

ERECTA family proteins: the bridge in plant aerial morphogenesis

Hengke Jiang^{1,2,3}, Yuhui Chen^{1,2,3}, Yuhan Liu^{1,2,3}, Jing Shang^{1,2}, Xin Sun^{1,2,3}, Junbo Du^{1,2,3}

¹ *College of Agronomy, Sichuan Agricultural University, Chengdu 611130, China*

² *Research Center for Modern Agriculture of the Middle East, Sichuan Agricultural University, Chengdu 611130, China*

³ *Key Laboratory of Crop Ecophysiology and Farming System in Southwest China, Ministry of Agriculture, Sichuan Agricultural University, Chengdu 611130, China*

Corresponding authors: Xin Sun (sunxin@sicau.edu.cn) and Junbo Du (junbodu@sicau.edu.cn)

Abstract

Receptor-like kinases (RLKs) were found to participate in multiple signaling pathways and are considered one of the most critical parts of the early event of intercellular signaling. Of the many, the *ERECTA* family (ERf) consists of three genes: *ERECTA*, *ERL1* and *ERL2*. Each of the three genes can combine with other proteins to regulate multiple signaling pathways from plant growth, development, and environmental adaptation. Although it is indispensable, the detailed information about ERf manipulated signaling pathways is still largely elusive. Here we are tempted to summarize the essential roles of ERf in aerial morphogenesis, including shoot apical meristem, stem, and reproductive organ development. This review would provide better insights into the role of ERf in modulating several intercellular signaling pathways.

Keywords: ERf, *ERECTA*, *ERL1*, *ERL2*, RLK, aerial morphogenesis

1 | INTRODUCTION

Multicellular organisms rely on intercellular signal transduction in response to environmental stimuli, and information exchange between cells depends heavily on the cell-surface located receptor protein kinases. Primarily, the definition of receptor protein appears in animal research and is called receptor tyrosine kinase (RTKs) (van der Geer *et al.*, 1994). In plants, researchers identified the proteins with similar structures to RTKs named receptor-like kinases (RLKs) (Walker & Zhang, 1990). Since then, RLKs have been popular in plant research. Currently, more than 610 RLKs are identified in *Arabidopsis thaliana* including at least 225 leucine-rich repeat RLKs (LRR-RLKs), which means plants have complex signals networks (Shiu & Bleecker, 2001; Liu *et al.*, 2017). Meanwhile, it has been found that some RLKs participate in multiple signal pathways, the LRR-RLK *ERECTA* (*ER*) is one of them.

In 1957, George Rédei *et al* isolated Landsberg *erecta* (*Ler*) from Landsberg (La-0) by X-ray mutagenesis (Rédei, 1992). *Ler* is erect with the phenotypes of dwarf, blunt siliques, short petioles, and compact inflorescence (Torii *et al.*, 1996). So *Ler* had been popular among scientists, but the parental Landsberg line La-1 was unfortunately lost (Zapata *et al.*, 2016; Tameshige *et al.*, 2017). And then, several mutant lines appeared subsequently with T-DNA insertion, and *ER* was cloned to notified its function in plant morphogenesis (Torii *et al.*, 1996). *ERECTA* family genes (*Erf*) include *ER*, *ERECTA-LIKE1* (*ERL1*), and *ERECTA-LIKE2* (*ERL2*) (Shpak *et al.*, 2004). Loss-function *erf* show many phenotypes, such as short internodes and pedicels (Fridborg *et al.*, 2001), compact inflorescence and blunt silique (Torii *et al.*, 1996; Shpak *et al.*, 2004), adaxial-abaxial leaf polarity (Qi *et al.*, 2004), sterile (Pillitteri *et al.*, 2007), drought tolerance and transpiration efficiency (Masle *et al.*, 2005; Schmalenbach *et al.*, 2014; Li, H *et al.*, 2019), thermotolerance (Shen *et al.*, 2015), shade avoidance (Patel *et al.*, 2013; Du *et al.*, 2018), seed germination (Nanda *et al.*, 2019), pathogen response (Godiard *et al.*, 2003; Llorente *et al.*, 2005; Häffner *et al.*, 2014; Jordá *et al.*, 2016; Takahashi *et al.*, 2016), and cluster stomata (Berger & Altmann, 2000; Shpak *et al.*, 2005). In this review, we principally focus on the function of *Erf* in plant morphogenesis, including SAM development, stem elongation, reproductive organ growth, and it will involve the

intercellular communication and so on.

2 | DOMAINS OF ERf

According to extracellular structure, plant RLKs can be divided into RLK and RLCK (receptor-like cytoplasmic kinases) with no apparent signal peptide or transmembrane domain. There are more than 225 LRR-RLKs: the largest subfamily of RLKs in Arabidopsis, including ER family members (Man *et al.*, 2020). Some structural differences among ERf exist: ERL1 has 21 leucine repeats, one more than that in ER and ERL2, while ER has five phosphorylation sites in the kinase domain, one less than that in ERL1 and ERL2 (FIGURE S1). Dominant-negative ER shows a similar phenotype with *er* mutation when it lacks the cytoplasmic kinase domain (Shpak *et al.*, 2003). In the cytoplasmic domain, the juxtamembrane domain has more impact on morphogenesis than the C-terminal tail (Kosentka *et al.*, 2017). Researchers thought intron isn't important years ago because introns are often cut off during transcription, but in recent years, introns were found to be required for their complete encoding for many genes, including *ER* (Karve *et al.*, 2011; Morgan *et al.*, 2019). The intronless *ER* has decreased transcript abundance, affects the mRNA stability, and ultimately affects the protein function (Karve *et al.*, 2011). And the introns of the extracellular domain seem to be extraordinarily important for ER, that's why people usually retain the introns when cloning *ER*.

3 | REGULATION OF SHOOT APICAL MERISTEM AND LEAF GROWTH BY ER-FAMILY

Vegetative growth is closely related to shoot apical meristem (SAM), which is the source of all above-ground organs (Mandel *et al.*, 2014). Scientists use *in situ* hybridization and histochemical analyses to examine the activity of promoters of *ER*, *ERL1* and *ERL2* driven the β -glucuronidase (*GUS*) reporter gene, and all showed intense staining in SAM, young leaves, and developing flower primordia (Yokoyama *et al.*, 1998; Shpak *et al.*, 2005; Uchida *et al.*, 2013).

3.1 | ER AND APICAL SUBTISSUE DEVELOPMENT

The triple mutant *er erl1 erl2* has a flatter and broader SAM than wild type (WT)

(Mandel *et al.*, 2014). The transcription factor WUSCHEL (WUS) is necessary for maintaining stem cell niche in SAM and plant cell totipotency (Jha *et al.*, 2020). SAM loss in *wus* plants can be rescued by deficiency of *ERf* (Kimura *et al.*, 2018). Besides, *WUS*, *CLV*, and *SHOOT MERISTEMLESS (STM)* have an increased expression level in *er erl1 erl2* triple mutant (Chen *et al.*, 2013; Uchida *et al.*, 2013; Kimura *et al.*, 2018; Zhang *et al.*, 2020), so ERf may affect these signal pathways directly or indirectly. The expression of *WUS*, but not *CLV3*, is sensitive to exogenous cytokinin treatment (Uchida *et al.*, 2013). Nonetheless, it is interesting to observe a drastic response of *CLV3* in *er erl1 erl2* after CK treatment (Uchida *et al.*, 2013). *ERf* control the proliferation of the peripheral zone, while *CLV3* controls the proliferation of stem cells (Uchida *et al.*, 2013). That means ERf determine the sensitivity of *CLV3* to cytokinin treatment, suggesting that there may be other RLKs or co-receptor of ER in the response of different CK concentrations. Loss-of-function of *CKX3* and *CKX5 (CYTOKININ OXIDASE)* also confers a broader SAM, elongated pedicel, and thicken stem with an increased expression of *WUS* (Bartrina *et al.*, 2011). Not too long ago, people found a new pathway that OsERECT1-OsMKKK10-OsMKK4-OsMPK6 in rice controls inflorescence development, and the DST-OsCKX2 module is downstream of the pathway (Guo *et al.*, 2020). Based on the prior results, it is essential to do follow-up researches, which would get deeper insights into roles in RLKs in response to different CK concentrations. For example, how does ER buffer the change of *CLV3* to CK concentration? Is the signal received by *WUS* passed to *CLV3* through ER? Furthermore, ER is expressed in the L1 layer of SAM, indicating that ER coordinates the communication between SAM tissue layers, and shoot-apex-expressed EPFL1 and EPFL2 may be the upstream of ERf (Kimura *et al.*, 2018). Recently, it has been reported that exogenous EPFL4 and EPFL6 treatments would downregulate the expression of *CLV3* and *WUS* in the periphery of the SAM under fully functional *ERf* (Zhang *et al.*, 2020). It is also interesting to check whether EPFLs protein in the feedback loop of *WUS-CLV3* (FIGURE 2).

SAM determines leaf number and phyllotaxy (Mandel *et al.*, 2014; Wang *et al.*, 2018). It is interesting to note that SAM of *er erl1 erl2* mutant, with an increased

number of stem cells, is accompanied by decreased leaf numbers and irregular phyllotaxy (Uchida *et al.*, 2012b), that is to say, the transformation of cells from the peripheral zone (PZ) to leaf primordium is delayed. The leaf shapes of *er* mutants are varied with different ecotypes and mutation sites. The leaf margin of *Ler* is smooth and tends to be round, and in the Columbia (Col) background, *er-102* has smaller and curled leaves with the shortened petioles, *er-101*, and *er-104* has more minor changes in leaf shape, while *er-103* is almost the same as the WT (Chen *et al.*, 2013). In *erf* mutants, the number of mesophyll cells was decreased and loosely arranged (Masle *et al.*, 2005).

ERf can sense a group of cysteine-rich peptide EPF/EPFLs. ERf and EPF/EPFLs regulate plant growth by acting as ligand-receptor pairs. Phenotype analyses revealed that the leaf margin of *epfl2* was not serrated, while deletion mutants of *ERf* also have similar phenotypes (Tameshige *et al.*, 2016). Auxin accumulates at the tip of the leaf tooth in Col, but in the *epfl2* and *erf* mutants, auxin branches become wider, and in *35S::EPFL2*, leaf tooth becomes insensitive to auxin (Tameshige *et al.*, 2016). As the time increase of 24-D treatment, *EPFL2* was down-regulated, and *ER* was up-regulated, while the tooth tip maintained a higher auxin concentration (Tameshige *et al.*, 2016). Further experiments showed that EPFL1, EPFL2, EPFL4 and EPFL6, as ligands of ERf, were redundant in the development of SAM. These encoding genes were expressed in both the leaf primordia and the PZ region of SAM (Kosentka *et al.*, 2019). The *epfl1/2/4/6* quadri-mutant is dwarf with a broader SAM as same as *erf* (Kosentka *et al.*, 2019). Tissue-specific promoters fusing with *ER* further demonstrated that ER is required for the communication between the border and CZ of SAM, and regulates the elongation of internodes and pedicels and leaf development (Kosentka *et al.*, 2019).

Then *ERf* was reported to regulate cotyledon development by promoting cell proliferation while inhibiting stomatal development (Chen & Shpak, 2014). *RLCK BOTRYTIS-INDUCED KINASE1 (BIK1)* is required for pathogen defense response and brassinosteroid (BR) signaling, but in morphogenesis, *bik1* and *er* show opposite phenotypes in leaf margin and inflorescence. BIK1 can phosphorylate ER, and the absence of ER smoothed the leaf margin of *bik1* (Chen *et al.*, 2019). It is interesting to note that *bik1* keeps a significant auxin concentration gradient in the leaf tooth, while

er is the opposite of *bik1*. Auxin distribution in *er* can be detected in a broader leaf margin (Chen *et al.*, 2019). The interaction between BIK1 and ER is worth examining in other developmental processes, and simultaneous auxin transporter can be considered.

The leaf morphology depends on the response of time and space to auxin, and the auxin concentration gradient of SAM is primarily dependent on the auxin transporter PIN-FROMED1 (PIN1). The deletion homozygous mutant of *PIN1* has an obvious SAM defect phenotype (Furutani *et al.*, 2004; Wang *et al.*, 2018). ERf is important for PIN1 subcellular localization in the midvein of leaf primordium and vascular of new leaves, the localization of PIN1 was abnormal in *erf* triple mutant, which led to the failure of the maximum concentration gradient of auxin in the L1 layer of SAM. It was also found that PIN1, located in vascular tissues, was dispersed around the periphery, which resulted in the blockage of the efflux channel of auxin from L1 and low auxin for hypocotyl development (Chen *et al.*, 2013). At the same time, the location of PIN1 protein in the vascular of newborn leaves was abnormal, and *erf* triple mutant has a defect phototropic bending. These are worthy for further study (Chen *et al.*, 2013). Morphological changes in response to the environment are exciting, and here, the defect phototropic bending may cover more auxin transporter or co-receptor. At least, the receptor kinase is involved in auxin transport, but there is very little evidence to show the direct interaction between receptor-like kinases and auxin transporters. Encouragingly, a team finally discovered that CAMEL-CANAR receptor complex regulate the phosphorylation of PIN1, which in turn regulates the polar localization of PIN1 (Hajny *et al.*, 2020). This makes us curious about the members of the ER complex that regulates the distribution of auxin in the plant development.

4 | ER FAMILY ARE ESSENTIAL FOR STEM ELONGATION

The most prominent phenotype of the *er* mutant is that the plant is short and erect and has compact inflorescence because of its shortened pedicels and internodes (Torii *et al.*, 1996). Here, we paid close attention to two aspects, one is stem cell growth, and the other is intercellular communication. Moreover, we also consider the pedicel (FIGURE 3).

4.1 | EPFLs ARE THE UPSTREAM OF ERF IN VASCULAR TISSURES

ERf is involved in cell proliferation in the pedicel, and the pedicel cell number of *er erl1 erl2* triple mutant is significantly lower than that of the WT (Shpak *et al.*, 2003; Shpak *et al.*, 2004; Bundy *et al.*, 2012). That is why the pedicel of the mutant is significantly shorter than that of the WT. However, although the pedicel became short, the cortex cell length was increased in the *er* mutant (Shpak *et al.*, 2004; Bundy *et al.*, 2012; Uchida *et al.*, 2012a). GUS staining showed that *ER*, *EPFL4* and *EPFL6* expressed in the pedicel, *epfl4 epfl6* double mutant also has a compact inflorescence (Uchida *et al.*, 2012a). Tissue-specific rescue experiments showed that ER expression driven by phloem-specific promoter *AtSUC2* could save defective phenotypes of *er*, including stem, leaf, and pod defects. However, the xylem-specific promoter *AtIRX3* and epidermal-specific promoter *AtMLI* has no significant effect though (Uchida *et al.*, 2012a). Further experiments demonstrated that the expression of *ER* in the phloem was not necessary for organ elongation and *EPFL1/2/4/6* affected organ elongation (Kosentka *et al.*, 2019). EPFLs peptides can move among cells, while ERf as transmembrane proteins cannot (Uchida *et al.*, 2012a). This means that phloem-expressed ER can respond to procambium-expressed EPFLs signal, and there is a signal exchange between the endodermis and phloem, which leads to one question: since ERf is expressed in the phloem to sense EPF/EPFLs, which signaling pathway is downstream of ERf to determine the organ elongation? CLAVATA3-LIKE/ESR-RELATED 41 (CLE41) and TDR/PXY pair were also reported to regulate vascular cell division (Etchells & Turner, 2010). Moreover, there is an interaction between TDR/PXY and ER in vascular development, and double mutant *er tdr/pxy* conferred a larger tangential/radial ratio of inflorescence stem vascular bundles than *er* and *tdr/pxy* single mutant (Etchells *et al.*, 2013). Cambium is a kind of meristematic tissue located between the xylem and phloem. The cell number of cambium in *er* and *erl1* single mutant is slightly lower than that in the WT, but cambium of *er erl1* double mutant was seriously damaged, loss-of-function of *ER* aggravated the phenotype of the *tdr/pxy* (Uchida & Tasaka, 2013), and *EPFL4/6* is still involved in this process (Uchida & Tasaka, 2013). Besides, the ethylene signaling pathway also made the defect phenotype

of *tdr/pxy* more severe (Etchells *et al.*, 2012), and it was previously reported that ER controls ethylene-induced hyponastic growth (van Zanten *et al.*, 2010). Therefore, it is necessary to study whether ethylene is the intersection between ERf and TDR/PXY signal pathways in vascular regulation (Etchells *et al.*, 2013). Then questions arise, does ERf block cell cycle progression during stem development, is it same as stomatal development? And it should be noted that though *epfl4 epfl6* mutant have a similar pedicel phenotype as *er* and *er erl*, but *epfl4 epfl6* did not affect procambium development while *er erl1* has a severe defect procambium, so ER and ERL1 may have more partner in one complex and the complex can sense more peptide except EPFL4 and EPFL6.

4.2 | DOWNSTREAM SIGNALS OF ER IN REGULATING STEM ELONGATION

It has been reported that *ERf* can regulate cell rate and proliferation in the epidermis and cortex (Bundy *et al.*, 2012). Loss-of-function mutation of *ARP6* (*ACTIN-PRIMED PROTEIN6*) in *er119 aeh1* background leads to shorter pedicels and siliques, which resulted from less cell proliferation, but it is accompanied by an extension of cortical cells (Cai *et al.*, 2017). *ARP6* and *SEF* (*SERRATED LEAVES AND EARLY FLOWERING*) form the ATP-dependent chromatin remodeling complex *SWR1*, and there is a genetic interaction between *ER* and *SWR1* in inflorescence architecture (Cai *et al.*, 2017). *er sefs* show a shorter pedicel and internode, in *arp6 er119* and *arp6 mpk6* and *er119 mpk6*, the expression of *PRE* (*PACLOBUTRAZOL RESISTANCE*) gene family *PRE1/2/4/5/6* decreased significantly (Cai *et al.*, 2017). *PRE*, which is sensitive to BRs, auxin and gibberellins (GAs), is a class of bHLH transcription factors which control hypocotyl elongation (Lee *et al.*, 2006; Zhang *et al.*, 2009), and it's reported that *PRE1* is downstream of the ER-MAPK signaling pathway to promote pedicel elongation (Cai *et al.*, 2017), and the MAPK cascade members downstream of ERf are *YDA*, *MKK4/5* and *MPK3/6* as well as that in stomata development (Meng *et al.*, 2012; Meng *et al.*, 2015; Lee & Bergmann, 2019), recently, more details had been revealed that *HBII* (*HOMOLOG OF BEE2 INTERACTING WITH IBHI*) is downstream of *PRE1*, and *HBII* can directly bind the promoter of the brassinosteroid (BR) biosynthesis gene

CYP85A2 and auxin response factor *ARF3* to promote their expression, besides, *ARF3* can directly bind the promotor of *CYP85A2*, some auxin transporter like *PIN1/3/4/7* and *AUXs* and auxin-induced *SAUR19* and *SAUR20* (Cai *et al.*, 2020), so BR or auxin hormone pathways related inflorescence architecture regulation is partially activated by *HBI1*, and the more detailed module is *SWR1-ER-MAPK-PRE1-HBI1* (Cai *et al.*, 2017; Cai *et al.*, 2020). Loss-of-function *bik1*, however, has a significantly increased pedicel phenotype opposite with *er* (Chen *et al.*, 2019), may *HBI1* is also a regulatory hub downstream of *BIK1*.

BREVI-PEDICELLUS (*BP*) can promote internode elongation by promoting cell division (Douglas *et al.*, 2002), while *BP* and *ER* could restrict the asymmetric localization and chlorenchyma repressor correlated vascular at the nodes (Douglas *et al.*, 2002). However, surprisingly, *BP* has a distinct mechanism of fiber differentiation between inflorescence stem and hypocotyl, and *BP* negatively regulates fiber differentiation (Mele *et al.*, 2003). This potential rewired and the flipped mechanism is similar to the *ER* function of stomata development between the hypocotyl and leaves (Bhave *et al.*, 2009; Abrash *et al.*, 2011). *ER* and *ERL1* redundancy inhibited the radial expansion of xylem in hypocotyls, which was due to the premature initiation of the fiber differentiation prevented by a lower expression of *NST1* and *NST3* (Ikematsu *et al.*, 2017), while *BP* positively regulates the expression of *NST1* and *NST3* (Liebsch *et al.*, 2014; Ikematsu *et al.*, 2017). Nevertheless, *BP* is reported to physically interact with *DELLA* in regulating xylem fibers differentiation (Felipo-Benavent *et al.*, 2018). Indeed, researchers took a step forward that *ER* has been demonstrated to physically interact with *LRR-RLK EVERSLED/ SUPPRESSOR OF BIR-1* (*EVR/SOBIR1*) in fiber differentiation, and *BP* is also involved in this process to regulate *EVR/SOBIR1* expression with down-regulation of GA signaling (Milhinhos *et al.*, 2019). So it also remains to be studied whether *EVR/SOBIR1* is the key factor of fiber development just like *TOO MAN MOUTH* (*TMM*) in *ER* pathways, whether *ER* or *EVR/SOBIR1* has other interactors? *GA* is reported to thicken stem (Ragni *et al.*, 2011), *ER* and *ERL1* were also found to delay *GA*-mediated fiber differentiation (Ikematsu *et al.*, 2017), and more studies need to figure out their internal relations. Another research showed that

overexpression of ER leads to hypocotyl elongation with the increased cell length and that the auxin content of *er erl1 erl2* decreased significantly with a lower expression level of the auxin biosynthesis gene *YUCCAs*, and the consistent phenotype was that the hypocotyl phenotype could be rescued by applying exogenous or increasing endogenous auxin content (Qu *et al.*, 2017). In addition to auxin, GA also promotes stem elongation (Dayan *et al.*, 2012; Binenbaum *et al.*, 2018). ER deficiency has also been reported to aggravate the short hypocotyl of GA insensitive mutants *short internode (SHI)* (Fridborg *et al.*, 2001), and inhibit the elongation hypocotyl of GA sensitive mutant *spindly (spy)* (Swain *et al.*, 2001). However, there is no direct evidence that ER is involved in GA signaling, and it has been found that SHI and SPY affect auxin biosynthesis and CK response (Swain *et al.*, 2001; Gomariz-Fernández *et al.*, 2017; Estornell *et al.*, 2018). Also, jasmonate (JA) and LONICERA may also contribute to the growth of cambium, which may be a future direction, suggesting new possible regulatory pathways.

5 | ERF IS REQUIRED FOR REPRODUCTIVE ORGAN GROWTH

Short fruits and compact shoot architecture characterize the *er* mutants, loss-function *er* has a more severe defect than *erl1/erl2* single or double mutant, and *er erl1 erl2* triple mutant is even sterile (Torii *et al.*, 1996; van Zanten *et al.*, 2009; Wu *et al.*, 2018). Pedicels development has been well discussed, so we will focus on other floral organs in this section. ERL2 was found to be the critical factor for normal ovule development (Pillitteri *et al.*, 2007), *er erl1 erl2/+* with haploinsufficiency of ERL2 has aberrant ovule growth and embryo sac development (Pillitteri *et al.*, 2007), but *er erl1/+ erl2* still keep fertile with defect integument outgrowth because of reduced cell numbers (Pillitteri *et al.*, 2007). Complete loss of ERf confers homeotic conversion of sepals to carpels, and *AGAMOUS (AG)* was detected in *er erl1 erl2* flower primordia (Bemis *et al.*, 2013), and ERf has genetic interaction with PRETTY FEW SEEDS 2 (PFS2), a *WUS*-related homeobox gene known as *WOX6*, loss-of-function of *PFS2/WOX6* would suppress *er erl1 erl2/+* ovule deficient phenotype, indicating that ovule development needs coordination between *ER* and *PFS2/WOX6* (Pillitteri *et al.*, 2007).

Same as stomata development, the mitogen-activated protein kinase (MAPK)

cascades are also involved in reproductive organ development. YDA, one member of the MAPKKK cascades, can rescue *er erl1 erl2* floral phenotype (Bemis *et al.*, 2013). ER also regulates petal shape and size through control of petal cell proliferation (Abraham *et al.*, 2013). ER-MAPK signal pathway has been confirmed in stomatal development, and the phenotype of *mpk3 mpk6* anther development is similar to that of *er erl1 erl2*, *MKK4/5* can rescue the defective inflorescence of *er-105*, which indicates that *MKK4/5* and *MPK3/6* are downstream of *ERf* signals to co-regulate anther lobe formation and anther cell differentiation (Hord *et al.*, 2008; Meng *et al.*, 2012). Another interesting phenotype during flower development was observed in the *er erl1 erl2/+* hybrid mutant with a larger pedicel angle than that in the WT, as well as in the loss-of-function of *BRASSINOSTEROID INSENSITIVE1 (BRI1)* and overexpression of *BRI1 KINASE INHIBITOR1 (BKII)*, mutation of *BKII* on the background of *er erl2* restored the pedicel orientation (Wang *et al.*, 2017), *BKII* is a receptor kinase inhibitor and negatively regulates *BRI1* in the BR pathway (Ye *et al.*, 2011). Moreover, a study had found an interaction between *BKII* and ER in vitro and planta (Wang *et al.*, 2017). *BKII* inhibits ER phosphorylation, while 24-epiBL treatment relieves the inhibition by *BKII*, indicating that the BR and ER signal pathways intersect (Wang *et al.*, 2017). In the BR pathway, *BIN2*, as a negative regulator, also interacts with YDA, *MKK* and *MPK* to regulate plant growth (Wang *et al.*, 2008; Kim & Wang, 2010; Khan *et al.*, 2013; Wang *et al.*, 2017), This may be one of the critical factors for the involvement of the BR and ER pathways in morphology. By constructing multiple mutants of *epfl6/5/4* with *erf*, the pedicel angle increased, and the siliques were shorter with the deletion of *EPFLs* (Wang *et al.*, 2017), indicating that it is a better clue to search for the upstream peptides of *ER* regulating pedicel orientation.

Class III homeodomain Leucine Zipper HD-ZIP Family JABBA (JBA) is reported to regulate SAM and lateral organs development (Weigel *et al.*, 2000; Williams *et al.*, 2005), here, loss-of-function *clv3-2* had 4 carpels, while *er clv3-2* had 5 carpels and *er clv3-2 jba-1d/+* had 8 carpels (Udi *et al.*, 2015), This suggests that ER, CLV and HD-III ZIP pathways are involved in carpel growth, but it is not known where the intersection of these pathways occurs (Udi *et al.*, 2015). *OsEPFL1* regulates

awnlessness in *Oryza sativa*, so it is very likely to find an OsERECTA binding with OsEPFL1 to control awnlessness (Bessho-Uehara *et al.*, 2016). It's also a reminder that EPFL1/2/3 may regulate undiscovered phenotypes in Arabidopsis. A recent study revealed that EPFL2 regulates spacing of ovules through ERL1 and ERL2, and loss-of-function *epfl2* has a shorter gynoecea and irregular spacing of ovules (Kawamoto *et al.*, 2020). Moreover, EPFL9 is a ligand for ERF receptors that controls fruit elongation (Kawamoto *et al.*, 2020), this is the first report about EPFLs regulating reproductive organ growth, and it also enriches the use of peptide hormones and has significant production value.

Determining the timing of seed germination is essential for agriculture, especially in environments that are vulnerable to drought and high salinity. Seed germination of loss-of-function *erf* was salt-hypersensitive, and the germination time of *erf* mutant was extended or even did not germinate until the conditions were suitable (Nanda *et al.*, 2019). The *erf* mutant germination was more sensitive to ABA treatment, and the up-regulation of ABA-INSENSITIVE-3, ABA-INSENSITIVE-5, DELLA-encoding RGL2, and DELAY OF-GERMINATION-1 were detected in the *erf* mutant (Nanda *et al.*, 2019). Therefore, some genetic engineering aimed at ERF modification has a great application prospect in crops.

6 | CONCLUDING REMARKS AND PERSPECTIVES

Different protein complexes of ERF can sense different ligands and various ligand-receptor pairs regulate distinct developmental processes (FIGURE 1). This is a fascinating but most complex point in the study of ERF and other receptor kinases. Furthermore, studies of ER are pretty scattered, so more studies are needed to integrate and modify these signal pathways. The ligand-receptor pairs of ERF/EPFLs-ERF, including *EPF1*, *EPF2*, *EPFL2/4/5/6/9* and *ERf*, have been identified to determine stomata, leaf margin, stem development, seed number and fruit size (Lee *et al.*, 2012; Lee *et al.*, 2015). Nevertheless, EPFL1/3/7/8 have not been identified yet in Arabidopsis morphogenesis, but encouraging is that OsEPFL1 is demonstrated in awnlessness of *Oryza sativa*, so that reminds us not to make *Arabidopsis thaliana* only our priority, and the application of peptide hormones in agriculture is also worthy of attention. It is

noteworthy that there is a switch in ERF sensing peptides, and the key is the co-receptor TOO MANY MOUTH (TMM) (Abrash *et al.*, 2011). However, EVR/SOBIR1 seems to be a potential co-receptor during stem growth. So that gives us more imagination that other receptor-like proteins or RLKs may interact with ERF in the phase transition of stem development. Besides these, there are still many problems to be solved for the time being. Plant hormones such as auxin, cytokinin, gibberellins, ethylene, and brassinosteroids are more or less related to ERF, and it lacks research about more detailed mechanisms between phytohormones and ERF.

Based on the above, the following three main questions remain to be answered. Q^{1st}: Does EPFLs-ERf model apply to other EPFL members? such as EPFL7 and EPFL8, and what physiological process can they control? Q^{2nd}: many experiments proved that there is a connection between ERF and auxin, including SAM development, leaf margin and stem development. So, does ERF affect auxin transport or synthesis? More detail, which auxin synthesis pathway is affected by ERF? Does ER affect the localization or transcription of auxin transporter? Q^{3th}: what is the key to affecting ERF function switching? secreted peptides or membrane protein?

In addition, there have been many applications of ER in crops, and ER function in biotic and abiotic stresses show that it is worth exploring, such as drought and thermotolerance (Masle *et al.*, 2005; Shen *et al.*, 2015; Blair, M. W. *et al.*, 2016; Li, H *et al.*, 2019), shade (Millenaar *et al.*, 2005; Millenaar *et al.*, 2009; Luciana *et al.*, 2013; Du *et al.*, 2018), seed germination (Nanda *et al.*, 2019) and plant disease resistance (Godiard *et al.*, 2003; Llorente *et al.*, 2005; Adie *et al.*, 2007; Sopena-Torres *et al.*, 2018). But ER may play distinct roles in different crops, it will be a quite challenging for the functional analyses and application of ER in crops in further.

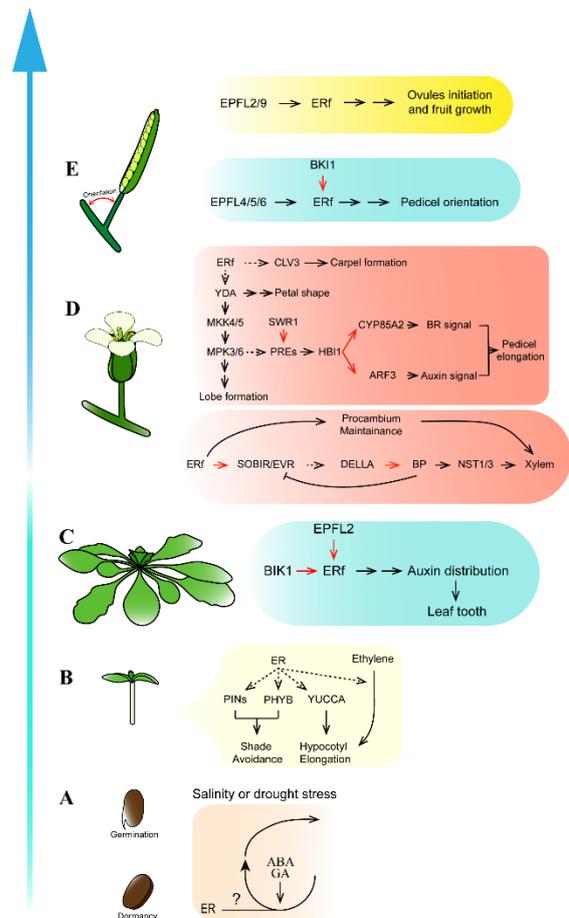


FIGURE 1 A schematic model of the diverse function of the ERECTA family (ERF) genes from seed germination to silique growth in plant growth and development.

- (A) ERf is involved in seeds germination under salinity or drought stress.
- (B) In the stage of seeding development, ERf participates in hypocotyl elongation and photo bending processes, in which PINs, PHYB and YUCCA may be covered.
- (C) BIK1 and EPFL2 directly bind to ERf to control leaf tooth development through auxin distribution in the leaf development stage.
- (D) In floral development, ERf and CLV3 co-regulate carpel formation, and MAPKs are involved in petal and lobe formation downstream of ERf and CLV3. Besides, the SWR1-PREs-HBI1 module is downstream of the ERf-MAPKs module to regulate pedicel elongation, and BR and auxin signals are also concluded. SOBIR/EVR can directly bind to ERf and positively regulate the BP-NST1/3 module through the binding of DELLA to BP in xylem formation. ERf is also essential for procambium maintenance, but the underlying mechanisms are still largely unknown.

(E) ERF binds to BKI1 and regulates pedicel orientation via the perception of the ligands EPFL4/5/6. ERF regulate ovule initiation and silique growth downstream of EPFL2/9.

Arrows with a solid line show direct regulation and arrows with dotted lines indicate indirect regulation whose mechanisms are unclear yet, double arrows indicate some unknown patterns. Arrows indicate positive regulation and bars indicate negative regulation. Red arrows show directly binding.

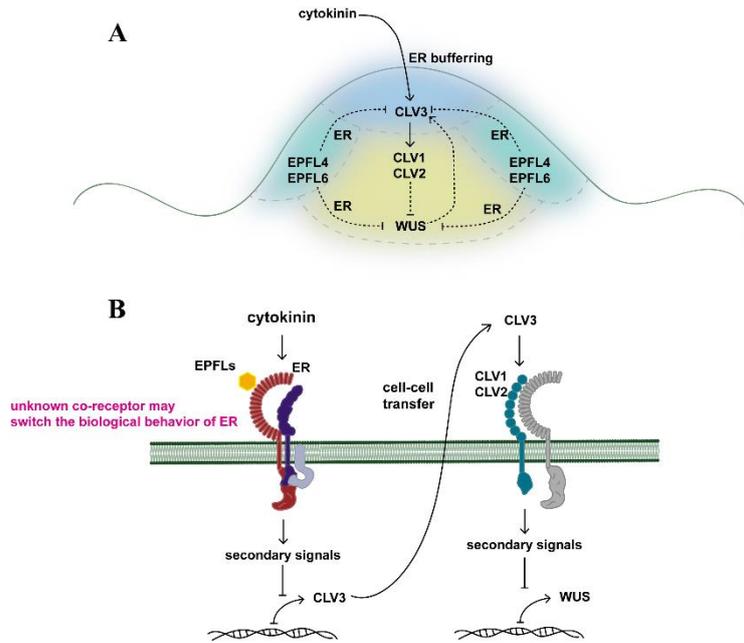


FIGURE 2 ERF participates in SAM development. (A) The shoot apical meristem (SAM) with the central zone (blue), peripheral zone (cyan) and rib zone (yellow) are shown. CLV3-WUS feedback loop regulates SAM development, while ER can buffer the change of CLV3 to CK concentration through an unknown pathway, and exogenous EPFL4 and EPFL6 can reduce the expression levels of both CLV3 and WUS. (B) A hypothetical signal pathway about EPFLs-ER-CLV3-WUS module.

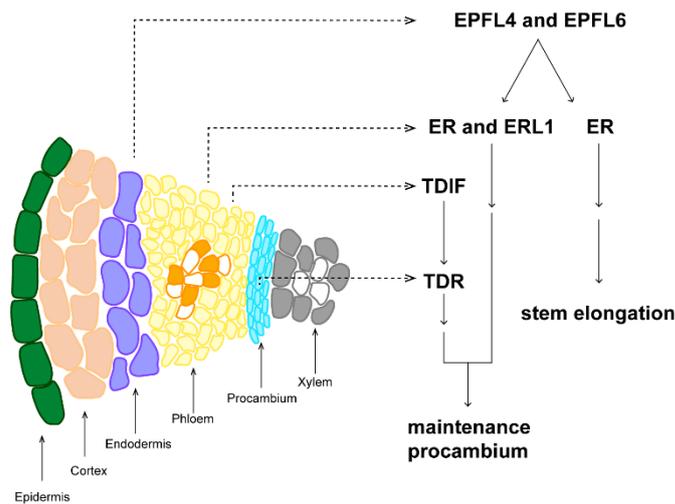


FIGURE 3 Network of ERf controlling stem development. Endodermis expressed EPFL4 and EPFL6 can be perceived by phloem expressed ER or ERL1 to regulate stem development. EPFL4/6-ER/ERL1 module and TDIF-TDR module are parallel. But there are two questions: is YDA-MKK4/5-MPK3/6 a common cascade for ER downstream signal? And which hormone signals are downstream of ER?

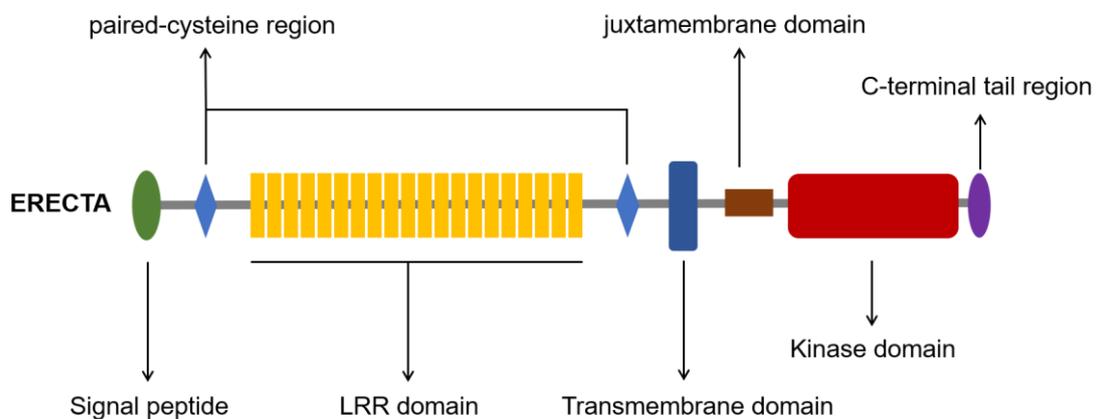


FIGURE S1 ER protein structure diagram. Complete ERECTA protein has one signal peptide, two paired-cysteine regions, 20 leucine repeats, one transmembrane domain, one juxtamembrane domain, one kinase domain, one C-terminal region. In addition, the intron in the extracellular domain is very important for the normal expression of ERECTA.

TABLE S1 *ERECTA*-application cases in crops.(Villagarcia *et al.*, 2012; Shen *et al.*, 2015; Blair, Matthew W. *et al.*, 2016; Junbo *et al.*, 2018; Zhang *et al.*, 2018; Li, Hanshuai *et al.*, 2019; M *et al.*, 2019; Zheng *et al.*, 2019; Guo *et al.*, 2020; Juneidi *et al.*, 2020; Shanmugam *et al.*, 2020; Yang *et al.*, 2020; Li *et al.*, 2021; Sakai *et al.*, 2021)

Gene names	Species	Function	Reference
<i>AtKinase</i>	<i>Glycine max</i>	The transgenic <i>AtKinase</i> soybean plants exhibited increased tolerance to water deficit stress due to the reduction of total leaf area and reduced transpiration compared to the wild-type plants.	Shanmugam <i>et al.</i> , 2020
<i>PvERECTA</i>	<i>Phaseolus vulgaris</i>	<i>PvERECTA</i> is related to drought resistance of <i>Phaseolus vulgaris</i>	Blair, Matthew W. <i>et al.</i> , 2016
<i>GmERECTA</i>	<i>Glycine max</i>	Truncated extracellular domain of GmERa might contribute importantly to shade avoidance.	Junbo <i>et al.</i> , 2018
<i>BdERECTA</i>	<i>Brachypodium distachyon</i>	A premature stop codon in <i>ERECTA</i> , a LRR receptor-like serine/threonine-protein kinase can severely affected the organization of vascular tissues,also displayed changes in cell wall composition, gene expression and hormone homeostasis.	Sakai <i>et al.</i> , 2021
<i>VvERECTA</i>	<i>Vitis vinifera</i>	<i>VvERECTA</i> gene family might play crucial roles in response to abiotic and biotic stresses.	M <i>et al.</i> , 2019
<i>AtERECTA</i>	<i>Lycopersicon esculentum</i> and <i>Oryza sativa</i>	Transgenic tomato and rice lines overexpressing <i>Arabidopsis ER</i> showed improved heat tolerance	Shen <i>et al.</i> , 2015
<i>AtKinase</i>	<i>Lycopersicon esculentum</i>	The transgenic plants also exhibited increased tolerance to water deficit stress, at least partially due to their diminished surface area.	Villagarcia <i>et al.</i> , 2012
<i>PdERECTA</i>	<i>Populus deltoides</i>	Overexpression <i>PdERECTA</i> can alter the development pattern of stomata to reduce stomatal density, which then restricts water consumption, conferring enhanced drought tolerance to poplar.	Li <i>et al.</i> , 2021
<i>OsER1, OsER2</i>	<i>Oryza sativa</i>	Loss-of-function mutants of <i>OsER1</i> and <i>OsER2</i> display shortened plant stature and reduced panicle size, suggesting they possibly also functioned in regulating cell proliferation and cell growth in rice.	Zhang <i>et al.</i> , 2018
<i>ERfs</i>	<i>Pinellia ternata</i>	Introduced a heat responsive receptor-like kinase <i>ERECTA (ER)</i> gene into <i>P. ternata</i> can disrupting the summer dormancy	Juneidi <i>et al.</i> , 2020
<i>SbER1-1, SbER2-1</i>	<i>Zea mays</i> and <i>Arabidopsis thaliana</i>	<i>SbER2-1</i> expression in <i>Arabidopsis</i> and maize conferred increased drought tolerance, especially in regard to water-use efficiency, increasing the net photosynthetic rate in maize under drought stress.	Li, Hanshuai <i>et al.</i> , 2019
<i>OsER</i>	<i>Oryza sativa</i>	The <i>oser1</i> mutant displayed increased spikelet number per panicle and reduced grain size without altered plant architecture, <i>oser1</i> mutant was markedly increased, with reduced grain length but enhanced grain width compared with the wild type.	Guo <i>et al.</i> , 2020
<i>TaERECTA</i>	<i>Triticum aestivum</i>	Reduced expression of <i>TaERECTA</i> caused an increased stomatal and epidermal cell density by average 13.5% and 3.3%, respectively, due to the significantly reduced size of leaf epidermal and stomatal cells, and this led to an increase in stomatal conductance.	Zheng <i>et al.</i> , 2019
<i>CmERECTA(CmSt)</i>	<i>Cucumis melo</i>	<i>ERECTA</i> family gene <i>CmSI</i> regulates stem elongation in melon through auxin signaling, which can directly affect polar auxin transport.	Yang <i>et al.</i> , 2020

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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