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REVIEW

Small signaling peptides mediate plant adaptions to abiotic environmental stress

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Abstract

Main conclusion **Peptide-receptor complexes activate distinct downstream regulatory networks to mediate plant adaptions to abiotic environmental stress.**

Abstract Plants are constantly exposed to various adverse environmental factors; thus they must adjust their growth accordingly. Plants recruit small secretory peptides to adapt to these detrimental environments. These small peptides, which are perceived by their corresponding receptors and/or co-receptors, act as local- or long-distance mobile signaling molecules to establish cell-to-cell regulatory networks, resulting in optimal cellular and physiological outputs. In this review, we highlight recent advances on the regulatory role of small peptides in plant abiotic responses and nutrients signaling.

Keywords Small peptides · Abiotic stress · Nutrients signaling

Introduction

Plants are frequently exposed to adverse environments such as multiple abiotic stresses and nutrients deficiency conditions. Abiotic stresses severely harm plant growth and reduce crop yield (Zulfiqar et al. 2019; van Zelm et al. 2020; Chen et al. 2021). The nutrient shortages, for instance, nitrate (N) or phosphate (P) deficiency influences plant architecture and growth (Motte et al. 2019; Huang and Zhang 2020; Luo et al. 2020). To better optimize plant development under fickle conditions, plants have evolved a plethora of mechanisms to integrate various environmental cues into coordination of cellular behaviors and overall growth. Activation or de-activation of plant phytohormone signaling pathway is one of the adaptive strategies for plants to modulate their growth under abiotic stress conditions (Skalak et al. 2021; Salvi et al. 2021). Nutrient deficiencies interfere with phytohormones biosynthesis, signaling and distribution to shape plant architecture (Motte et al. 2019; Luo et al. 2020). Notably, small peptides act as local or long-distance signals to coordinate plant adaptations to abiotic stress and nutrients availability (Lay and Takahashi 2018; Takahashi et al. 2019; Gautrat et al. 2021).

Many different approaches have been carried out to identify the existence of small peptide, and mass spectrometry has been used to dissect the small peptide structure (Matsubayashi 2014, 2018). Based on the peptide structure, bioinformatic approach has been implemented to uncover gene members of distinct peptide family from genome sequences. More than 7000 small peptide encoding genes have been identified in the *Arabidopsis thaliana* genome, and most of them are likely to encode hormone-like peptides (Takahashi et al. 2019). In general, plant peptides are derived from unfunctional precursor proteins, functional proteins, or directly translated from a short open reading frame (Tavormina et al. 2015). Peptides are usually less than 120 amino acids, and the bioactive form is generally shorter than 20 amino acids in length (Murphy et al. 2012; Tavormina et al. 2015). Based on structural

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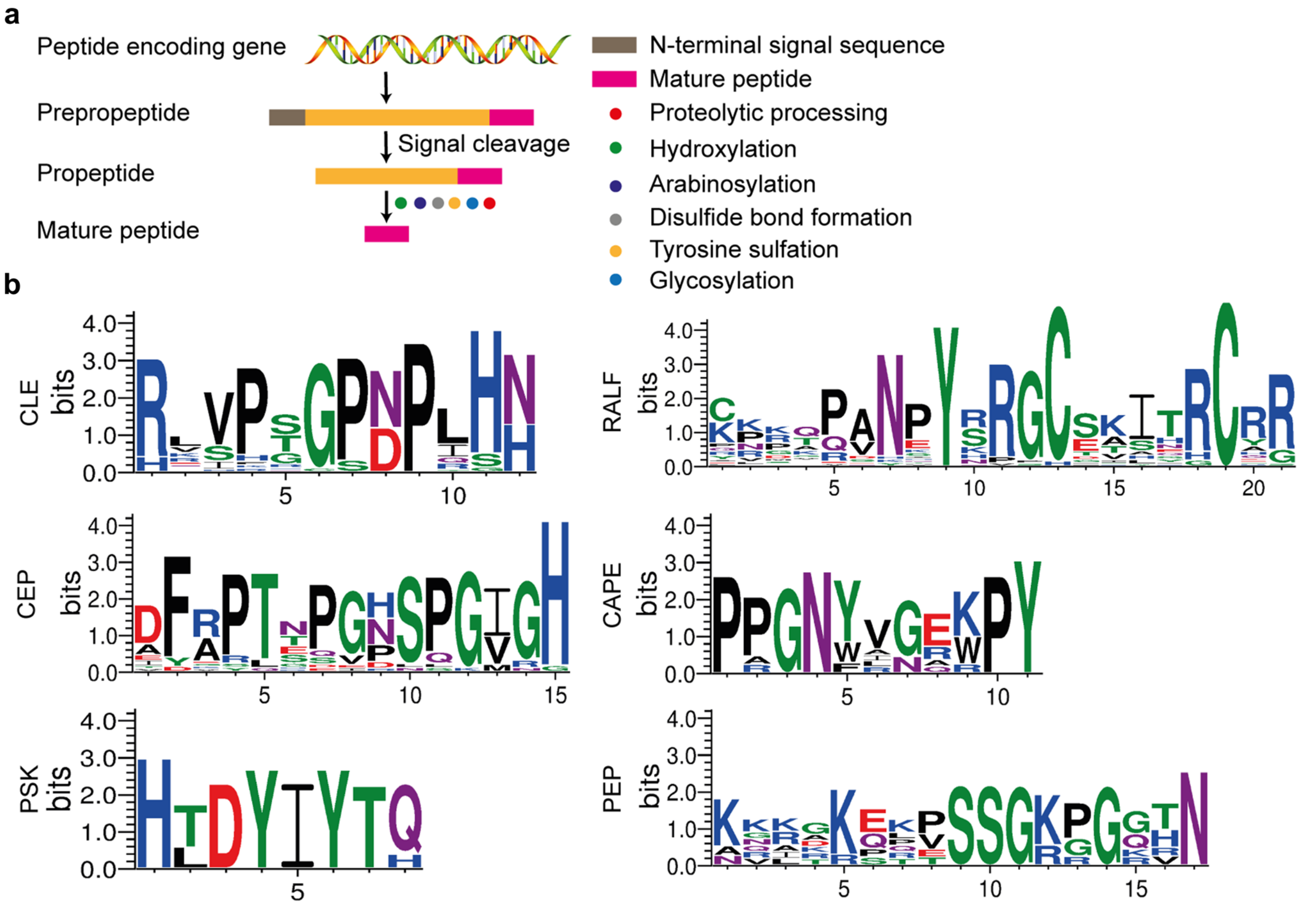

Fig. 1 Biogenesis of post-translationally modified small peptides. **a** Peptide encoding genes are translated into prepropeptides. The signal peptide is cleaved to ensure it enters into the secretory pathway. Propeptides undergo at least one type of post-translational modifications including tyrosine sulfation, proline hydroxylation, arabinosylation and glycosylation to generate mature peptide. **b** WebLogo alignment showing the sequences of representative motifs of CLE, CEP, PSK RALF, CAPE and PEP peptide family

differences, plant secretory peptides are classified into two main groups as follows: (1) post-translationally modified peptides (PMTs) and (2) cysteine-rich peptides (CRPs) (Olsson et al. 2019). Generally, PMTs and CRPs contain an N-terminal secretory sequence, a central variable region and a conserved motif or cysteine-rich domain at or near C-terminus. Mature PMTs and CRPs are generated by enzyme-mediated processing or modifications from their precursors-prepropeptides (Matsubayashi 2014, 2018). To date, numerous enzymes involved in peptide processing and post-translational modifications have been identified, although their impacts on peptides bioactivity and signal transduction are not fully understood (Matsubayashi 2014, 2018; Stührwohldt and Schaller 2019).

Receptor-like kinases (RLKs) and co-receptor proteins perceive the corresponding small peptides to integrate both external and internal signals into complex regulatory networks to achieve optimal responses and growth. Although some of the small peptides also play essential roles in biotic stress via distinct mechanisms (Segonzac and Monaghan 2019), it is out of the scope of this review. This review mainly aims to provide an overview of recent advances on small peptide-mediated plant adaptions to abiotic stresses. And their roles in plant response to nutrients are also discussed.

Small secretory peptides mediate plant drought stress

CLE peptide

The CLAVATA3(CLV)/EMBRYO-SURROUNDING REGION-RELATED (CLE) peptide family is well known for its role in regulation of meristem differentiation and proliferation as well as other developmental processes (Hirakawa and Sawa 2019; Fletcher 2020; Willoughby and Nimchuk 2021; Song et al. 2022). Typically, the length of bioactive CLE peptide is 12–14 amino acids generated with post-translational modifications (Fig. 1; Olsson et al. 2019;

Table 1 Summary of small peptides involved in plant abiotic stresses

Species	Peptide	Members are identified from	Gene expression products	Receptor	Stress response or nutrient signaling
Arabidopsis thaliana	CLE25	Genome sequence	Yes	BAMs	Drought
	CLE9	Genome sequence	Yes	Unknown	Drought
	CLE45	Genome sequence	Yes	SKM1/2	High temperature
	CLE3	Genome sequence	Yes	CLV1	Low nitrate
	CLE14	Genome sequence	Yes	CLV2/PEPR2	Low phosphate
	CLE2/CLE3	Genome sequence	Yes	CLV1	Sulfur starvation
	CEP5	Genome sequence	Yes	CEPR1/2 or unknown	Drought/osmotic stress
	CEP3	Genome sequence	Yes	unknown	Salinity
	CEP	Genome sequence	Yes	CEPR1/2	Low nitrate
	CEP	Genome sequence	Yes	CEPR1 or unknown	Sucrose
	RALF1/22/23	Genome sequence	Yes	FER	Salinity
	PSK1	Genome sequence	Yes	Unknown	Salinity
	CAPE1	Genome sequence	Yes	Unknown	Salinity
	PEP3	Genome sequence	Yes	PEPR1	Salinity
Medicago truncatula	MtCLE	Genome sequence	Yes	MtSUNN	Nodule number
	MtCEP	Genome sequence	Yes	MtCRA2	Nodule number
Lotus japonicus	LjCLE-RS	Genome sequence	Yes	LjHAR1	Nodule number

Stührwohldt et al. 2020). Recently, CLE9 and CLE25 have been reported to play roles in dehydration stress, which is dependent on ABA signaling (Table 1; Figs. 2, 3a, b; Takahashi et al. 2018; Zhang et al. 2019).

Root specifically expressed CLE25 peptide acts as a long-distance mobile signal during drought response. When roots sense lower water potential, the transcriptional level of *CLE25* is elevated, subsequently, CLE25 peptide is transported from roots to leaves. In leaves, plasma membrane-localized BARELY ANY MERISTEM (BAM) receptors bind to CLE25 peptide and transmit the drought signal to accelerate expression of *NINE-CIS-EPOXY-CAROTENOID DIOXYGENASE 3* (*NCED3*), an ABA biosynthesis enzyme. Consequently, the leaf produces more ABA to close stomata, thus enabling plants adapt to the drought stress (Fig. 3a; Takahashi et al. 2018). CLE25 peptide also binds to CLE-RESISTANT RECEPTOR KINASE (CLERK) and CLAVATA2 (CLV2), but their role in CLE25-mediated stomatal closure and drought response is elusive (Ren et al. 2019). On the other hand, other signaling components downstream of the CLE25-BAM signaling pathway in the regulation of plant drought stress require further clarification.

CLE9 is highly expressed in leaf guard cells, and its expression is prominently induced by abiotic stresses such as NaCl and mannitol. Exogenous application of synthetic CLE9 peptide or overexpression *CLE9* (*CLE9*^{OE}), resulted in leaf stomatal closure. Accordingly, the *CLE9*^{OE} transgenic plant shows much stronger resistance to drought stress (Zhang et al. 2019). Further study indicated that the CLE9 peptide-mediated stomatal closure involves a signaling cascade including MITOGEN-ACTIVATED PROTEIN KINASE 3/6 (MPK3/6), reactive oxygen species (ROS), and ABA signaling-related components, OPEN STOMATA 1 (OST1) and SLOW ANION CHANNEL-ASSOCIATED 1 (SLAC1). However, MPK3/MPK6 mediated stomatal closure is independent of ABA signaling (Montillet et al. 2013; Su et al. 2017). Hence, CLE9 induced stomatal is mediated parallelly by MPK3/MPK6 and ABA signaling (Fig. 3b; Zhang et al. 2019). In the future, the identification of receptors and co-factors involved in CLE9 peptide-induced stomatal closure would further clarify the CLE9 role in drought resistance.

CEP peptide

The C-TERMINALLY ENCODED PEPTIDE (CEP) genes encode proteins which contain an N-terminal signaling peptide, a variable central region, a 15 amino acids of CEP motif with post-translational modifications at C-terminus (Fig. 1; Delay et al. 2013; Roberts et al. 2013; Taleski et al. 2018). The bioactive CEP peptides are perceived by their receptors CEP RECEPTOR 1/2 (CEPR1/CEPR2) to regulate a variety of plant developmental processes (Djordjevic et al. 2015; Okamoto et al. 2016; Taleski et al. 2018; Jeon et al. 2021). Among the CEP peptides, CEP5 plays an essential role in conferring plant stress resistance (Table 1; Figs. 2; 3c; Smith et al. 2020). *CEP5* transcription is induced by osmotic stress, and *CEP5*^{OE} overexpression plant shows a tolerance to both drought and osmotic stresses. Seedlings treated

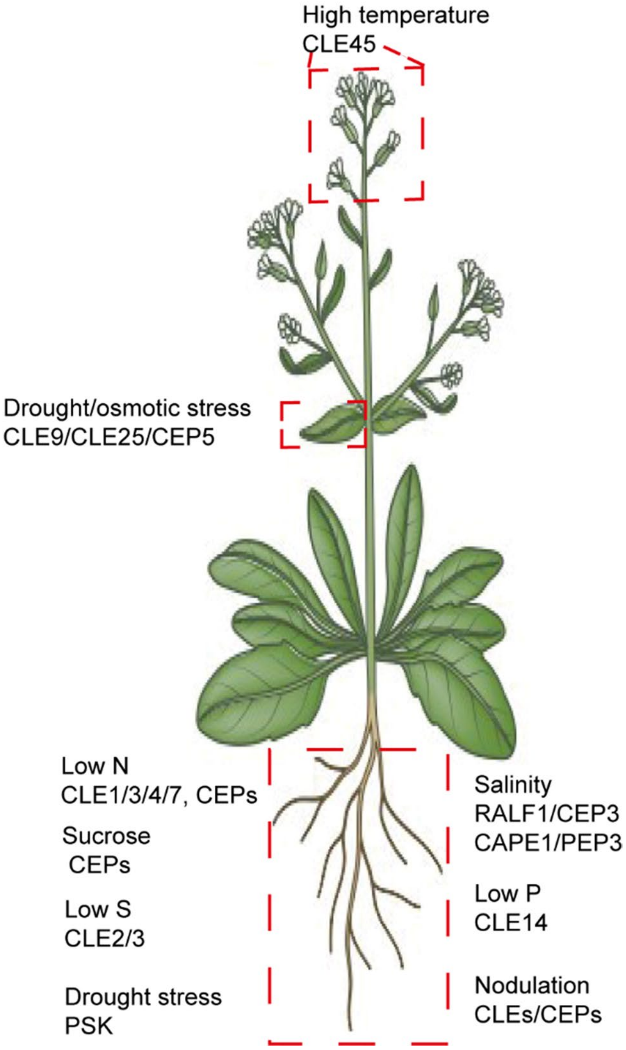

Fig. 2 An overview of small peptides in plant abiotic stress and nutrient signaling. The CLE, CEP, PSK, RALF, CAPE, and PEP peptides play distinct roles in plant response to abiotic stress and nutrient availability

with synthetic CEP5 peptide yield a similar tolerance. However, the function of CEP5 in stress tolerance does not fully depend on its well-known receptors, CEPR1 or CEPR2, because no obvious phenotype was observed in *cepr1 cepr2* double mutant under osmotic conditions. In contrast, CEP5 peptide promotes the stability of AUX/IAA, a key regulatory component of SCF$^{TIR1/AFB}$ nuclear auxin signaling pathway, partially via the CEPR receptors, resulting in repression of auxin-mediated gene expression, which in turn may confer plants resistance to stress (Shani et al. 2017; Sadok and Schoppach 2019; Smith et al. 2020). Thus, CEP5 peptide regulates plants stress responses through two mechanisms, dependent or independent of the CEPR receptors (Fig. 3c). Whether CEP5 peptide can be transported to leaves to regulate ABA signaling and stomatal closure during drought stress remains an open question, as *CEP5* is also expressed in root phloem (Roberts et al. 2013, 2016; Takahashi et al. 2018).

PSK peptide

PHYTOSULFOKINE (PSK), a group of sulfated peptides (Fig. 1), are perceived by plasma membrane localized PSK RECEPTOR 1 (PSKR1) and PSKR2, together with SOMATIC EMBRYOGENESIS RECEPTOR KINASE 3 (SERK3) coreceptors to modulate multiple physiological processes including stress response (Table 1; Fig. 2; Sauter 2015; Ladwig et al. 2015; Wang et al. 2015; Kaufmann et al. 2021). Osmotic stress prominently induces the expression of PSK precursor genes and PSK cleavage genes the SUBTILISIN (SBT). The overexpression transgenic plant *proPSK1*^{OE} or *SBT3.8*^{OE} displayed significantly improved osmotic stress tolerance, which is evident by its enhanced root and shoot growth under osmotic stress. Additionally, PSK1 peptide treatment recovers the osmotic stress-induced sensitive phenotypes in *sbt3.8* mutant. Thus, SBT3.8 cleaves the proPSK1 protein to generate biologically activated PSK1 peptide, which positively regulates plant resistance to drought stress. However, the involvement of PSKRs or SERK3 in PSK1-mediated drought/osmotic tolerance needs to be defined in future (Fig. 3d; Stührwohldt et al. 2021).

Small peptide-mediated response to salinity stress

RALF peptide

The Rapid Alkalinization Factor (RALF) peptides belong to the CRP family with post-translational modifications (Fig. 1) that are perceived by the receptors FERONIA (FER) and THESEUS1 to regulate various plant developmental processes including salt stress (Table 1; Stegmann et al. 2017; Yu and Assmann 2018; Gonneau et al. 2018; Blackburn et al. 2020; Gjetting et al. 2020). The *ralf1* mutant showed a comparable growth inhibition to wild-type upon NaCl treatment; however, the overexpression *RALF1*^{OE} transgenic line exhibits relative resistance to salt treatment, implying a positive role of RALF1 peptide in salt stress (Feng et al. 2018). On the other hand, *RALF1* expression in root is downregulated by salinity, and exogenous application of active RALF1 peptide triggers an accumulation of Na^+ via inhibiting the ARABIDOPSIS H^+-ATPASE 2 (AHA2) and Na^+/K^+ transporters

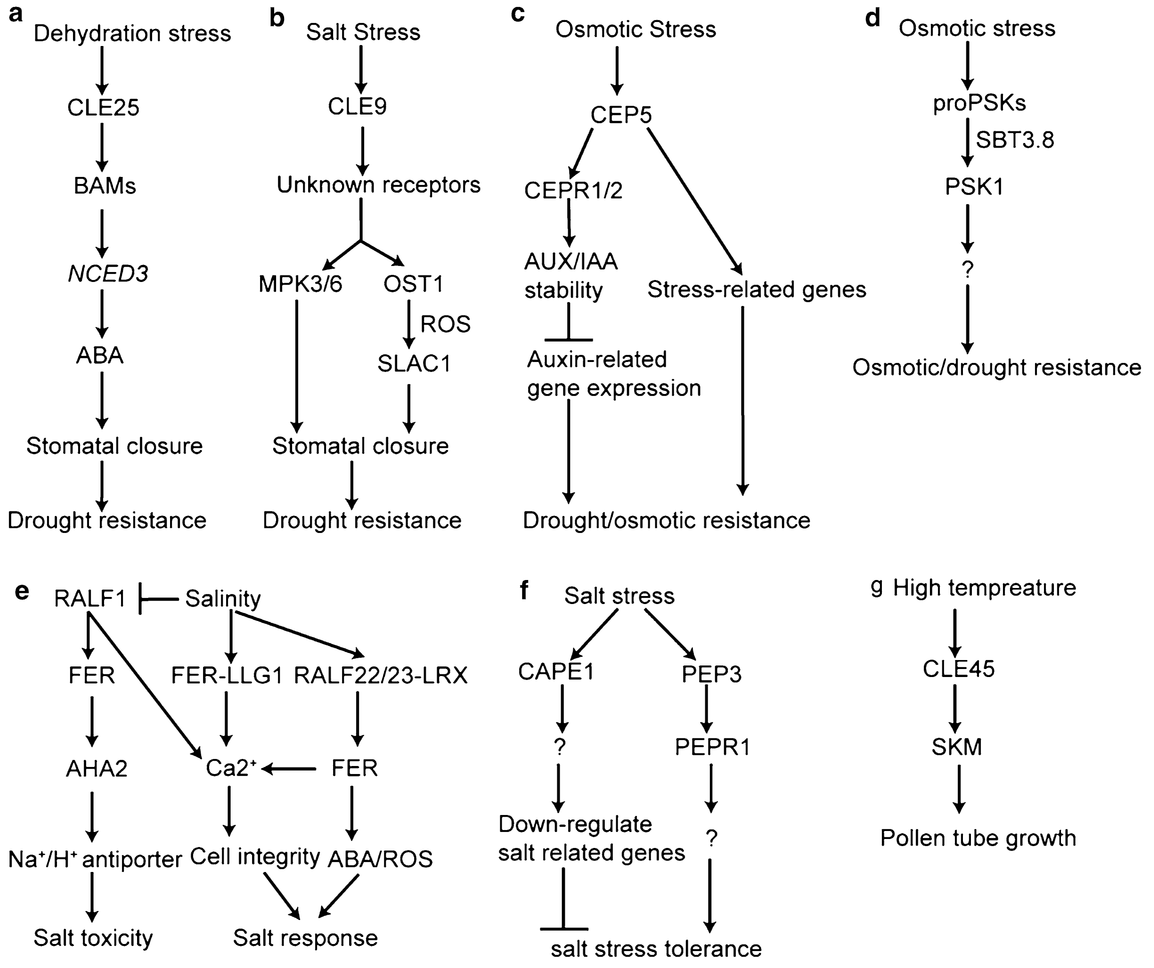

Fig. 3 Summary of small peptides in plant abiotic stress response. **a** Dehydration stress triggers accumulation of CLE25 peptide in roots, CLE25 is then transported to leaves, and is perceived by BAMs receptors to induce ABA biosynthesis via promoting *NCED3* expression, resulting in stomatal closure and drought resistance. **b** Drought stress triggers accumulation of CLE9 peptide, CLE9 is perceived by unknown receptors to simultaneously active MPK3/MPK6 and OST1-ROS-SLAC1 signaling cascade to close stomatal, resulting in drought resistance. **c** *CEP5* expression is induced by osmotic stress to confer plants drought/osmotic tolerance via two distinct mechanisms. On the one hand, CPE5 is recognized by CEPR1/CEPR2 to stabilize AUX/IAA transcriptional repressors, which suppresses transcriptional auxin response. On the other hand, CEP5 alters the expression of stress-related genes via undefined receptors. **d** Osmotic stress elicits expression of *proPSKs* and *SBT3.8*, and the SBT3.8 then cleaves proPSK1 to generate mature PSK1 peptide. PSK1 binds to unidentified receptors to confer plants the drought tolerance. **e** Salinity downregulates *RALF1* expression in roots. Bioactive RALF1 peptide is perceived by FER receptor to regulate AHA2 and N^{+}/K^{+} antiporter activity, resulting in accumulation of Na^{+} and enhanced salt toxicity. On the other hand, salinity triggers accumulation of RALF22/23 peptide, which interacts with LRX protein. Salinity causes dissociation of mature RALF22/23 peptides from LRX proteins, thereby triggering FER internalization, and resulting in the change of cell wall integrity, ABA and ROS signaling and salt tolerance. Salinity also regulates FER-LLG1-Ca^{2+} signaling cascade to maintain cell wall integrity during salt stress response. **f** Under salt conditions, *CAPE1* level is downregulated, and undefined receptors perceive CAPE1 peptide signal to downregulate salt-related genes, thus negatively regulating plant salt tolerance. Salt stress also induces *PEP3* expression, PEP3 then binds to PEPR1 receptor to improve salt tolerance via an unknown mechanism. **g** High temperature induces *CLE45* expression, and CLE45 binds to SKM receptor to protect pollen tube growth under high temperature

activity, leading to enhanced salt toxicity. RALF1 induced salt toxicity requires its receptor FERONIA (FER) (Yu and Assmann 2018). Interestingly, *fer* mutant is insensitive to RALF1 peptide treatment, but displays a hypersensitivity to salinity (Feng et al. 2018; Yu and Assmann 2018). It has been suggested that *fer* mutant rapidly loses cell integrity under salt stress and this defect depends on the Ca^{2+} signaling and its co-receptor LORELEI-like GPI-AP1 (LLG1) (Feng et al. 2018). RALF1 peptide treatment also induces an increase of cytoplasmic Ca^{2+} (Haruta et al. 2008), indicating a potential linkage between RALF1 peptide and salt tolerance. Notably, salinity also induces accumulation of RALF22/23 peptides which interact with LEUCINE-RICH REPEAT EXTENSINS (LRX) proteins to regulate FER-mediated cell wall integrity, ABA signaling, and Reactive Oxygen Species (ROS), resulting in salt tolerance (Zhao et al. 2018, 2020; Feng et al. 2018). RALF1-FER module is also involved in regulating ABA signaling (Yu et al. 2012; Chen et al. 2016) and GLYCINE-RICH RNA BINDING PROTEIN 7 (GRP7) splicing dynamics (Wang et al. 2020), which in turn, ensures plant responses to stress. Overall, RALF peptide signaling regulates salinity response via distinct mechanisms (Fig. 3e). However, through what precise mechanisms plants integrate these complex stress-related signaling networks mediated by RALF peptides are beyond our understanding.

CEP3 peptides

The CEP peptide family has also been implicated in salt response. The expression of *CEP* genes is differentially regulated by environmental clues such as salinity (Delay et al. 2013; Aggarwal et al. 2020). In *Arabidopsis*, *CEP3* is strongly upregulated by NaCl treatment. In addition, the *Arabidopsis cep3* mutant partially exhibits resistance to NaCl, indicated by a longer primary root of the mutant upon NaCl treatment (Delay et al. 2013). However, the molecular mechanism of CEP3-mediated salt stress response is still elusive.

CAPE1 peptide

CAP-DERIVED PEPTIDE 1 (CAPE1) is a member of the CRP family (Fig. 1; Chen et al. 2014). Nine *CAPE*s have been identified as precursor *Arabidopsis thaliana* CAPEs (PROAtCAPEs), and *PROAtCAPE1* specifically is downregulated under salt stress (Chien et al. 2015). The *proatcape1* knock-out mutant exhibits resistance to high salinity; in contrast, overexpression of *PROAtCAPE1* or exogenous application of synthetic AtCAPE1 peptide restores the salinity response in *proatcape1* mutant. Transcriptome analysis further shows that AtCAPE1 negatively regulates the expression of salt stress response genes (Table 1; Figs. 2, 3f; Chien et al. 2015). Hence, AtCAPE1 plays a negative role in plant salt stress response via undetermined mechanism.

PEP3 peptide

PLANT ELICITOR PEPTIDEs (PEPs) are endogenous elicitors of plant immunity (Fig. 1); however, it has been shown that PEPs are involved in plant salt stress (Fig. 2; Table 1). Among the eight members of *Arabidopsis* precursor PEP (AtPROPEP), *AtPROPEP3* is prominently induced by high salt concentration (Nakaminami et al. 2018). Knock down the *AtPROPEP3* expression results in the hypersensitivity to salt stress. In contrast, overexpression of *AtPROPEP3* or application of the synthetic AtPEP3 peptide induces plant resistance to the salinity. Further analysis shows that AtPEP3 binds to the receptor PEP RECEPTOR 1 (PEPR1) to confer plant tolerance to salinity, but the precise mechanisms require more investigations (Fig. 3f; Nakaminami et al. 2018).

CLE45 peptide mediates high-temperature response

CLE45 is expressed in stigma, and its expression is induced by high temperature. CLE45 peptide is capable of mediating pollen tube growth in response to high temperature (Table 1; Fig. 2; Endo et al. 2013). CLE45 peptide treatment prolongs pollen tube growth without affecting pollen germination at high temperature. By screening the T-DNA insertion lines, two candidate proteins, STERILITY-REGULATING KINASE MEMBER1 (SKM1) and SKM2, are recognized as the CLE45 receptors. Biochemical experiments demonstrated that the CLE45 physically binds to SKM1. *SKM1* and *SKM2* are expressed in pollen tube and their transcription is also induced by high temperature. Additionally, the *skm* mutants are insensitive to CLE45 peptide treatment in pollen tube growth. Collectively, these findings suggest CLE45-SKM pathway involves in a successful seed production under high temperature (Fig. 3g; Endo et al. 2013).

CLE peptides mediate nitrogen, phosphate and sulfur signaling

The availability of nitrogen (N) affects various plant developmental processes such as shoot branching, flowering and root development (Luo et al. 2020; Jia and von Wirén 2020). Nitrogen consists of two forms: inorganic (nitrate [NO^3-], and ammonium [$NH4^+$]) and organic (amino acids and urea). The discovery of N transport and key genes in N uptake and signaling using biochemical and genetic studies in the past decades provided fundamental insights into the nitrogen use efficiency in plants (Vidal et al. 2020). A regulatory network between N and phytohormones has also been established (Ristova et al. 2016). Interestingly, the CLE peptides also participate in N-mediated root growth (Araya et al. 2014).

CLEs gene expression is enhanced by N signaling (Patterson et al. 2010; Ruffel et al. 2011). Indeed, *CLE1/3/4/7* transcription levels are elevated in roots under low N conditions. The phloem-localized receptor kinase CLAVATA1

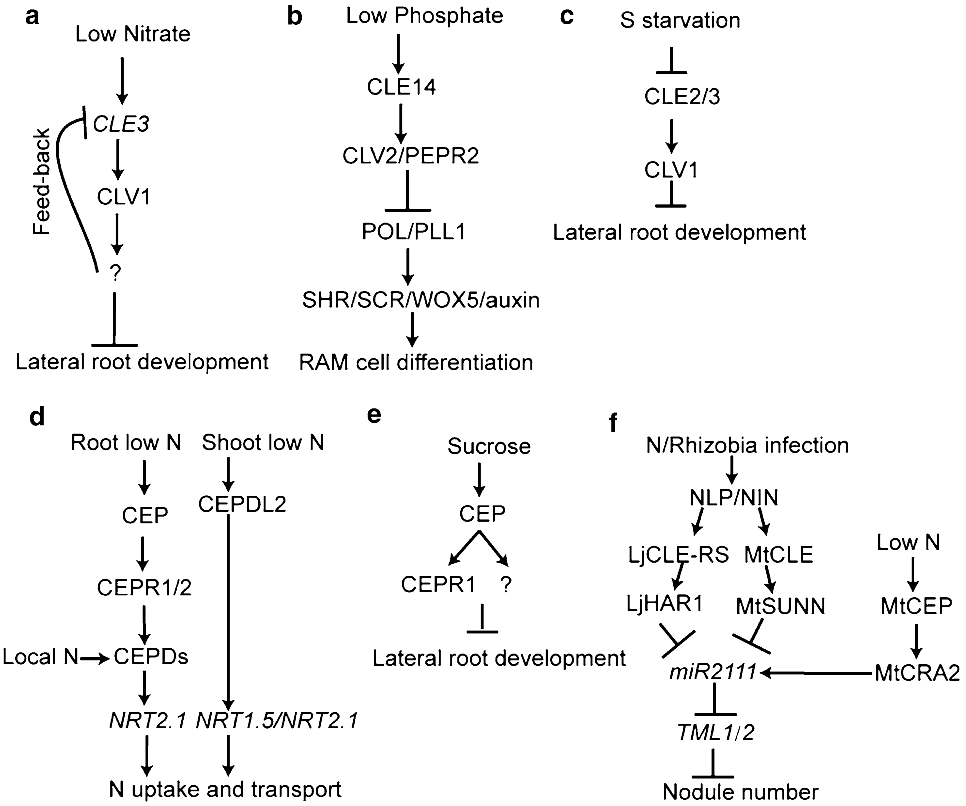

Fig. 4 Summary of small peptides that mediate plant nutrient signaling and nodulation. **a** Under low nitrate environment, *CLE3* expression is increased, and CLV1 recognizes CLE3 peptide to repress lateral root development via unknown downstream players. A feedback signal is activated by the CLV1-mediated N-demanding signal to repress *CLE3* expression. Hence a feedback loop is formed to control CLE-CLV1 cascade during lateral root development under a nitrate starvation environment. **b** Under low phosphate conditions, CLE14 peptide binds to CLV2 and PEPR2 receptors to attenuate POL and PLL1 function, which in turn affects the function of transcription factor SHR, SCR, WOX5, and auxin signaling, leading to root apical meristem (RAM) cell differentiation. **c** Under sulfur starvation, *CLE2/3* expression is suppressed, and CLV1 functions as CLE2/3 receptor to repress lateral root development. **d** In roots, *CEP* expression is promoted under N deficiency condition. CEP is then transported to shoots and is recognized by CEPRs receptors. CEPDs act as downstream players of CEP-CEPR signaling to accelerate N transporter *NRT2.1* expression, thus activating N acquisition. While in shoots, N deficiency enables CEPDL2 to promote *NRT2.1* or *NRT1.5* expression, which activates N acquisition. **e** Sucrose treatment increases *CEP* expression, and CEP binds to CEPR1 and unknown receptors to simultaneously repress lateral root development. **f** N/rhizobia infection promotes the expression of transcription factor *NLP* or *NIN*, which then binds to *LjCLE* and *MtCLE* promoters to control the expression of *LjCLE* and *MtCLE*, respectively. LjCLE and MtCLE are then separately perceived by LjHAR1 and MtSUNN to inhibit *miR211* expression, thus promoting *TML1/2* expression, resulting in a reduction of nodule numbers. Under low N conditions, *MtCEP* expression is increased, and MtCRA2 perceives MtCEP peptide to promote *miR211* expression. *miR211* then represses *TML1/2* expression, resulting in an increased number of nodules. Hence, CLE and CEP peptides play antagonistic roles in nodulation

(CLV1) perceives the bioactive CLE3 peptide to inhibit lateral root development (Table 1; Figs. 2, 4a; Araya et al. 2014). In turn, a yet unknown signal activated by CLV1-mediated N-demanding signal represses *CLE3* expression. Therefore, CLV1-CLE signaling forms a feedback loop to balance the *CLE* transcription in response to N availability (Fig. 4a). Many other receptor-like kinases (RLKs) are also suggested to transmit CLE signal (Fletcher 2020); however, it is unknown whether these RLKs also participate in CLE-mediated N signaling during plant development.

To adapt to low-phosphate (P) environments, plants develop intricate and adaptive mechanisms to maintain P homeostasis, which are regulated by intricate gene networks involving the plasma membrane-localized P transporters and P starvation-induced genes (Wang et al. 2018). Plants modify their root system architecture by an increase of lateral root number, promotion of root hair growth and termination of cell differentiation in root meristem to enlarge the contact surface with the soil for P uptake (Liu 2021). Recently, CLE14 peptide has been reported to be downstream of P signaling to regulate root apical meristem (RAM) cell differentiation (Gutiérrez-Alanís et al. 2017). Under P starvation, CLE14 transcription is upregulated. CLAVATA2 (CLV2) and PEPR2 perceive CLE14 peptide, to inhibit POLTERGEIST (POLL) and POLTERGEIST-LIKE 1 (PLL1) function, which in turn affects the major players involved in root meristem differentiation including the transcription factors SHORT ROOT (SHR), SCARECROW (SCR) and WUSCHEL-RELATED HOMEOBOX 5 (WOX5), and plant hormone auxin, leading to root meristem exhaustion (Table 1; Figs. 2, 4b; Gutiérrez-Alanís et al. 2017). Nevertheless, the mechanism regarding how the CLE14-CLV2/PEPR2 signaling regulates downstream players during P starvation is still not clear.

The macronutrient sulfur (S) has various effects on plant growth (Li et al. 2020; Aarabi et al. 2020). Despite the involvement of phytohormones in the regulation of S nutrient (Li et al. 2020), additional evidence supports the function of CLE peptide in regulation of root development in response to S (Table 1; Dong et al. 2019). *CLE* expression is controlled by the availability of S (Czyzewicz et al. 2015; Dong et al. 2019). S deprivation represses *CLE2* and *CLE3* expression levels, resulting in a reduction of lateral root density. However, this repression of *CLE* expression and lateral root density is diminished in *clv1* mutant. Hence, CLE-CLV1 module controls lateral root development under S deprivation (Table 1; Figs. 2, 4c; Dong et al. 2019), but the precise mechanism requires further investigations.

CEP peptides mediate nitrogen acquisition and sucrose signaling

N distribution is often heterogenous in soil; CEP peptides function as systemic long-distance signaling to ensure plants' efficient N uptake (Tabata et al. 2014; Ohkubo et al. 2017). The expression of seven *CEP* genes is prominently upregulated in roots under N-starvation condition, then the synthesized CEP peptides are transported to leaves. The leaf expressed CEPR1/2 receptors sense the root-derived CEP peptides to regulate the transcription of nitrate transporters *NRT2.1*, resulting in the promotion of N acquisition (Table 1; Figs. 2, 4d; Tabata et al. 2014). The polypeptides CEP DOWNSTREAM1 (CEPD1) and CEPD2, belonging to the glutaredoxin family, act as a second signal in shoot-to-root N signaling downstream of the CEPR-CEP signaling pathway (Ohkubo et al. 2017). Perception of CEP peptide by CEPR on the leaf phloem cells surface leads to the production of CEPDs polypeptides in shoots. CEPDs then act as phloem-mobile descending signals directed to roots exposed to sufficient N, where they accelerate *NRT2.1* expression and N uptake (Fig. 4d; Ohkubo et al. 2017). CEPD-LIKE2 (CEPDL2) is a leaf-derived signal to regulate root N uptake and transport. When roots are unable to absorb enough N to meet shoots N demand, *CEPDL2* expression is significantly upregulated, which helps roots to take up and transport N via upregulating the transcription of *NRT1.5* and *NRT2.1* (Ota et al. 2020). Taken together, CEP-CEPR-CEPD-CEPDL module forms a root-to-shoot-to-root regulatory network to control N uptake and transport dependent on the environmental N availability (Fig. 4d).

Sucrose is the product of photosynthesis, it breaks down into several forms of sugars such as glucose, fructose and trehalose 6-phosphate (T6P), and it is transiently stored in compartments for further use. Sucrose is transported from the source tissues to sink tissues via the phloem, which is mediated by multiple sucrose transporters (Fichtner et al. 2021). Sucrose is involved in various plant developmental processes including lateral root development. High sucrose concentration dramatically represses lateral root initiation, whereas low sucrose promotes lateral root development (Malamy and Ryan 2001). Sucrose upregulates multiple *CEP* genes expression; then CEP binds to the CEPR1 receptor and subsequently inhibits lateral root development. Notably, the sucrose-mediated upregulation of *CEP* gene expression is independent of CEPR1 receptor, implying that some unknown mechanisms also exist to mediate sucrose-CEP signaling involved in lateral root development. Additionally, RNA-seq analysis showed that many genes respond differently to sucrose in the *cepr1* mutant as compared to wild type, which suggests an alternative sucrose response dependent on the CEP-CEPR signaling pathway (Table 1; Figs. 2, 4e; Chapman et al. 2019).

Antagonistic roles of CLE and CEP peptide in Nodulation

Legumes fix atmospheric N_2 through a specific root organ, the nodule. As fixing N_2 is an energy-consuming biological process, the nodule number is tightly regulated via the autoregulation of nodulation (AON) and nitrate-dependent signaling pathway (Ferguson et al. 2019; Gautrat et al. 2021). The AON signaling initiates the synthesis of CLE peptides in *Medicago truncatula* (MtCLE12, MtCLE13 and MtCLE35) (Mortier et al. 2010; Mens et al. 2021; Moreau et al. 2021), and in *Lotus japonicus* (LjCLE-RS1, LjCLE-RS2 and LjCLE-RS3) (Okamoto et al. 2009, 2013; Nishida et al. 2018). The induction of *CLE* expression by N or rhizobia relies on the transcription factor NODULE INCEPTION (NIN) and NIN-LIKE PROTEIN (NLP) family. NIN or NLP binds to the *CLE* gene promoter to upregulate *CLEs* expression (Mortier et al. 2010; Nishida et al. 2018; Lin et al. 2018; Laffont et al. 2020; Moreau et al. 2021); then CLE peptides are transported to shoots and sensed by *Medicago truncatula* SUPER NUMERIC NODULES (MtSUNN) and *Lotus japonicus* HYPERNODULATON AND ABERRANT ROOT 1(LjHAR1) receptors (Mortier et al. 2010; Mens et al. 2021; Okamoto et al. 2013). The MtCLE-MtSUNN and LjCLE-RS-LjHAR1 modules repress the key shoot-to-root microRNA, *miR2111* expression (Fig. 4f; Tsikou et al. 2018; Gautrat et al. 2020). TOO MUCH LOVE 1/2

(TML1/2) are targets of *miR2111* (Magori et al. 2009; Takahara et al. 2013). The low expression level of *miR2111* leads to an elevated *TML1/2* expression and thus reduces nodule numbers (Magori et al. 2009; Takahara et al. 2013; Tsikou et al. 2018; Gautrat et al. 2020).

In contrast to the negative impact of CLE peptides on nodulation, CEP peptides positively regulate the nodulation formation. Under N starvation, the *CEP* expression is elevated and then binds to the COMPACT ROOT ARCHITECTURE 2 (CRA2) receptor to stimulate nodulation (Imin et al. 2013; Huault et al. 2014; Mohd-Radzman et al. 2016). Under low N condition, *miR2111* expression is upregulated, whereas the *TML1/2* transcription is decreased, which results in an increase of the nodule number (Fig. 4f; Gautrat et al. 2020). This transcriptional regulation of *miR211* and *TML1/2* expression depends on the CEP-CRA2 pathway (Gautrat et al. 2020).

In short, plants activate either CLE or CEP signaling to antagonistically regulate *miR2111* and *TML1/2* expression (Laffont et al. 2020; Gautrat et al. 2020). As a result, the nodule numbers are tightly controlled depending on the local environmental N status (Table 1; Figs. 2, 4f).

Conclusions and further perspectives

Plants have developed a plethora of pathways, notably including small peptides to enable optimal cellular and physiological outputs under constantly changing environments. The RLKs and co-receptor proteins perceive small peptides and translate the environmental signals to activate the complex downstream regulatory networks and thus modulate plant growth accordingly. Although many small peptides have been identified in many crops, the physiological roles of these peptides, particularly their roles in abiotic stress and nutrient signaling-related developmental processes are still untapped.

Arabidopsis genome contains more than 7000 small peptide encoding genes and 600 RLKs; the corresponding ligands for most of RLKs have not been identified yet (Takahashi et al. 2019). This suggests that various potential peptide-receptor signaling cascades enable plants to transmit a wide range of environmental signals under diverse conditions. Due to the redundancy among large family members, only a few members of identified peptides or RLKs have been characterized with a clear biological function. The application of novel genome editing technology to obtain multiple gain-of-function and loss-of-function mutants will enable us to understand the critical roles of small peptides and their interacting receptors in various aspects of plant development and stress responses (Wu et al. 2016; Yamaguchi et al. 2017). In addition, photoaffinity labeling peptides can be used to screen RLK expression library, which will enable to identify peptide-receptor pairs and to elucidate their biological functions (Tabata et al. 2014; Shinohara et al. 2016; Nakayama et al. 2017).

Recently, the emerging roles of small peptides in abiotic stress have been uncovered (Kim et al. 2021), but the mechanistic basis is still largely unknown. Despite their participations in plant response to drought, salinity, and nutrient starvation outlined above, they are also differentially induced by other environmental stimuli (Delay et al. 2013; Czyzewicz et al. 2015; Wang et al. 2016), whereas the undefined roles of small peptides in these unclarified environmental stimuli remain uncharted, which will be of great interest in future. In addition, to discover the downstream key players involved in these small peptide-mediated various abiotic stress will provide novel strategies to genetically engineer crops and hence improve their growth under adverse environments.

Moreover, when and how plants acquired these peptides signaling networks during evolution is currently unsolved; therefore, the study of peptides in early land plants (Delay et al. 2013; Roberts et al. 2013; Goad et al. 2017; Campbell and Turner 2017) will greatly help to elucidate the evolutionary mechanisms of small peptides in plant abiotic stress and nutrients signaling. Additionally, dissection of the crosstalk between phytohormones and small peptides would provide us novel strategies to improve plant tolerance to adverse environments.

The small peptides play essential roles in response to nutrients such as N and P; however, the mechanisms are still far from fully understood. On the other hand, antagonistic and synergistic interactions also exist among different nutrients (Kumar et al. 2021), while how the signaling of different nutrients is integrated by the peptide-receptor system remains obscure. Other phytohormones also take part in the regulation of plants' reactions to nutrients starvation; thus mechanistic basis of crosstalk between the phytohormone and peptide signaling are also attractive subjects for further investigation. Additionally, how small peptides shape plant architecture in response to other micronutrients, for example, iron (Fe) and zinc (Zn), is also untapped.

In the future, a comprehensive understanding of small peptides-mediated plant abiotic and nutrient responses will require the knowledge regarding the role of small peptides in environmental sensing and the subsequent signal transduction. The basic knowledge obtained from *Arabidopsis* will provide a blueprint to engineer crops for better growth and yield under unfavorable environmental conditions.

Author contribution statement HPX, WZ and WLL wrote the draft manuscript. HBH, YZZ, and JH designed the figures, wrote and edited the manuscript. All authors contributed to this article and approved the submitted version.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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