhibits BES1 activity to release the inhibitory effect on CYC U4;1 transcription, and meanwhile, BIN2 can also phosphorylate CYC U4;1 to activate the CYC U4;1/CDKA complex, leading to enhanced abaxial sclerenchyma cell division and erect leaves (Figure 4; Sun et al., 2015). This study for the first time established a direct link between BR signalling and cell proliferation in the lamina joint during determination of LA size in rice.

In addition, it has been shown that a number of genes modulate LA through regulating BR biosynthesis or signalling (Figure 4). For example, OsSRAV-Like1 (OsSRAVL1, a B3 domain transcription factor) could directly bind to the promoters of OsBR1, OsDWARF2 (OsD2), OsDWARF1 (OsD11) and OsBRD1 to promote their expression, thus increasing the size of LA in rice (Je et al., 2010), whereas a transmembrane protein OsELT1 positively regulates LA size through stabilizing OsBR1 (Yang et al., 2017). In addition, a mediator OsMED25 and an APETALA2 domain-containing transcription factor OsRLA1 regulate the size of LA through interacting with OsBR1 and enhancing its activity, while a negative BR signalling regulator U-box E3 ubiquitin ligase OsUPB24 represses lamina joint inclination through ubiquitination and degradation of OsB2R1. The AtBIN2 homolog OsSK2 regulates the stability of OsPUB24 through phosphorylation (Min et al., 2019; Qiao et al., 2017; Ren et al., 2020a). Moreover, it was shown that OsBU1 and OsBUL1 (both of them encode typical HLH proteins) and OsGRAS19 (encoding a homolog of DLT) positively regulate LA (Chen et al., 2013; Jang et al., 2017; Tanaka et al., 2009). Furthermore, it was shown that
OsBUL1, LO9-177 and OsBC1 form a tri-protein complex that positively regulates LA in rice through regulating BR signalling and cell elongation in the lamina joint (Chen et al., 2013; Jang et al., 2017). Furthermore, it was reported that OsLC2 (encoding a VIN-3 like protein), OsPLA1 (encoding a cytochrome P450 protein) and OsMDP1 (encoding a MADS-DOMAIN-CONTAINING PROTEIN) negatively regulate LA through controlling expansion and division of adaxial parenchyma cells of the lamina joint (Duan et al., 2006; Xiong et al., 2021; Zhao et al., 2010). However, the detailed molecular mechanisms linking these genes to BR signalling remain to be elucidated in future studies.

Similarly, maize mutants defective in BR biosynthesis (such as Zmna1, Zmna2 and Zmbrd1) or signalling (such as ZmBRI1-RNAi and Zmii1) also display more erect leaves (Best et al., 2016; Hartwig et al., 2011; Kir et al., 2015; Makarevitch et al., 2012; Ren et al., 2020b), indicating a conserved positive role of BRs in LA regulation in maize. However, less is known about BR signalling mechanisms in maize, compared with rice. In a recent illuminating study, Tian et al. (2019) demonstrated that ZmAFLV1 directly activates ZmBRD1 expression, leading to increased BR levels and larger LA. Both ZmDRL1 (a YABBY protein with a C2C2 zinc-finger DNA-binding domain, a negative regulator of LA, Strable et al., 2017) and ZmLG1 can directly bind to the upstream regulatory sequence of ZmAFLV1 (a positive regulator of LA). Moreover, ZmDRL1 can physically interact with ZmLG1 to suppress transcriptional activation of ZmAFLV1 by ZmLG1, thus reducing LA. This study fills in a significant gap between LG1 and BR signalling in LA regulation.

Interestingly, two OsBRI1-independent BR signalling pathways regulating LA were also reported in rice. Oki et al. (2009) reported that a rice α-subunit of heterotrimeric G protein, OsD1/RGA1, mediates BR signalling independent of OsBRI1 and could enhance leaf inclination and grain size in rice. Similarly, Liu et al. (2016) demonstrated that OsLPA1, which encodes an INDETERMINATE DOMAIN protein, regulates lamina joint bending by suppressing auxin signalling that interacts with C-22-hydroxylated and 6-deoxo BRs in rice, in an OsBRI1-independent manner. They further showed that the expression levels of OsPIN1a, OsPIN1c and OsPIN3a are positively correlated with those of OsLPA1. Nevertheless, the detailed molecular mechanisms remain to be elucidated.

**Regulation of LA formation by other hormones**

Numerous studies suggest that auxin plays a negative role in regulating LA size (Figure 4), as a number of rice mutants defective in auxin biosynthesis or signalling (such as Osfibs, OsAA1-OE, OsGH3s-OE, Ostir1 and OsAFB2-RNAi) display enlarged LA (Bian et al., 2012; Du et al., 2012; Song et al., 2009; Yoshikawa et al., 2014). For example, a gain-of-function mutant for OsGH3-1 encoding an indole-3-acetic acid-amido synthetase exhibits increased LA due to accelerated cell elongation at the lamina joint, likely caused by decreased free IAA levels (Zhao et al., 2013). At the mechanistic level, it has been shown that two positive regulators of auxin signalling, OsARF6 and OsARF17, could directly bind to the promoter of OsLIA1 (encoding a Raf-like MAPKKK) and promote its expression, resulting in reduced mechanical tissue formation at the lamina joint, thus producing more upright flag leaf (Huang et al., 2021; Ning et al., 2011). In contrast, three negative regulators of auxin signalling, OsARF1, OsARF11 and OsARF19, were shown to promote OsBR1 and OsGH3s expression, thus enlarging the size of LA (Attia et al., 2009; Liu et al., 2018; Zhang et al., 2015).

OsLC3, encoding a SPOC domain-containing transcription suppressor, also influences OsGH3 expression to inhibit elongation of adaxial cells of the lamina joint, thus reducing LA size (Chen et al., 2018). In addition, auxin induces expression of OsMIR393s and OsMIR394, and OsMIR393s could enhance leaf inclination through suppressing their target genes OsTIR1 and OsAFB2, while OsMIR394 suppresses the expression of OsLC4 (encoding an F-box protein and a target of OsMIR394), thus reducing LA through inhibiting elongation and expansion of adaxial parenchyma cells at the lamina joint (Bian et al., 2012; Qu et al., 2019). Moreover, a role of auxin in regulating LA in maize is supported by the observations that ZmPGP1, an auxin efflux carrier P-glycoprotein, is involved in the regulation of LA in maize (Li et al., 2019; Wei et al., 2018).

Several studies suggest that GA plays a promoting role in LA formation (Figure 4). For example, knockdown mutants of OsSPY (a negative regulator of GA signalling) have increased BR levels and hence increased LA (Shimada et al., 2006). In addition, a positive regulator of GA signalling, OsGSR1, positively regulates LA size through directly interacting with the BR biosynthetic enzyme OsBRD2 and enhancing its activity (Wang et al., 2009). Moreover, a recent study showed that transgenic rice plants expressing OsBCL1 and OsBCL2, two homologous genes of OsBC1, under the control of OsBUL1 promoter, exhibit larger LA and contain higher GA3 levels than the wild type plants, suggesting that both OsBCL1 and OsBCL2 promote cell elongation at the lamina joint at least partially through increased GA biosynthesis (Jang et al., 2021). However, another study showed that treatment with exogenous GA inhibits BR biosynthesis and signalling and hence reduces LA in plants, suggesting a negative role of GA in LA regulation (Tong et al., 2014). Therefore, the precise function of GA on LA regulation needs to be further clarified.

Several rice mutants defective in SLs biosynthetic and signalling (d10, d17, d27, d3 and d14) display increased LA, indicating a negative role of SLs in LA regulation (Li et al., 2014). Accumulating evidence suggests that SLs may regulate LA through interacting with other hormone signalling pathways. For example, the SLs positive regulator OsDWARF3 (a F-box protein) was shown to interact with OsBZR1 and trigger its degradation, thus decreasing LA size, whereas the SLs negative regulator OsDWARF53 could enhance the transcriptional repression activity of OsBZR1 to increase LA size (Fang et al., 2020). In addition, a recent study showed that mutations in the ethylene biosynthetic gene ZmAACS7 and its closest paralog ZmAACS2 cause increased LA through promoting the longitudinal cell elongation of the auricle tissue in maize (Li et al., 2020a), suggesting a negative role of ethylene in LA regulation. Nevertheless, the detailed molecular mechanisms of SLs and ethylene regulation of LA formation remain to be further elucidated.

**Perspective**

As summarized above, despite the great progress made in recent years on elucidating the cellular and molecular mechanisms regulating LA formation in cereal crops (mainly in rice and maize), a number of pressing questions still stand out. First, the signal (s) that dictates the BSB formation and triggers the formation of PLB has not been unequivocally determined. Second, how the signal (s) is perceived and propagated from the midvein to the leaf margins still remain to be elucidated. Third, the detailed molecular mechanism regulating the outgrowth of ligule and auricle still...
remain poorly understood. Fourth, from a view of plant breeding, despite a large number of LA-associated genes have been cloned (Table S1), the majority of them have not been exploited in plant breeding practice. A likely reason is that many LA genes pleiotropically regulate many other plant developmental processes besides LA. Therefore, changes, either loss-of-function or overexpression, in these LA genes often result in some unfavourable effects, such as plant dwarfism, reduced tillers and smaller grains (Hong et al., 2002, 2003, 2005; Tanabe et al., 2005, Tong et al., 2012). One approach to mitigate the negative effects of pleiotropic genes is to carefully manipulating their expression levels or patterns. For example, RNAi-OsBRI1 transgenic plants obtained a 30% increased grain yield under dense planting conditions (Morinaka et al., 2006). In addition, identification and utilization of superior alleles in natural populations might be a preferred strategy. For instance, a recent study elegantly demonstrated that two QTLs that confer reduced LA, Upright Plant Architecture1 (UPA1), encodes BRD1, an enzyme essential for bioactive BR biosynthesis and UPA2 (UPA2 is controlled by a 2-bp nucleotide difference located 9.5kb upstream of ZmRAV1.1), can be successfully leveraged from its ancestor, teosinte, to maize to breed maize cultivars with more compact plant architecture and enhanced grain yields (Tian et al., 2019). Therefore, continued identification of new LA regulatory genes with minimal adversary effects on plant architecture may provide promising targets for genetic manipulation of LA and plant architecture for high-density planting. Moreover, with a better understanding of the regulatory network of LA formation, biotechnological approaches can be utilized to more precisely manipulate gene expression in a tissue- or developmental-specific manner to tailor plant architecture for high-density planting. The increased toolkits (such as genome editing) available now should greatly empower us to molecular design and create new germplasm that can better adapt to high-density planting and increased yield per unit land area in the years to come.

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Conflict of interest

The authors declare they have no conflict of interest.

Author’s contributions

All authors contributed to the writing of this review article.

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### Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table 1** Blade-Sheath Boundary (BSB), preligule band (PLB) formation and leaf angle regulation related genes in maize and rice.