Trends in Plant Science

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Review

Sugar codes for plant fitness: arabinosylation in small peptide signaling

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Arabinosylation, a critical post-translational modification (PTM) ubiquitous in plants, has received insufficient scientific attention relative to its biological significance. While small secreted peptides (SSPs) are crucial signaling molecules that orchestrate plant growth, stress adaptation, and host-microbe communication, emerging evidence positions arabinosylation as a key regulatory mechanism modulating SSP functionality. In this review we synthesize current knowledge on arabinosylated SSPs, emphasizing their regulatory roles in developmental programming and reprogramming, stress resilience, and symbiotic interactions. We discuss biochemical mechanisms through which arabinosylation enhances peptide biological activity or stability, including receptor interaction modulation, structural stabilization, and proteolytic resistance. We also evaluate future opportunities for leveraging arabinosylation engineering in developing climate-smart crops through targeted arabinosylated SSPs.

Highlights

An increasing number of studies have demonstrated that arabinosylated peptides are the bioactive forms of small secreted peptides (SSPs).

Arabinosylation is critical for the functions of SSPs and plays a role in fine-tuning plant development, stress resilience, and symbiosis.

Innovative strategies – including endogenous regulation of the expression and arabinosylation of SSPs, and exogenous application of arabinosylated peptides – hold significant promise for improving crop yields and stress tolerance.

There are still thousands of glycopeptides in plant genomes that have yet to be discovered and identified.

Arabinosylation: a ubiquitous biological mechanism with multidisciplinary implications

Arabinosylation, an enzymatic process mediating L-arabinose conjugation to biological substrates, exhibits remarkable phylogenetic conservation across plants, bacteria, and viral systems [1]. In plants, this modification plays crucial roles in cell wall polymer construction and functional modulation of SSPs, thereby governing growth, stress responses, and symbiotic interactions [2–4]. Pathogenic microorganisms have evolutionarily coopted arabinosylation mechanisms to enhance virulence. For instance, *Mycobacterium tuberculosis* arabinosylates virulence factors to facilitate host cell adhesion and immune evasion [5,6]. Targeted inhibition of arabinosyltransferases that mediates arabinan biosynthesis disrupts bacterial cell wall integrity, synergistically improving antimicrobial efficacy and informing novel therapeutic regimens [7]. Pharmacologically, arabinose moieties significantly potentiate drug bioactivity. For example, it significantly enhances the anticancer efficacy of the pentacyclic triterpenoid betulinic acid [8]. Beyond conventional roles, arabinosylation can be an epigenetic safeguard in T4-like bacteriophages, conferring nuclease resistance to viral DNA through site-specific arabinosylation [9].

Despite its cross-kingdom functional significance, key knowledge gaps persist regarding enzymatic regulation, substrate specificity, and the evolutionary trajectory of arabinosylation pathways. These limitations currently constrain its systematic application in drug discovery and agricultural biotechnology, underscoring the need for mechanistic studies integrating structural and systems biology approaches. In this review we focus on plant arabinosylation systems, with emphasis on SSP regulation as a paradigm for understanding their biological versatility.

Arabinosylation in plants

In plants, the arabinosylation of cell wall protein **extensins** (see Glossary) and SSPs predominantly occurs on hydroxyproline (Hyp) [1]. The proline hydroxylation in extensins is mediated

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primarily by **prolyl-4-hydroxylases (P4Hs)**, whereas the enzyme responsible for proline hydroxylation associated with SSPs currently remains unknown [10–12]. Although contiguous proline-rich motifs have been implicated in facilitating efficient proline hydroxylation in extensins, the precise consensus sequence required for proline hydroxylation of SSPs in plants remains to be elucidated [13]. Building on proline hydroxylation, arabinosylation exhibits even more complex diversity among different biopolymers due to the variations in the modified motifs, glycosidic linkages, and number of arabinose units. For example, cell wall protein extensins contain a repeating motif consisting of serine residues followed by three to five Hyp residues, with each Hyp modified by one to five β- or α-linked **L-arabinofuranose (L-Ara*f*)** units (Ara*f*1–5) [1] (Figure 1A). By contrast, SSPs feature instead a Hyp–Ara*f*3 side chain attached to non-contiguous Hyp residues [1] (Figure 1B).

Hyp arabinosylation was first identified in extensins and has since been progressively discovered in numerous SSPs [14]. There is general agreement that the biosynthesis of arabinoside chains involves the initial attachment of L-Ara*f* to a specific Hyp residue, followed by chain elongation [15]. The initial attachment step is catalyzed by hydroxyproline arabinosyltransferases (HPATs), which were originally identified in arabidopsis (*Arabidopsis thaliana*) and are encoded by three genes *HPAT1*, *HPAT2*, and *HPAT3* of the glycosyltransferase 95 (GT95) family [16]. Phylogenetic analyses have suggested that HPATs are conserved in plants and are represented by several HPAT homologs in different species, including the tomato (*Solanum lycopersicum*) FASCIATED INFLORESCENCE (FIN), *Lotus japonicus* PLENTY (LjPLENTY), *Medicago truncatula* ROOT DETERMINED NODULATION 1 (MtRDN1), and *Pisum sativum* NODULATION 3 (PvNOD3) [17–20]. In arabidopsis, *hpats* mutants display elongated hypocotyls, premature leaf senescence, and compromised male fertility, phenotypes linked to cell wall abnormalities [16,21]. By contrast, in tomato, *fin* mutants result in enlarged shoot meristems, branched

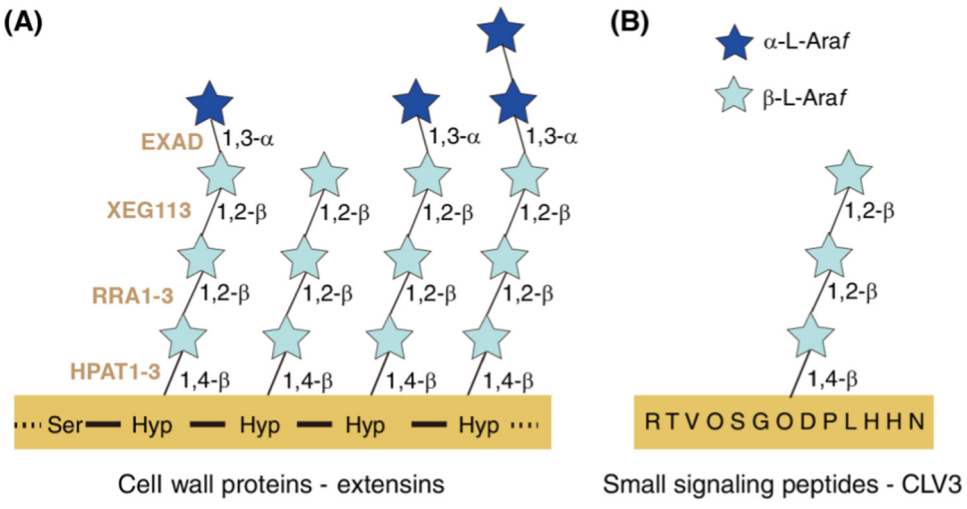

Figure 1. Arabinosylated patterns in cell wall protein extensins and small secreted peptides (SSPs). (A) Extensins contain contiguous hydroxyproline (Hyp) residues, and each of these Hyp residues undergoes arabinosylation with three to five arabinose units, leading to the formation of multiple arabinoside chains. (B) The arabinosylation of SSPs forms an Hyp–arabinofuranoside3 (Ara*f*3) chain on non-consecutive Hyp. The enzymes mediating the cascade arabinosylation of cell wall extensins are indicated in brown. Dark blue stars: α-linked L-arabinofuranoside; light blue stars: β-linked L-arabinofuranoside. Abbreviations: ExAD, extension-deficient arabinose; HPAT1–3, hydroxyproline arabinosyltransferase 1–3; O, Hyp residues; RRA1-3, reduced residual arabinose 1–3; XEG113, xyloglucan endoglucanase 113.

Glossary

L-Arabinofuranose (L-Ara*f*): L-arabinose residues are present in two tautomers in nature: arabinofuranose (Ara*f*) and arabinopyranose (Ara*p*). L-Ara*f* is primarily involved in building biopolymers, while L-Ara*p* is commonly regarded as an intermediate in synthesizing Ara*f*.

Autoregulation of nodulation (AON): a root-to-shoot-to-root negative feedback mechanism to achieve a balanced symbiotic relationship. It balances the number and activity of root nodules through the interaction of multiple signal molecules and regulatory factors such as small signaling peptides, nitrate, and miRNA.

CLAVATA–WUSCHEL (CLV–WUS) pathway: a negative feedback mechanism to maintain shoot meristem homeostasis. CLAVATA3 (CLV3) and its cognates are perceived by receptors to repress the expression of *WUSCHEL* (*WUS*). WUS in turn promotes the *CLV3* expression, forming the negative feedback loop.

CLV3/endosperm surrounding region-related (CLE) peptides: a currently well-known and the largest family of small peptides; they play critical roles in plant growth, development, defense responses, and symbiosis.

Extensins: a class of plant cell wall hydroxyproline-rich glycoproteins involved in reinforcing structure via tyrosine-mediated intramolecular and intermolecular cross-linking; they are often glycosylated with arabinose residues, forming short oligosaccharide chains. This glycosylation contributes to their structural stability and interactions with other cell wall components like cellulose and pectins.

Prolyl-4-hydroxylase (P4H): P4H belongs to the family of 2-oxoglutarate-dependent dioxygenases, which require 2-oxoglutarate and oxygen as co-substrates. As a transmembrane protein, P4H localizes in both the endoplasmic reticulum and the Golgi complex. Thirteen *P4H* genes have been identified in arabidopsis to date, and they are closely associated with plant root hair growth and hypoxic stress. The enzymes responsible for proline hydroxylation in small signaling peptides remain unclear.

Receptor-like kinases (RLKs): a class of proteins with a predicted signal sequence, single transmembrane region, and cytoplasmic kinase domain;

inflorescences, increased floral organs, and larger fruits [17]. These phenotypes are related to the abnormal arabinosylation of tomato CLAVATA3 (CLV3) and related **CLV3/endosperm surrounding region-related (CLE) peptides** [17]. In legumes, loss-of-function mutations in *LjPLENTY*, *MtRDN1*, and *PsNOD3* disrupt arabinosylation of nodulation-associated CLE peptides, resulting in hypernodulation phenotypes [18–20]. These divergent phenotypes suggest that arabinosyltransferase homologs have evolved species-specific substrate preferences, adapting their roles in arabinosylation to distinct developmental contexts.

RLKs mediate many signaling events by recognizing ligands such as small signaling peptides.

Shoot apical meristem (SAM): a tissue composed of innately undifferentiated cells that determines the morphology of all aerial parts of the plant.

A second class of arabinosyltransferases is responsible for extending arabinoside chains. The first identified enzymes responsible for arabinoside chain elongation are REDUCED RESIDUAL ARABINOSE 1–3 (RRA1–3), XYLOGLUCAN ENDOTRANSGLUCOSYLASE 113 (XEG113), and EXTENSIN ARABINOSE-DEFICIENT (EXAD) in arabidopsis [22–24]. Among these, RRA1–3 and XEG113 belong to the GT77 family, whereas EXAD is classified as a member of the GT47 family. They form an enzymatic cascade that elongates the arabinoside chains of cell wall extensins (Figure 1A). Although there is no evidence to suggest that they modify SSPs in arabidopsis, genetic analysis in tomato indicates that their orthologs, SlRRA3a and FASCIATED AND BRANCHED 2 (FAB2, a homolog of XEG113), together with FIN, may function in adding arabinoside chains to SlCLV3 and related SlCLE peptides (Figure 1B). Elucidating the mechanisms underlying functional conservation and diversification of arabinosyltransferases among different species is crucial but remains unresolved.

Arabinosylated SSPs in plants

SSPs are a class of crucial signaling molecules that can be transported over either short or long distances. There are thousands of genes in plants that encode potential SSPs [25,26]. SSPs typically act as ligands that bind to plasma membrane **receptor-like kinases (RLKs)**, activating or inhibiting their kinase activity to regulate plant development and environmental responses [27–29]. Arabinosylated SSPs are initially synthesized as long, inactive prepropeptides that subsequently undergo various PTMs, such as proteolytic cleavage, proline hydroxylation, hydroxyproline arabinosylation, and tyrosine sulfation, ultimately generating mature glycopeptides that usually comprise no more than 20 amino acids (aa) [30]. Accumulating evidence demonstrates the critical roles of arabinosylation in governing SSP functions. Here, we review recent advancements in SSP arabinosylation, discussing the molecular mechanisms underlying this modification and its potential applications in agricultural improvements.

Arabinosylated peptides in plant shoot development

The development of all aboveground plant structures relies on the continued activity of the **shoot apical meristem (SAM)**. Forward genetic studies identified non-cell-autonomous ligand CLV3 and the receptor CLAVATA 1 (CLV1) as key regulators of SAM proliferation in arabidopsis [31,32]. *CLV3* is specifically expressed in the outermost cell layers of the SAM central zone and is secreted into the underlying organizing center where it is perceived by CLV1 [31]. The BARELY ANY MERISTEM (BAM) receptors function as redundant receptors for CLV1 and can perceive CLV3 in *clv1* null allele mutants [33,34]. Another receptor-like protein CLAVATA 2 (CLV2) combined with pseudokinase CORYNE (CRN), and receptor-like protein kinase 2 (RPK2) are also involved in the CLV signaling pathway [35,36]. CLAVATA 3 INSENSITIVE RECEPTOR KINASEs (CIKs) function as co-receptors of CLV1, CLV2/CRN, and RPK2 to mediate CLV3 signaling [37]. When CLV3 binds to these receptors, it represses expression of WUSCHEL (WUS) transcription factor [38,39]. WUS promotes stem cell proliferation and non-cell-autonomously upregulates *CLV3*, thereby forming a **CLAVATA–WUSCHEL (CLV–WUS) pathway** negative feedback loop that maintains SAM homeostasis [39,40].

The secreted CLV3 has an extremely low abundance in the SAM [41]. Matrix-assisted laser desorption/ionization–time-of-flight mass spectrometry (MALDI–TOF MS) was initially applied for *in situ* analysis of arabidopsis *CLV3*-overexpressing calli [41]. Using this method, a 12-aa peptide containing two Hyp residues within a conserved motif of the CLV3 propeptide was identified [41]. However, application of this 12-aa peptide failed to fully rescue the enlarged SAM of arabidopsis *clv3* mutants at physiologically relevant concentrations [42]. Further analysis of CLV3 peptides in submerged arabidopsis cultures using nano-liquid chromatography–tandem mass spectrometry (nano-LC–MS/MS) found that the bioactive form of CLV3 is a 13-aa glycopeptide in which Hyp7 is modified by three β-linked L-Ara*f*s [42]. This glycopeptide showed stronger interaction with CLV1, compared with the non-glycosylated CLV3 peptide at an equivalent concentration [42]. The functional significance of CLV3 arabinosylation is further supported by comparative analysis of chemically synthesized mono-, di-, and tri-arabinosylated CLV3 variants, revealing that CLV3 bioactivity increases with arabinose chain length in arabidopsis [43] (Figure 2A).

In the tomato, although the endogenous active structure of SlCLV3 remains unclear, application of chemically synthesized 12-aa SlCLV3 glycopeptides has demonstrated that arabinosylation significantly enhances its bioactivity [17]. Recent studies revealed that sugar transport protein 2 (STP2), a monosaccharide transporter, influences tomato fruit locule number under low temperature by regulating SlCLV3 arabinosylation in the SAM, linking the critical role of SlCLV3 arabinosylation to stress responses [44]. Furthermore, arabinosylation also enhances the bioactivity of its homolog SlCLE9, which acts as a backup peptide of SlCLV3 to maintain SAM developmental robustness through transcriptional compensation [17,45]. Genetic analysis of tomato *fin*, *slrra3a*, and *fab2* mutants indicated that these arabinosyltransferases might form an enzymatic cascade to modify SlCLV3 and SlCLE9 [17]. Although *CLV3* is highly conserved across flowering plants, the endogenous active forms of CLV3 in different species remain poorly characterized [46]. The key questions are whether arabinosylation constitutes an evolutionarily conserved mechanism modulating CLV3 function, and whether this modification targets specific Hyp residues in the CLV3 peptide via a universal biochemical pathway.

Arabinosylated peptides in balancing the growth–defense trade-off

Researchers initially isolated PLANT PEPTIDE CONTAINING SULFATED TYROSINE 1 (PSY1)–a key sulfated signaling peptide that promotes cell elongation and root growth–from arabidopsis cell suspension cultures through ion-selective enrichment. Structural characterization revealed the mature PSY1 peptide as an 18-aa polypeptide featuring a sulfated tyrosine residue and an Ara*f*3 side chain linked to Hyp16 [47]. Overexpression of *PSY1* or exogenous application of PSY1 peptides purified from arabidopsis cell suspensions significantly increased root length [47]. By contrast, a chemically synthesized form of PSY1 lacking Ara*f*3 showed substantially weaker effects on root elongation at equivalent concentrations, indicating that arabinosylation is essential for full PSY1 bioactivity [47]. Recent studies have shown that PSY1 glycopeptides mediate trade-off between plant growth and stress response through their cognate PSYR receptors [27]. Interestingly, although arabidopsis contains nine PSY1 homologs, only PSY1 exhibits Hyp arabinosylation [27]. This suggests that arabinosylation of SSPs may depend not only on proline residues but also on specific peptide sequence contexts. Whether arabinosylation confers functional specificity to PSY1 in balancing plant growth and stress responses merits further exploration.

Arabinosylated peptides in stomatal and xylem development

The arabidopsis CLE peptide family member AtCLE9 was found to regulate stomatal lineage development and xylem file formation [48]. It also enhances drought tolerance by mediating abscisic acid (ABA)-dependent stomatal closure under osmotic stress (mannitol or NaCl) via core ABA

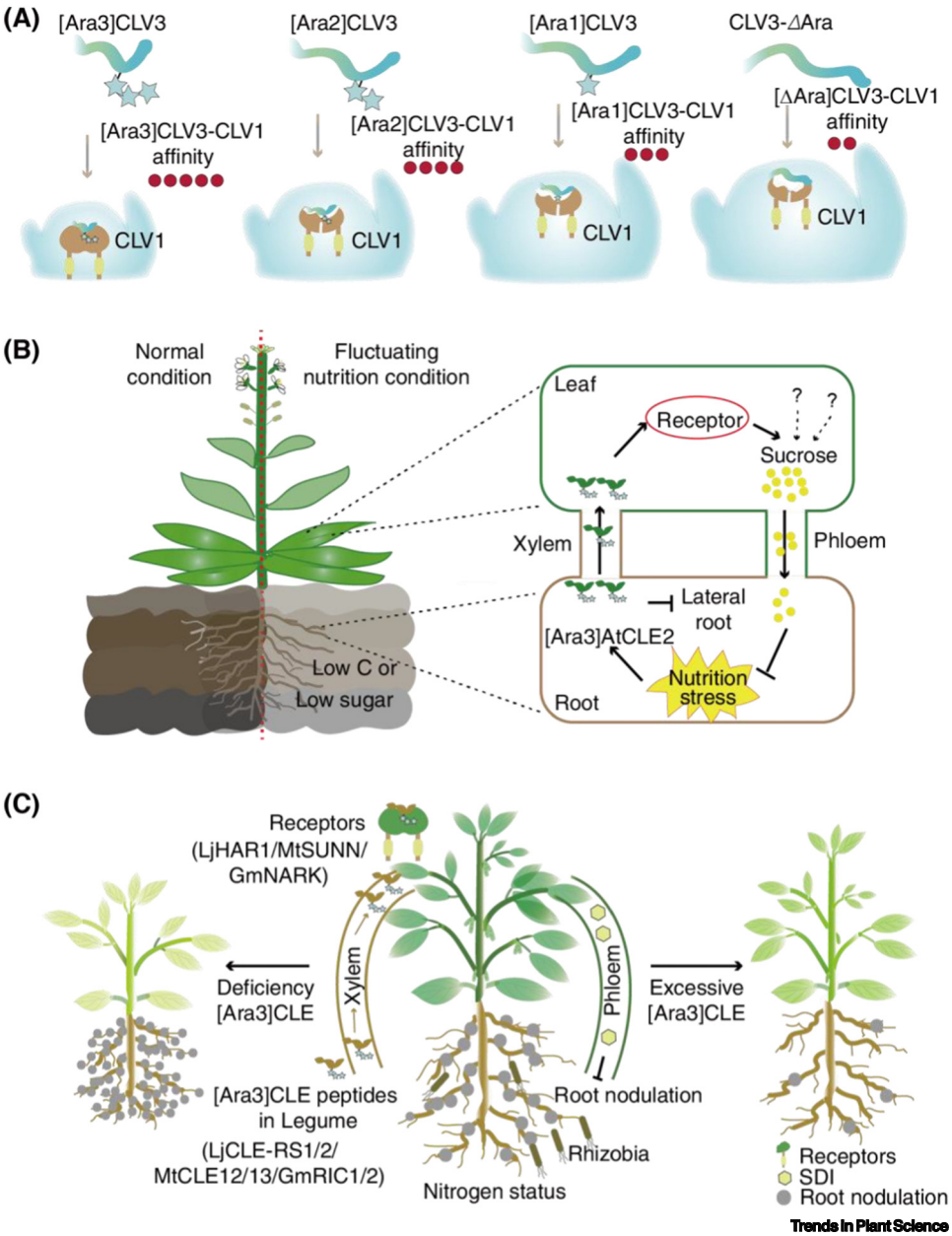

Figure 2. Arabinosylated peptides mediate plant development, stress resilience, and symbiosis. (A) In arabidopsis, the longer arabinoside chain of CLV3 correlates with higher biological activity. Incomplete arabinoside chains cause shoot meristem enlargement. The CLV3–CLV1 interaction model is conceptual (not based on structural data). (B) Tri-arabinosylated AtCLE2 peptide systematically boosts root sucrose levels during nutrition fluctuations (e.g., sugar/carbon deficiency). (C) In legumes, tri-arabinosylated CLE peptides (LjCLE-RS2, MtCLE12/13, GmRIC1/2, etc.) are induced by rhizobia and nitrate. They regulate nodulation autoregulation by suppressing root nodulation (excessive or insufficient nodules harm plant growth). Abbreviations: C, carbon source; SDI, shoot-derived inhibitor.

signaling components OPEN STOMATA 1 (OST1) and SLOW ANION CHANNEL-ASSOCIATED 1 (SLAC1) [49]. Notably, AtCLE9 operates through distinct receptor complexes: it binds HAESA-LIKE 1 (HSL1) and BAM1 to modulate stomatal development, while regulating xylem development through BAM1 and CLV1 [48,50]. Nano-LC–MS/MS analysis of apoplastic peptides

derived from *AtCLE9*-overexpressing arabidopsis plants revealed that AtCLE9 is secreted as a 12-aa glycopeptide in which either or both of the two Hyp residues are modified with multiple L-Ara*f* residues [51]. Elucidating the biological significance of the diverse arabinoside chains on AtCLE9 and their underlying biochemical mechanisms will facilitate a deeper understanding of how plants utilize arabinosylation to achieve developmental plasticity for environmental adaptation.

Arabinosylated peptides in nutrient deficiency responses

AtCLE2, another member of the arabidopsis CLE family, is found to act as a key regulator of sugar starvation, darkness, and nitrogen deficiency [52]. The root-derived AtCLE2 not only systematically increases root sucrose levels via its long-distance translocation to leaves, but also inhibits excessive lateral root development to limit energy consumption through short-distance movement [53] (Figure 2A). AtCLE2 regulates lateral root growth primarily through CLV1, while the receptors that perceive AtCLE2 to regulate root sucrose levels remain elusive [54]. The active mature form of AtCLE2 is a 12-aa glycopeptide with the Hyp7 residue modified by three L-Ara*f* residues [42,53]. The arabinosylation of AtCLE2 is primarily executed by HPAT3, but how the arabinoside chain extends is still unclear [16]. *In vitro* experiments revealed that arabinosylated AtCLE2 displays stronger binding affinity to the CLV1 receptor than the non-arabinosylated forms, demonstrating the critical role of arabinosylation in its function [42]. Similarly, the soybean (*Glycine max*) XYLEM SAP-ASSOCIATED PEPTIDE 4 (GmXAP4/GmCLE32) – which responds to root sucrose levels – was identified as a tri-arabinosylated peptide in xylem exudates [53,55]. These findings suggest the crucial roles of arabinosylation in determining the functions of these SSPs in regulating nutrient stress across different species.

Arabinosylated peptides in plant defense

Systemin and Hyp-rich systemin (HypSys) are two types of plant defense signaling peptides that mediate plant responses to wounding by inducing early defense signals in the jasmonate pathway to activate defense gene expression against herbivory [56,57]. Systemin, initially isolated from tomato leaves, activates defensive gene expression by binding to a leucine-rich repeat receptor kinase (LRR-RK) termed systemin receptor 1 (SYR1) and somatic embryogenesis receptor-like kinase (SERK) co-receptors [58–60]. Systemin is a 18-aa peptide derived from the C terminus of a 200-aa pro-systemin, which does not contain a signal peptide for secretion and is not produced through the secretory pathway [61]. Unlike systemin, HypSys, first identified in tobacco (*Nicotiana tabacum*) suspension cells via MALDI MS, is derived from a precursor protein with a signal peptide [62]. It matures through proline hydroxylation and Hyp arabinosylation into a glycopeptide that contains 3–12 pentose units [62]. Although there is no evidence to confirm that the pentose is arabinose, the Hyp-rich sequences in HypSys resemble characteristic arabinosylation motifs, implying that arabinosylation might occur in HypSys. Importantly, the bioactivity of chemically synthesized HypSys is significantly reduced without these pentose moieties, suggesting that the pentose moieties are critical for HypSys bioactivity [62]. Notably, the tobacco HypSys precursor yields multiple mature glycopeptides, a trend conserved across various plants: species of the Solanaceae (tomato, *Solanum nigrum*, *Petunia hybrida*) generate three HypSys glycopeptides per precursor, while species of the Convolvulaceae (*Ipomoea batatas*) produce six [63–66]. Despite the receptors of systemin being identified, the perception mechanism of HypSys in plant defense responses remains unknown. A critical question is whether multiple glycopeptides with diverse pentose attachments derived from the same precursors are recognized by distinct receptors.

Arabinosylated peptides in plant–microbe symbiosis

Plants frequently engage in symbioses with beneficial microbes, a trait especially prevalent and functionally significant within the legume family. To establish balanced symbiotic relationships,

plants have evolved sophisticated regulatory mechanisms such as the **autoregulation of nodulation (AON)** in legumes. CLE peptides are key regulators of AON; they include: *L. japonicus* CLE-RS1/2, *M. truncatula* CLE12/13 and C-TERMINALLY ENCODED PEPTIDE (CEP), and soybean RIC1/2 [20,67–71]. These peptides are root-specifically expressed in response to rhizobial infection and environmental nitrogen levels, and are perceived by CLV1 orthologs in the shoots of different species, including *L. japonicus* HAR1 (LjHAR1), *M. truncatula* SUPER NUMERIC NODULES (MtSUNN), soybean and *P. vulgaris* NODULE AUTOREGULATION RECEPTOR KINASE (GmNARK and PvNARK), and *Pisum sativum* SYMBIOSIS 29 (PsSYM29) [20,67,68,71] (Figure 2B). Ligand–receptor recognition initiates a secondary signal that functions as a shoot-derived inhibitor (SDI) of nodulation. This SDI is systemically transported to roots where it inhibits subsequent nodule formation [72].

Structural analyses confirm that mature bioactive LjCLE-RS1 and LjCLE-RS2 from xylem sap are 13-aa glycopeptides featuring Hyp7 modified by three L-Ara*f* residues [67]. Non-arabinosylated LjCLE-RS2 fails to bind LjHAR1 receptor and lacks bioactivity even at elevated concentrations, demonstrating direct functional dependence on arabinosylation [67]. This modification dependency is evolutionarily conserved: MtCLE12/13 and GmRIC1/2 similarly require tri-arabinosylation for function [20,68]. Essential arabinosyltransferases, such as LjPLENTY, MtRDN1, and PsNOD3, catalyze this modification on their cognate peptides such as LjCLE-RS1/2, MtCLE12, and GmRIC1/2 [18–20]. Beyond legumes, SlCLE11 arabinosylation mediated by FIN regulates arbuscular mycorrhizal colonization in tomato [73]. Together, these findings demonstrate that functions of these SSPs in symbiosis homeostasis rely on arabinosylation. Interestingly, arabinosylation of MtCEP1 conversely regulates nodulation symbiosis [69]. Multiple hydroxylated and monoarabinosylated MtCEP1 derivatives isolated from root exudates retain bioactivity, while tri-arabinosylated forms are inactive [69], suggesting that the degree of arabinosylation can either enhance or inhibit the activity of SSPs.

The biochemical mechanisms of arabinosylation in regulating SSP functions

Although arabinosylation is critical for the function of plant SSPs, how arabinosylation modulates their activities has been a longstanding mystery. Due to the lack of direct structural evidence for the glycopeptide–receptor complex, there is currently no definitive conclusion regarding the biochemical function of Hyp arabinosylation. Here, we summarize the biochemical and genetic evidence for arabinosylation conferring bioactivity to SSPs, and propose potential biochemical mechanisms.

Arabinosylation may increase the binding affinity of SSPs to their cognate receptors

Although no structural data on Hyp arabinosylation have been reported, *in vitro* binding and bioassays have shown that most arabinosylated CLE peptides are more active than non-arabinosylated CLE peptides [17,19,20,42,68]. Thus, the Hyp residues subjected to arabinosylation in CLE peptides are very likely to interact directly with residues on the receptors to promote binding affinity. It is also possible that tri-arabinosylation imposes an allosteric regulation of peptide conformation, as evidenced by nuclear magnetic resonance (NMR) analysis of arabidopsis CLV3 glycopeptide [43], to fit into the receptor binding grooves and promote binding affinity. Notably, several SSPs exhibit various forms of arabinosylation, such as AtCLE9 and HypSys [51,62]. It is intriguing to investigate whether different arabinosylation patterns can induce SSPs to adopt distinct conformations for binding multiple receptors.

Arabinosylation may protect SSPs from protease degradation

Arabinosylation may provide physical protection for SSPs from protease breakdown. For example, *in vitro* degradation assays showed that arabinosylated GrCLE1 peptide from the parasitic

nematode *Globodera rostochiensis* is more resistant to subtilisin A (a Ser endoproteinase) treatment than its non-glycosylated isoform [74]. Moreover, the arabinosylated GmCLE40 peptide, whose arabinosylation does not affect its conformation, exhibited stronger inhibitory potency in repressing soybean root growth than its non-glycosylated isoform [75]. Whether arabinosylation endows GmCLE40 with greater hydrolytic stability warrants further investigation. Notably, SSPs function as non-cell-autonomous signals undergoing local or systemic transport via the apoplastic compartment [76]. Elucidating whether arabinosylation facilitates efficient apoplastic trafficking by enhancing their aqueous phase mobility – particularly for systemically acting SSPs – represents a compelling research direction.

Arabinosylated SSPs in crop improvements: insights and potential applications

The CLV3 pathway is evolutionarily conserved across different crops and regulates key agronomic traits: tomato fruit size, rice (*Oryza sativa*) panicle architecture, *Brassica napus* seed number, and maize (*Zea mays)* kernel number [77–80]. Complete CLV3 loss of function typically compromises yield, whereas natural variation in regulatory elements or hypomorphic alleles can enhance crop productivity [81]. For instance, the *fasciated* (*fas*) locus associated with tomato fruit size domestication represents a partial loss-of-function mutation caused by a 294 kb inversion that disrupts the SlCLV3 promoter, thereby leading to more locules and increased fruit yield [17]. This supports the targeted editing of gene regulatory regions to generate quantitative trait variation for yield improvement, as demonstrated in tomato CLV3 and maize CLE7 [82,83]. However, nonlinear transcriptional–phenotypic relationships in SlCLV3 and unpredictable *cis*-regulatory interactions within the CLV–WUS network complicate deterministic yield prediction [84,85]. Notably, arabinoside chain length is tightly related to bioactivities of CLV3 in arabidopsis and tomato [17,43], implying potential for fine-tuning arabinosylation levels through rational design of arabinosyltransferases to quantitatively control yields (Figure 3, Key figure).

Arabinosylated SSPs modulate plant responses to diverse environmental stresses, including drought, carbon and nitrogen deficiency, mechanical damage, and rhizobial infection. Elevated SSP expression can enhance stress resilience, as demonstrated by *AtCLE9* overexpression inducing stomatal closure and improving drought tolerance [49]. However, constitutive overexpression may incur growth penalties. Recent advances in targeted engineering of spatial–temporal gene expression facilitate development of climate-smart crops. For example, targeted insertion of heat-responsive *cis*-elements into promoters of CELL WALL INVERTASES (CWINs), key regulators of source-sink relations, confers heat-responsive upregulation to this gene in both controlled and field environments, which enhances carbon partitioning to grains and fruits and achieves higher yields under favorable conditions and stable yields under adverse conditions [86]. This supports targeted *in situ* integration of stress-responsive regulatory elements into SSP promoters to achieve context-dependent expression enhancement, potentially optimizing stress tolerance without compromising yield (Figure 3). Complementary to genetic approaches, exogenously applied chemically synthesized glycopeptides offer promising crop protection strategies (Figure 3). Despite the high challenge of chemically synthesizing glycopeptides, researchers have achieved significant advances in enhancing the efficiency of synthesizing arabinosylated peptides [75,87]. Further refinements in chemical synthesis or development of biosynthetic platforms will accelerate glycopeptide applications for sustainable stress resilience enhancement of crop production.

Concluding remarks and future perspectives

Arabinosylation of SSPs determines their bioactivity in regulating plant development, stress resilience, and symbiosis (Table 1). Optimizing SSP arabinosylation represents a promising strategy to enhance crop productivity and resilience, albeit with numerous unresolved questions persisting regarding arabinosylation of SSPs (see Outstanding questions).

Outstanding questions

Why did arabinosylation evolve as a post-translational modification for SSPs, and how does it generate functional diversity in peptide signaling?

How can we achieve sensitive *in situ* detection of endogenous glycopeptides – particularly at single-cell resolution – during environmental stress or microbial challenge?

Does SSP arabinosylation exhibit stereochemical specificity (e.g., α/β anomeric configurations)? If so, what enzymatic machinery establishes this configuration, and how does it determine biological function?

Are SSP maturation (proteolytic processing) and arabinosylation spatiotemporally coupled, or do they occur sequentially within distinct subcellular compartments?

Is arabinosylation dynamically reversible? What enzymes mediate de-arabinosylation, and what physiological roles does this regulation serve?

Can we leverage artificial intelligence (AI)-guided structural modeling to engineer multifunctional 'super' glycopeptides that optimize growth–defense trade-offs in developing climate-smart crops?

How did arabinosyltransferases evolve substrate specificity for SSPs, and does their functional diversification across species correlate with morphological diversity?

Can chemical biology approaches translate SSP arabinosylation mechanisms into design principles for sustainable, exogenously applied glycopeptide agents?

Key figure

Diverse strategies for utilizing arabinosylated small secreted peptides (SSPs) in crop improvement

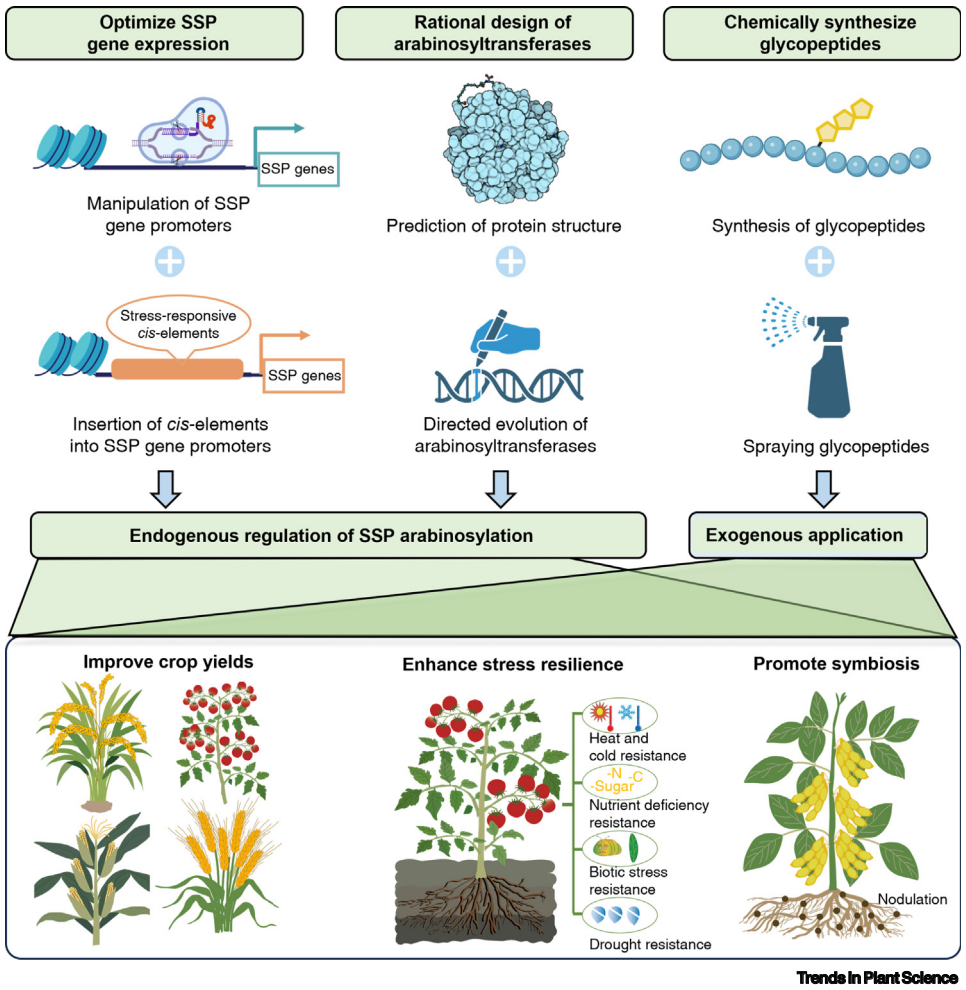

Figure 3. Endogenous regulation of the expression and arabinosylation of SSPs and exogenous application of SSPs allow for the fine-tuning of crop yields, stress resilience, and symbiotic interactions. For specific SSPs, gene expression levels can be optimized by manipulating promoter regions or targeted introduction of stress-responsive *cis*-elements to quantitatively control yields and induce climate-smart responses. The function of SSPs depends on arabinosylation, a process that can be optimized through directed evolution of arabinosyltransferases for quantitative yield control. Figure created with BioRender.

To fully exploit the potential of arabinosylation in SSPs, several key research areas should be prioritized. First, comprehensive discovery of arabinosylated SSPs is needed. Genetic redundancy and low peptide abundance hinder classical characterization. Integrated multi-omics – including genomics, transcriptomics, peptidomics, and chemical biology techniques – will accelerate identification of novel SSPs. Moreover, developing efficient arabinose-specific glycopeptide enrichment methods will be crucial for identifying new glycopeptides. Second, the structural basis of arabinosylation-dependent peptide function remains unclear. Resolving glycopeptide–receptor

Table 1. Plant glycopeptides, associated arabinosyltransferases, receptors, and their biological functions[a]

Species	Glycopeptides	Pentose units	Arabinosyl-transferases	Receptors	Function	Refs
Arabidopsis thaliana	CLV3	3	ND	CLV1/BAMs/CLV2/RPK2	SAM homeostasis	[31–36,42,43]
	PSY1	3	HPATs	PSYRs	Cell proliferation and expansion, trade-off between plant growth and stress responses	[27,47]
	AtCLE9	3,4,6	ND	BAMs/HSL1	Stomatal and xylem development, drought response	[48–51]
	AtCLE2	3	HPAT3	CLV1	Lateral root development, root sucrose level	[16,42,53]
Solanum lycopersicum	SlCLV3	3	FIN, SlRRA3a, FAB2	SlCLV1	SAM homeostasis	[17,45]
	SlCLE9	3	FIN, SlRRA3a, FAB2	ND	SAM homeostasis	[17,45]
	SlHypSys I/II/III	8–17 /6/12–16	ND	ND	Defense response	[63]
Lotus japonicas	LjCLE-RS1/2	3	LjPLENTY	LjHAR1	Autoregulation of nodulation	[18,67]
Medicago truncatula	MtCLE12	3	MtRDN1	MtSUUN1	Autoregulation of nodulation	[19,68]
	MtCLE13	3	ND	MtSUUN1	Autoregulation of nodulation	[19,68]
	MtCEP1	3	ND	ND	Autoregulation of nodulation	[69]
Glycine max	GmRIC1a	3	PsNOD3	GmNARK/PsSYM29/PsSYM28	Autoregulation of nodulation	[20,71]
	GmRIC2a	3	PsNOD3	GmNARK/ PsSYM29/ PsSYM28	Autoregulation of nodulation	[20,71]
	GmCLE40	3	ND	ND	Root growth	[75]
Nicotiana tabacum	HypSys I/II	9/6	ND	ND	Defense response	[62]
Solanum nigrum	SnHypSys I/II/III	6/6/6,9	ND	ND	Defense response	[64]
Petunia hybrida	PhHypSys I/II/III	10/10/3,6	ND	ND	Defense response (pathogen)	[65]
Ipomoea batatas	IbHypSys I-VI	6–12	ND	ND	Defense response	[66]

[a]Abbreviation: ND, not determined.

complex structures would enable the elucidation of molecular recognition principles and functional significance. Third, most SSP arabinosylation pathways are uncharacterized. Identifying dedicated arabinosyltransferases and deciphering their regulatory networks will enable precise engineering of crop yield and abiotic stress resilience traits. Elucidating these mechanistic details is critical for addressing global agricultural challenges posed by climate volatility and population growth.

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Declaration of interests

The authors have no interests to declare.

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