

Phytohormones during tuber and storage root formation

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Abstract

Understanding the molecular mechanism of tuber and storage root (SR) development is crucial for designing effective strategies to enhance tuber and SR crops' yield. In the past, numerous molecular factors have been shown to directly or indirectly converge at phytohormones and influence crucial physiological changes happening in the stolon (potato), or adventitious roots transitioning to SRs (sweetpotato). In general, the potato tuber development pathway has been widely studied for the functions of phytohormone-related genes, whereas similar studies in sweetpotato and other SR crops are just emerging. However, a comprehensive understanding of the hormonal network underlying both tuber and SR development is limited. In this review, the updated information regarding the changes of endogenous phytohormone levels, functions of phytohormone metabolism, transport and signalling pathway-associated genes during tuber or SR development are summarized. The expression patterns of different phytohormones (auxin, cytokinin, gibberellin, abscisic acid, ethylene, salicylic acid, jasmonic acid, brassinosteroid and strigolactone) and their pathway components during development of potato tubers and sweetpotato SRs are also highlighted. The regulation of key phytohormone pathway genes during tuber development (or SR developmental stages) by various epigenetic mechanisms, such as DNA methylation, histone modifications, and small non-coding RNAs, especially microRNAs and phased short-interfering RNAs are discussed.

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Introduction

According to the Food and Agriculture Organization of the United Nations, four of the top ten staple food crops globally are either tuber or storage root producers. Belowground storage organs of these crops are vital for human nutrition^[1]. The most widely cultivated tuber crops are potato (*Solanum tuberosum*) and yam (*Dioscorea alata*), which are stem tubers, while the major storage root crops include sweetpotato (*Ipomoea batatas*), cassava (*Manihot esculenta*), beetroot (*Beta vulgaris*), carrot (*Daucus carota*), radish (*Raphanus sativus*), and turnip (*Brassica rapa*)^[1] (Fig. 1). These crops are rich sources of carbohydrates, calcium, vitamins, minerals, fibers, and provide medicinal and industrial benefits, making them valuable for global food security. Two key agronomic traits influencing yield are: (i) an earliness for induction of belowground storage organ formation; and (ii) the size of the storage organs^[2].

Tuber formation (tuberization) in potato is a multifaceted physiological phenomenon which is under the influence of various environmental cues (light, photoperiod, temperature, humidity, fertilizer application) and intrinsic factors (molecular, genetic, and biochemical). Tubers are formed from stolons, which are the belowground modified stems that arise from lateral buds and grow diageotropically. In recent decades, tuberization research has focused primarily on enhancing tuber productivity. It is now well established that, under tuber-inductive short-day (SD) conditions, crucial tuberization signals transport from leaf to stolon and initiate an intricate series of developmental events; wherein the stolon undergoes various transitions (swollen stolon and mini-tuber) and accumulate starch, before maturing to a tuber^[3].

Storage root (SR) development in sweetpotato is also a complex, well-regulated process involving anatomical, cellular, and physiological changes that convert slender adventitious roots into

thick, starch-rich storage organs^[4]. This transition begins with the cessation of root elongation and the activation of the vascular cambium, which drives radial growth through increased cell division and expansion in parenchymatous tissues. Anatomical changes include stele enlargement and formation of additional vascular cambia, coupled with upregulation of genes related to starch biosynthesis, sugar transport, and storage proteins, leading to massive starch accumulation^[4]. Overall, this shift from elongation to radial growth underpins SR formation and yield potential.

Over the years, research has revealed that multiple molecular factors influencing tuber and SR development converge at the phytohormone level, impacting key physiological and developmental transitions, such as swelling of the stolon sub-apical region in potato, and adventitious root thickening in sweetpotato. This review summarizes current knowledge on the changes in endogenous phytohormone levels, expression of genes involved in phytohormone metabolism, transport, and signaling, and how modulation of these pathways affects yield. While potato tuber development is extensively studied, insights into phytohormone roles in sweetpotato SR formation are more recent. The focus of the present review are the major phytohormones and their regulatory networks during tuber or SR development. Further, the epigenetic regulation of phytohormone pathway genes via DNA methylation, histone modifications, and small RNAs are highlighted.

Phytohormone-mediated regulation of tuber development in potato

Role of gibberellins

Gibberellin (GA) exerts a control over plant growth and differentiation by tightly regulating its concentration^[3]. In potato,

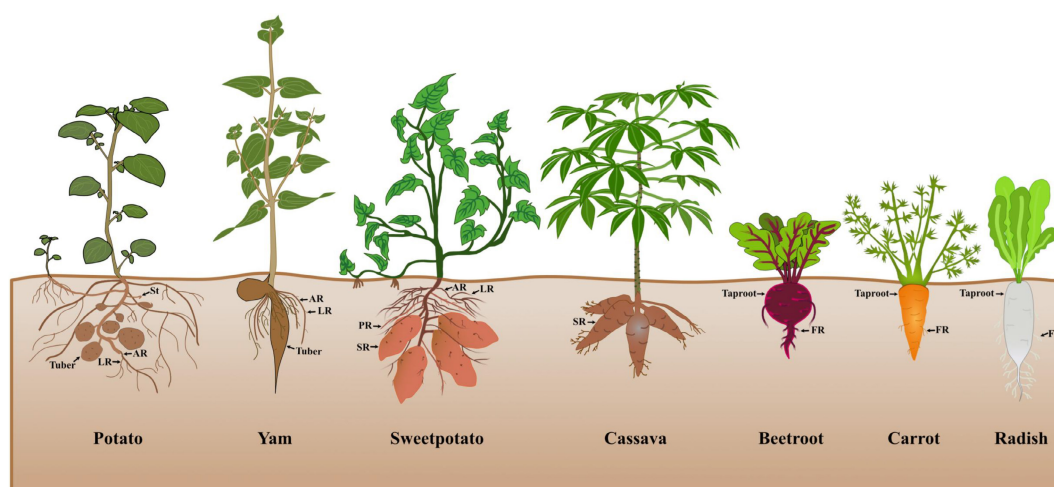


Fig. 1 Schematics of tuber and storage root crops. Stem tuber crops, such as potato (*Solanum tuberosum*), and yam (*Dioscorea alata*), and five storage root crops like sweetpotato (*Ipomoea batatas*), cassava (*Manihot esculenta*), beetroot (*Beta vulgaris*), carrot (*Daucus carota*), and radish (*Raphanus sativus*) are illustrated along with their below ground storage organs. Potato tubers are formed from belowground modified stem, known as stolon, whereas yam tubers are belowground thickened stems. Adventitious roots can thicken and store carbohydrates to develop into storage roots in sweetpotato. Cassava develops tubers from fibrous roots. Beetroot, carrot, and radish have single, enlarged taproots modified to store carbohydrates. Abbreviations: AR, adventitious root; FR, fibrous root; LR, lateral root; PR, pencil root; SR, storage root; St, stolon.

endogenous GA levels decrease sharply at the onset of tuberization from the stolon to swollen stolon stage, and the levels further remain low in the subsequent tuber development stages (Fig. 2a, b). Application of bioactive GA₃ inhibited tuber formation, while a GA biosynthesis inhibitor - paclobutrazol enhanced tuber formation, suggesting inhibitory role of GAs during tuberization^[5]. Manipulation of the *StGA20ox1* gene (encoding GA 20-oxidase 1) altered levels of the GA precursor (GA₂₀) and bioactive GA₁, affecting tuber formation; notably, *StGA20ox1* overexpression lines showed delayed tuberization under SD conditions^[6]. Further, microarray analysis from SD induced stolons showed increased *StGA20ox1* (a GA catabolic enzyme) transcripts in tuberizing stolons ensuring minimal GA levels^[7]. Another study has identified GA biosynthesis genes *StGA3ox1* and *StGA3ox2* in potato^[8]. Of which, *StGA3ox2* was identified as a rate limiting enzyme which catalyzes GA₁ production in stolon. Overexpression lines of *StGA3ox2*, as expected, exhibited taller phenotype, but also showed a delayed tuber formation in potato^[8]. While *StGA3ox2* RNAi potato lines displayed no change in tuberization timing^[9], they produced a greater number of tubers per plant compared to wild-type (WT) that may result from an altered GA:auxin ratio in stolons^[10] (Table 1). In a similar line, a recent study identified a homolog of *AtGA3ox3*, termed as *StGA3ox3* and catalyzes GA₃ production in stolons. *StGA3ox3* knock-down potato lines produced more tubers^[11], like *StGA3ox2*-RNAi lines (Table 1).

Role of auxin

Auxin application to *in vitro* single nodal potato explants resulted in early tuberization and formation of sessile tubers^[5], suggesting it's putative role in tuber formation. Microarray analysis of stolon developmental stages identified differentially expressed auxin-related genes^[5]. Auxin levels increase at the onset of tuberization (Fig. 2a, b), coinciding with the increased expression of the auxin biosynthesis gene (*StYUC-LIKE1*), auxin transporters (*PIN* family members) and a signalling gene *ARF6* (*AUXIN RESPONSE FACTOR 6*) in swollen stolons, indicative of auxins' positive role in swollen stolon formation^[12]. Specifically, *StPIN2* and *StPIN4* expression peaks after 4 d of tuber induction, indicating their role in auxin distribution in stolons. Furthermore, a constitutive expression of *StYUCCA-8* resulted in altered auxin content with an increase in tuber number, but a reduction in tuber size^[13]. The authors correlated the

increased auxin levels, possibly due to an altered GA-to-auxin ratio, may lead to stolon branching, resulting in more tubers per plant, highlighting the importance of auxins during tuber development.

Role of cytokinin

Application of cytokinin (CK) to the *in vitro* nodal potato explants promoted tuberization, but failed to replicate results in soil-grown plants^[14]. Endogenous CK levels increase during potato tuberization (i.e. from the stolon to swollen stolon and mini-tuber stages), but the levels decrease slightly during tuber maturation (Fig. 2a, b). However, CK alone, was insufficient to induce tuberization. In a study, overexpression potato lines of a CK biosynthesis gene *ISOPENTENYL TRANSFERASE (IPT)* showed severe growth phenotype with a few and small tubers. Whereas *CYTOKININ OXIDASE/DEHYDROGENASE1 (CKX)* expressing potato lines resulted in reduced CK levels leading to small drop shaped tubers^[14]. In another study, CK was shown to enhance starch accumulation in tobacco cells, suggesting that CK might be involved in regulation of starch accumulation in tuber; thus, enhancing the sink potential of developing tubers. While earlier studies primarily revealed the role of CK in starch synthesis, more recent research has begun to uncover its broader functions in tuber development. Overexpression of a CK biosynthesis gene *LOG1 (LONELY GUY1)* resulted in aerial tuber production from the axillary meristems of tomato plant, which usually do not produce any tubers^[15], suggesting the ability of CK to modulate developmental plasticity of meristem to generate sessile mini-tubers. Notably, CK has also been demonstrated to regulate cell differentiation in other plant species^[16]. Therefore, the possible involvement of CK in the regulation of cell division during tuber formation cannot be ruled out, and requires further study.

Role of abscisic acid

Abscisic acid (ABA) levels in stolon/tuber increase continuously during tuberization in potato (Fig. 2a, b). Application of ABA to potato plants in soil, caused early tuberization and higher tuber numbers^[17], implicating its tuber promoting effects in potato. In the presence of ABA, nodal explants tuberized earlier than controls, while the ABA-deficient line of *Solanum phureja* tuberized like WT, indicating that ABA is not required for the tuberization process, but it can promote it^[17]. Heterologous expression of *AtABF4* (ABRE-BINDING FACTOR) positively regulates tuberization accompanied by

deregulation of the GA metabolism gene^[17]. Furthermore, overexpression lines of ABA 8'-hydroxylase (*StCYP707A1*), a catabolic gene,

resulted in reduced tuber yield and average tuber weight per plant; whereas antisense lines exhibited enhanced tuber yield^[18] (Table 1).

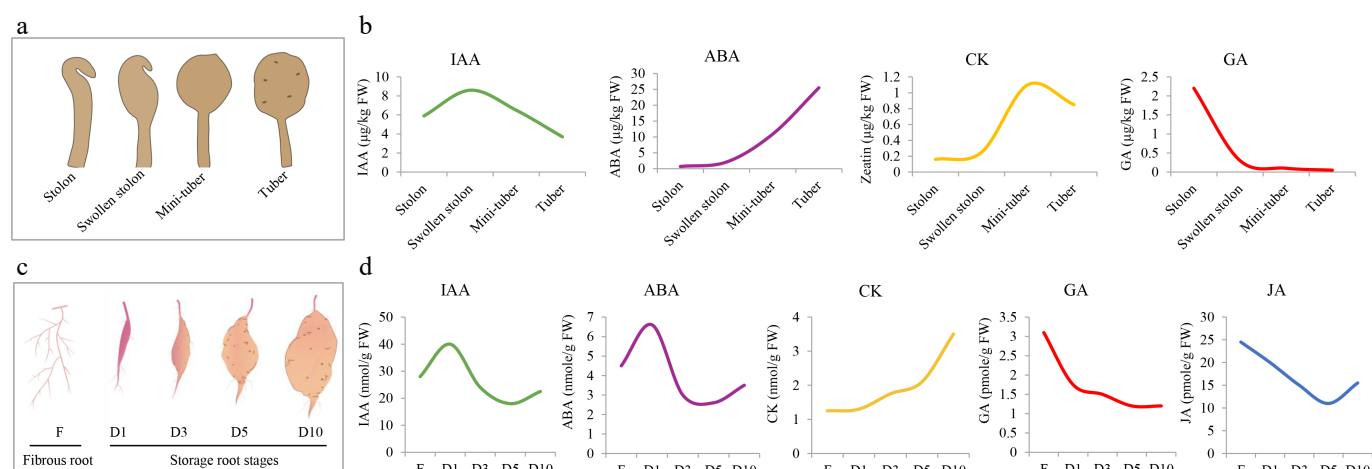


Fig. 2 Dynamics of phytohormone levels during the developmental stages of potato tubers and sweetpotato storage roots. (a) Schematic of stolon-to-tuber transition stages in potato. (b) Endogenous phytohormone levels during tuber development in potato^[101]. Phytohormones were measured from the respective root tissue type-fibrous root or developing storage roots. (c) Schematic of different stages of storage root development in sweetpotato. F, fibrous roots with diameter 1 mm; D1, initiating storage root with diameter 1 cm; D3, storage root with diameter 3 cm; D5, storage root with diameter 5 cm; D10, storage root with diameter 10 cm. Phytohormones were measured from tuberizing stolons/tubers. (d) Endogenous levels of phytohormones during storage root developmental stages in sweetpotato^[74].

Table 1. List of phytohormone related genes characterized for their role in tuber development in potato and storage root formation in sweetpotato. The associated phenotypes of gene expression modulation are also described.

Gene	Function	Mutant phenotype
Potato		
<i>StCYP707A1</i>	ABA catabolism	Overexpression and antisense potato lines showed reduced tuber yield ^[18] .
<i>StABL1</i>	ABA signalling	Overexpression potato lines exhibited an early tuberization phenotype ^[19] .
<i>AtABF4</i>		Heterologous overexpression in potato positively regulated tuberization ^[17] .
<i>iaaL</i>	Auxin biosynthesis	Overexpression potato lines of <i>Pseudomonas syringae iaaL</i> showed an remarkable increase in tuber numbers; however, average tuber weight was reduced ^[104] .
<i>StYUCCA-8</i>		Constitutive overexpression displayed increased tuber numbers with reduction in tuber size ^[13] .
<i>AtYUCCA6</i>		<i>AtYUCCA6</i> expressing potato lines exhibited lower tuber yield compared to untransformed control plants ^[105] .
<i>tms1</i>		Overexpression of <i>Agrobacterium tms1</i> gene enhanced tuber productivity ^[106] .
<i>StIAA2</i>	Auxin signalling	RNAi potato lines displayed no clear difference on stolon length and tuber weight ^[107] .
<i>StBRI1</i>	BR signalling	RNAi potato lines exhibited a reduced tuber yield, whereas overexpression increased tuber yield ^[22,24] .
<i>StBIN2</i>		Overexpression potato lines exhibited an increase in tuber number and weight ^[23] .
<i>IPT</i>	CK biosynthesis	Transgenic potato lines with moderate IPT expression (under native promoter) influenced tuberization, whereas its expression under constitutive promoter prevented tuber formation ^[108] .
<i>AtIPT</i> and <i>AtCKX</i>	CK metabolism	<i>AtIPT</i> overexpression potato lines produced few and small tubers, whereas <i>AtCKX</i> overexpression potato lines exhibited small, drop-shaped tubers ^[14] .
<i>StGA20ox1</i>	GA biosynthesis	Overexpression potato lines resulted in delayed tuber formation under short-day conditions ^[6] .
<i>StGA3ox2</i>		Overexpression potato lines showed delayed tuber formation, whereas RNAi lines produced tubers with smaller average tuber weight ^[8,9] .
<i>StGA3ox3</i>		Antisense potato lines displayed increased tuber numbers with the total tuber weights remaining unchanged ^[11] .
<i>StGA2ox1</i>	GA catabolism	Overexpression potato lines exhibited an earliness for <i>in vitro</i> tuberization ^[7] .
<i>AtGA20ox</i> and <i>AtGA2ox</i>	GA metabolism	Overexpression of <i>AtGA20ox</i> and <i>AtGA2ox</i> in potato resulted in reduced total number of tubers and the overall tuber weight ^[14] .
<i>StSN2</i>	GA signalling	Overexpression potato lines showed increased tuber numbers and size of the tubers ^[109] .
<i>StCCD8</i>	SL biosynthesis	RNAi potato lines showed a reduction in stolon formation ^[26] .
<i>StJAZ1-like</i>	JA signalling	Overexpression potato lines attenuated tuber forming potential, leading to reduced stolon numbers and average tuber weights ^[29] .
Sweetpotato		
<i>lbCYP714A1</i>	GA catabolism	Overexpression sweetpotato lines exhibited inhibition of storage root formation ^[88] .
<i>lbYUCCA4</i>	Auxin biosynthesis	Overexpression sweetpotato lines showed reduced storage root yield ^[90] .
<i>AtYUCCA6</i>		Overexpression sweetpotato lines showed reduced storage root yield ^[89] .
<i>lbARF11L</i>	Auxin signaling	' <i>lbMYB52/lbARF11L-lbDRM1</i> ' module negatively regulates storage root development ^[91] .

* ABA8'H: ABSCISIC ACID HYDROXYLASE 8; ABF4: ABSCISIC ACID RESPONSIVE ELEMENT-BINDING FACTOR; ABL1: ABSCISIC ACID INSENSITIVE 5-LIKE 1; ARF11L: AUXIN RESPONSE FACTOR 11-LIKE; At: ARABIDOPSIS THALIANA; BIN2: BRASSINOSTEROID INSENSITIVE 2; BRI1: BRASSINOSTEROID INSENSITIVE 1; CCD8: CAROTENOID CLEAVAGE DIOXYGENASE 8; CKX: CYTOKININ OXIDASE; CYP714A1: CYTOCHROME P450 encoding a GA deactivation enzyme; GA3ox2: GIBBERELLIN 3-OXIDASE 2; GA3ox3: GIBBERELLIN 3-OXIDASE 3; GA2ox1: GIBBERELLIN 2-OXIDASE 1; GA20ox1: GIBBERELLIN 20-OXIDASE 1; IAA2: INDOLE-3-ACETIC ACID INDUCIBLE 2; iaaL: bacterial auxin biosynthesis gene encoding INDOLEACETAMIDE HYDROLASE; lb: *Ipomoea batatas*; IPT: ISOPENTENYL TRANSFERASE; JAZ1-LIKE: JASMONATE ZIM-DOMAIN PROTEIN 1-LIKE; SN2: SNAKIN/GASA family gene encoding SN2 PROTEIN; St: *Solanum tuberosum*; tms1: bacterial auxin biosynthesis gene encoding TRYPTOPHAN-2-MONOOXYGENASE.

Specifically, the GA₃ content in the overexpression lines was higher compared to WT, suggesting that ABA works antagonistically with GA. A recent study demonstrated the function of StABI5-like1 (StABL1) transcription factor (TF) as a positive regulator of tuberization^[19]; wherein, StABL1 forms an alternate tuberigen complex with StSP6A in a St14-3-3 dependent manner. Overexpression lines of *StABL1* resulted in early tuberization, and showed binding on a tuberization marker gene *StGA2ox1*^[19]. Moreover, a potato *PROTEIN PHOSPHATASE 2C* (PP2C) gene, hypersensitive to ABA1 (StHAB1), is highly expressed in tubers and axillary buds of potato. PP2Cs are negative regulators of the ABA signalling pathway. Overexpression of StHAB1 leads to increased shoot branching and stolon development due to the activation of axillary buds, probably regulated by the interplay between auxin and ABA^[20].

Role of brassinosteroid and strigolactone

Exogenous application of brassinosteroid (BR) increased potato tuber numbers and weight^[21]. Three BR receptors have been identified in potato, mainly StBRI1, StBRI2, and StBRI3. Of them, *StBRI1* expresses in stolons and knockdown lines of *StBRI1* showed impaired tuberization in potato, e.g., reduced tuber numbers and weight^[22]. Further, a negative regulator of BR signalling, *StBIN2* (*BR INSENSITIVE 2*) was shown to positively regulate tuberization. Overexpression of *StBIN2* led to enhanced stolon numbers and tuber weight by increasing activities of ABA signalling, sucrose transporters, and starch synthases^[23]. A recent study demonstrated the mechanism for StBRI-driven tuber development. StBRI1 phosphorylates PHA2, a plasma membrane proton ATPase2 and enhances its activity, which subsequently promotes tuber development^[24]. PHA2 activity contributes to higher proton motive force leading to BR-mediated cell expansions and starch accumulation in potato tubers.

Strigolactones (SLs) work together with auxins, and show inhibitory effects on shoot branching contributing to apical dominance^[10]. *In vitro* application of SL to nodal explants resulted in the inhibition of axillary bud outgrowth and subsequent tuber production^[10]. SLs have been detected in root extracts of potato plants, but not from stolons possibly due to their negligible levels. *CAROTENOID CLEAVAGE DIOXYGENASE 8* (*CCD8*) is a key gene in the SL biosynthesis pathway^[25]. *CCD8*-RNAi potato lines exhibited reduced stolon formation^[26]. Interestingly, *CCD8*-RNAi lines lost the diageotropic growth of stolons resulting in many stolons emerging from the soil and forming shoots when exposed to light. Since SL can modulate auxin levels and its redistribution, this may disrupt the SL-auxin balance in stolons, potentially influencing diageotropic stolon growth^[10,27]. Therefore, it is conceivable that SLs have a potential role during tuberization, possibly in coordination with auxin.

Role of jasmonic acid, salicylic acid, and ethylene

Jasmonic acid (JA) exerts a positive effect on tuber formation. When *in vitro* nodal cuttings of potato plants were treated with different concentrations of JA, it induced tuber formation in stolons at optimum concentration^[28]. JA induces cell expansions in tuber buds^[28]. JA can act on young cells, and induce radial expansion of meristematic cells, indicating that JA may contribute to stolon transition stages^[28]. In a recent study, *StJAZ1-LIKE*-mediated signalling is attenuated at tuber induction as it functions as a negative regulator of the JA response^[29]. Moreover, overexpression lines of *StJAZ1-LIKE* negatively regulate tuber initiation in potato plants and its phenotype can be partially rescued by ABA treatment, suggesting potential ABA–JA regulation during tuber development.

An early report showed tuber-inducing activities of salicylic acid (SA) and related compounds under *in vitro* conditions^[30]. SA has not yet been detected in potato stolons, probably due to its minute

amounts. However, foliar SA application in potato fields increased tuber yield^[31]. Similarly, ethylene was shown to induce swelling in stolons due to lateral cell expansions^[32]. However, other reports showed inhibitory effect of ethylene on tuberization. Later, in 1989, it was demonstrated that ethylene inhibits stolon elongation, and causes radial expansions in the stolon sub-apical region; however, a mature tuber formation is inhibited^[33], suggesting the dual role of ethylene in tuberization. The lack of studies on the molecular network between SA/ethylene signalling and tuber development, highlights the need for further research. While SA and ethylene may not directly regulate tuberization, it could influence the process through interactions with other phytohormones.

Crosstalk of various hormones during stolon-to-tuber transitions

The hormonal control of the tuberization process has been recently reviewed across several crop plants^[3,34–36]. For example, GA and auxin work in a concerted manner to regulate the stolon-to-tuber transition phase. Under non-inductive long-day conditions, high GA levels promote stolon elongation through transverse cell division, while low auxin levels help to maintain growth of the stolon apical meristem. At the onset of tuberization, GA levels reduce, while auxin levels rise (Fig. 2a, b) owing to enhanced expression of auxin biosynthesis genes^[5]. This hormonal shift alters the cell division plane in the sub-apical region of stolons, leading to a reduction in longitudinal growth, and the initiation of radial expansion, marking the transition from stolon to a swollen stolon^[5]. Reduction in GA content is a key step for this developmental event. Auxin levels rapidly increase during tuber initiation and decline as the swollen stolon transitions to a mini-tuber or mature tuber^[5], suggesting that the auxin maxima are essential for the cell division switch occurring during tuber induction. However, the molecular mechanisms behind auxin-driven cell division during tuberization remain poorly understood. cDNA microarrays and recent transcriptome studies have presented several phytohormone-related genes to be differentially expressed during tuberization^[37–39], suggesting a more complex hormonal network orchestrating the tuber development process. A detailed analysis of this network governing the transition can help in understanding the dynamics of stolon-to-tuber transitions in potato.

To gain insights into potential gene networks regulating these transitions, the expression profiles of hormone-related genes from the transcriptome of stolon-to-tuber transition stages of potato (Fig. 3a–j), available in the SpudDB database (<https://spuddb.uga.edu/expression.shtml>), were analyzed. The expression patterns of GA (Fig. 3b), and auxin (Fig. 3c) metabolic genes were consistent with earlier findings, downregulation of GA biosynthesis genes (*StGA20ox2*, *StGA3ox2*, and *StGA3ox3*), and upregulation of the GA catabolic gene (*StGA2ox1*). Induction of *StYUCCA4*, -5, and -10 might have contributed to enhanced auxin levels in swollen stolon (SS), and mini-tuber (TS1) stages. Auxin efflux transporters, such as *StPIN1*, *StPIN3*, and *StPIN4*, exhibited higher expression during early tuber stages. Several *ARFs*, *AUX/IAAs*, and *SAURs* showed higher expression throughout tuber formation, suggesting active auxin signalling that might regulate key genes of tuberization. Surprisingly, the expression of *StSHY2*, a member of the *AUX/IAA* family, is drastically reduced from the SS to the TS5 stages (Fig. 3c). *SHY2* plays a key role in maintaining auxin homeostasis by downregulating the expression of PIN transporters and preventing the activation of auxin responsive genes^[40]. *SHY2* also acts as a central component of auxin, CK, and BR signalling during root development in *Arabidopsis*^[40]. Therefore, regulation of *SHY2* during tuber development appears to be interesting and needs further investigation.

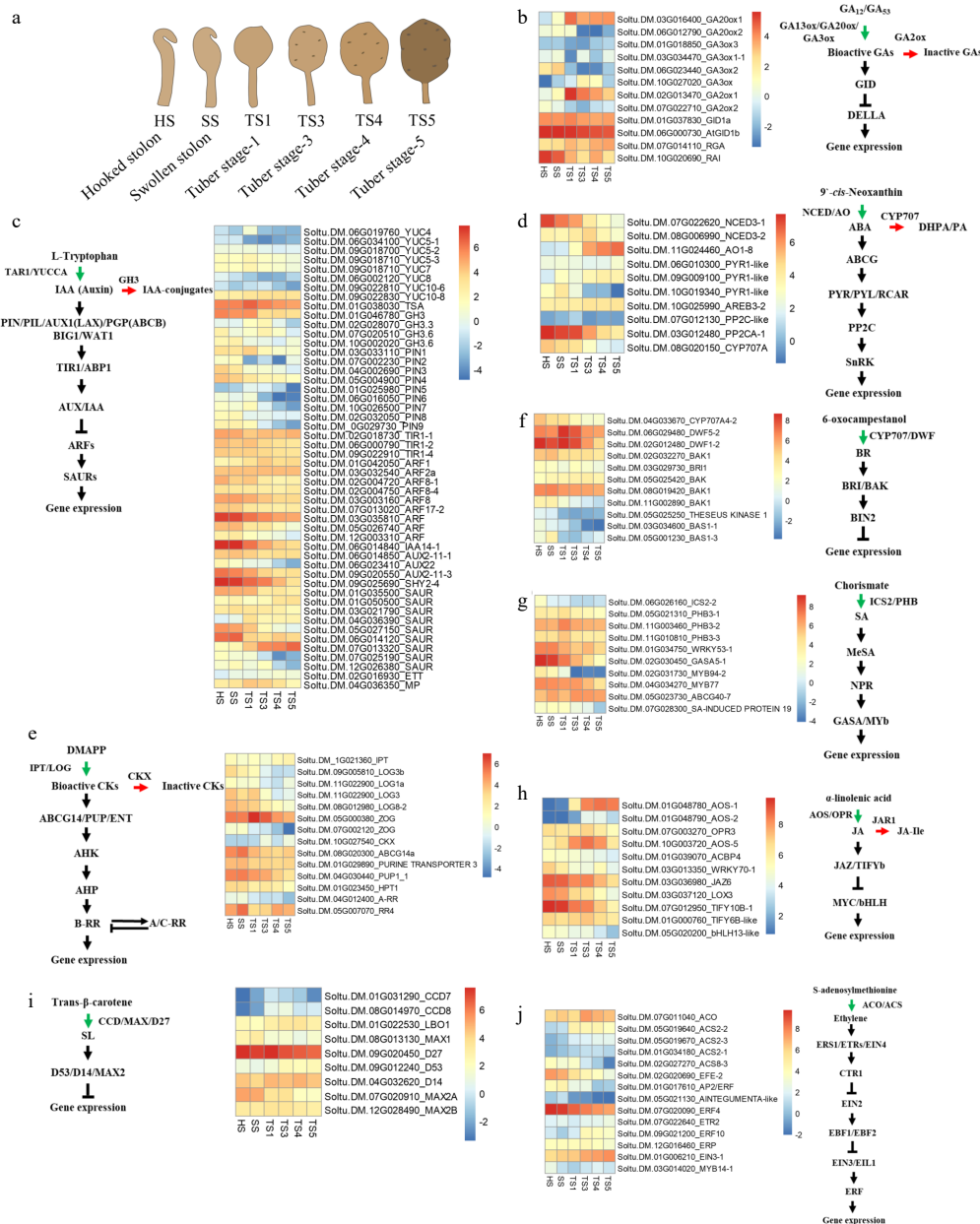


Fig. 3 Heat maps showing the expression profiles of key phytohormone-related genes during tuber developmental stages of potato. (a) Schematic of six tuber developmental stages used for transcriptome profiling as a part of NCBI BioProject PRJNA753086. These stages and the samples harvested for RNA sequencing are as follows. HS: hooked stolon, 0.5 cm of tip; SS: Swollen at the base of the tip but no roundness, 2 cm of the tip; TS1: stolon rounded off, harvested tuber part; TS3: round tuber, 5–15 mm; TS4: round tuber, 15–30 mm and TS5: larger and mature tuber, 30 mm plus. Heat maps of genes are categorized based on the type of phytohormones. (b) gibberellin, (c) auxin, (d) ABA, (e) cytokinin, (f) brassinosteroid, (g) salicylic acid, (h) jasmonic acid, (i) strigolactone, and (j) ethylene. The scale bar represents normalized read counts (log2 values). Detailed information of all these and related genes along with their expression values are shown in [Supplementary Table S1](#). Abbreviations used: GA13/20ox: GIBBERELLIN 13/20-OXIDASE; GA20ox: GIBBERELLIN 2-OXIDASE; GA3ox: GIBBERELLIN 3- β -DIOXYGENASE; GID: GIBBERELLIN INSENSITIVE DWARF 1; RGA: REPRESSOR OF GA1-3; TAR1/YUC: TRYPTOPHAN AMINOTRANSFERASE-RELATED PROTEIN1/FLAVIN-CONTAINING MONOOXYGENASE; GH3: GRETCHEN HAGEN3; PIN: PIN-FORMED; TIR1: TRANSPORT INHIBITOR RESPONSE 1; ARF: AUXIN RESPONSE FACTOR; AUX/IAA: AUXIN/INDOLE-3-ACETIC ACID PROTEIN; SAUR: SMALL AUXIN-UP RNA; ETT: ETTIN; MP: MONOPTEROS; NCED: 9-CIS-EPOXYCAROTENOID DIOXYGENASE; AO: ALDEHYDE OXIDASE; ABA8H: ABSCISIC ACID HYDROXYLASE 8; ABI: ABSCISIC ACID INSENSITIVE; DHPA/PA: DIHYDROPHASEIC ACID/PHASEIC ACID; ABCG: PYR/PYL: PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL); RCAR: REGULATORY COMPONENTS OF ABA RECEPTOR; PP2C: PROTEIN PHOSPHATASE 2C; SnRK: SNF1-RELATED PROTEIN KINASE; DMAPP: DIMETHYLLALLYL DIPHOSPHATE; IPT: ISOPENTENYL TRANSFERASE; LOG: LONELY GUY; ZOG: ZEATIN O-GLUCOSYLTRANSFERASE; CKX: CYTOKININ OXIDASE/DEHYDROGENASE; PUP: PURINE PERMEASE; AHK: ARABIDOPSIS HISTIDINE KINASE; AHP: ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN; A/B-RR: Type A/B RESPONSE REGULATOR; CYP707A: CYTOCHROME OXIDASE P450 TYPE A; DWF: DWARF; BRI: BRASSINOSTEROID INSENSITIVE1; BAK: BRI1-ASSOCIATED RECEPTOR KINASE; BIN: BRASSINOSTEROID-INSENSITIVE 2; BAS: BRASSINOSTEROID-DEFICIENT1; ICS: ISOCHORISMATE SYNTHASE; PHB: PROHIBITIN; NPR: NON-EXPRESSOR OF PATHOGENESIS-RELATED 1; AOS: ALLENE OXIDE SYNTHASE; OPR: OXOPHYTODIENOATE REDUCTASE; JAR: JASMONIC ACID-AMIDO SYNTHETASE; JAZ: JASMONATE ZIM-DOMAIN; LOX: LIPOXYGENASE; CCD: CAROTENOID CLEAVAGE DIOXYGENASE; MAX: MORE AXILLARY GROWTH; LBO: LATERAL BRANCHING OXIDOREDUCTASE; D27/53: DWARF27/53; ACO: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID OXIDASE; ACS: 1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID SYNTHASE; ERF: ETHYLENE RESPONSE FACTOR; ETR: ETHYLENE RECEPTOR; EIN: ETHYLENE INSENSITIVE; CTR1: CONSTITUTIVE TRIPLE RESPONSE 1; EIL: ETHYLENE INSENSITIVE3-LIKE; ERP: ETHYLENE RESPONSE PROTEIN.

Notably, ABA is known to promote tuber formation by antagonizing GA signalling. In line with this, the expression of ABA biosynthesis genes, such as *9-CIS-EPOXYCAROTENOID DIOXYGENASE (NCED)*, and *ALDEHYDE OXIDASE (AO)* were induced at the SS and TS1 stages, and remained high through TS5 (Fig. 3d). A few ABA signalling genes were expressed at all stolon stages. Especially, *StAREB (StABI5-LIKE1)* levels remain high through all tuber stages, implying its importance during tuber formation as previously described^[19].

CKs are positive regulators of tuberization, well indicated by increased expression of CK biosynthesis genes, such as *StIPT*, *StLOG*, and *ZEATIN O-GLUCOSIDASE (StZOG)* (Fig. 3e) whereas the expression of a CK catabolism gene *CKX* remains low in early stolon stages. CK transporters and CK signalling genes like *HISTIDINE PHOSPHOTRANSFER PROTEIN 1 (StHPT1)* and *RESPONSE REGULATOR 4 (StRR4)*, show higher expression in all tuber stages. Type-A response regulators function as negative regulators of CK signalling, which is consistent with their decreasing expression from the stolon to the tuber stages. The expression profiles of CK-related genes suggest that CK may regulate cell division during tuber development. BR has been shown to promote tuber formation via exogenous application^[21]. Also, *StBRI1* had higher expression in potato tubers^[24]. BR biosynthesis (*StDWF5*) and signalling (*StBRI1* and *StBAK1*) genes show higher expression in all tuber stages, suggesting their importance during tuber development (Fig. 3f). BR can regulate *PIN* genes by repressing *SHY2* expression^[40]. *SHY2* expression exhibits a complementary pattern to BR and CK signalling genes, suggesting potential crosstalk among auxin, BR, and cytokinin pathways during tuberization.

JA and SA biosynthesis and signalling genes were induced at the SS/TS1 stages (Fig. 3g, h) and their expressions remain relatively high, aligning with their reported roles as positive regulators of tuber induction^[29,30]. SL biosynthesis genes did not show any peculiar pattern; however, SL signalling genes showed higher expression throughout tuber development (Fig. 3i), suggesting SL could have an effect on tuber formation, in conjunction with other hormones. Ethylene inhibits stolon elongation and can lead to localized swelling^[33]. However, except the *1-AMINOCYCLOPROPANE-1-CARBOXYLIC OXIDASE (ACO)* gene, other ethylene biosynthesis gene expression remains low in tuber stages (Fig. 3j). Interestingly, ethylene signalling seems to be active during tuberization, probably due to the regulation via other phytohormones. Enhanced ethylene signalling in the late tuber stages might facilitate swelling of expanded cortex cells of tubers as ethylene delays cell differentiation^[38].

Photoperiodic signals integrate into phytohormone signalling during tuberization

The photoperiod is one of the major external cues that influences tuberization, and is perceived by light receptors, such as phytochromes and cryptochromes^[3]. In potato, where tuberization is strictly SD-dependent, phytochromes PHYB and PHYF negatively regulate this process by stabilizing CONSTANS1-like (*StCOL1*) protein^[41,42]. *StCOL1* has been shown to repress Flowering Locus T ortholog *StSP6A (SELF-PRUNING 6A)*, a positive regulator of tuberization, by activating another FT family member, *StSP5G*, which, in turn, suppresses *StSP6A* expression^[43]. Under SD conditions, *StSP6A* protein is induced in leaves and transported to stolons through the phloem, where it forms the tuberigen activation complex (TAC), along with *StFDL1* (FD-like) and *St14-3-3* proteins, activating the transcription of key tuberization genes^[44]. *BEL1-LIKE* TF, *StBEL5*, and *KNOTTED1-LIKE (KNOX)* protein *POTH1* are also SD-inducible and their mRNAs are phloem-mobile, transporting from leaf to stolon^[45,46]. *StBEL5* and *POTH1* form a heterodimer to regulate

expression of key tuberization genes in leaves and stolon by binding to their promoters^[47]. Numerous phytohormone-related genes and *StSP6A* have been identified as targets of TAC complex and/or *StBEL5-POTH1* heterodimer. Specifically, the TAC complex regulates the expression of *StGA2ox1*, while the *BEL5-KNOX* complex influences the expression of several auxin transporter genes, activates *StGA2ox1*, and represses *StGA2ox1*, indicating that both complexes are involved in the regulation of GA metabolism^[44,47]. *StBEL5* also induces *StSP6A* expression, thereby contributing to the TAC complex functionality. Alternatively, *StABL1* (a member of the *AREB/ABF/ABI5* subfamily; *StABI5*-like 1) TF interacts with *StFT*-like proteins to form an alternative TAC (aTAC) promoting tuberization by regulating *StGA2ox1* expression^[19]. Moreover, *StCEN (TERMINAL FLOWER 1/CENTRORADIALIS)* has shown to suppress tuberization by competing with *StSP6A* as a member of the TAC complex^[48]. Furthermore, a *TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTOR (TCP)* protein *StBRC1b* has been shown to regulate tuber-inducing activity of *StSP6A*, and restricts symplastic sucrose transport in axillary meristems; thereby making them weak sinks under tuber-inducing conditions^[49]. As a result, sucrose is redirected to stolon for starch deposition. Additionally, *StBRC1b* regulates ABA levels to maintain dormancy of axillary meristems. Overall, these findings suggest that tuberization is coordinated through a complex network of TFs that ultimately converge into phytohormone pathways.

Epigenetic regulation of phytohormone pathway key genes mediating tuber development

Numerous reports over the past few years have shown that epigenetic modifications, such as DNA methylation^[50,51], histone modifications^[3,52,53], and gene silencing mediated by small non-coding RNAs like microRNAs^[54–56] and siRNAs^[3,11,57], regulate the expression of tuberization marker genes. Many of them include phytohormone metabolism, transport, and signaling genes. Here, the regulation of phytohormone-related genes by these epigenetic modifications are highlighted.

DNA methylation

In plants, DNA methylation appears to be a conserved epigenetic mark caused by the simultaneous activity of methyltransferases and demethylases at the cytosine residues of CpG islands, and it not only regulates gene expression, but also provides genomic stability^[58]. From the potato genome, 10 genes encoding DNA methylase and eight genes encoding demethylase have been identified^[51]. This study further suggested the role of DNA methylases and demethylases in regulating the expression of tuberization genes under high temperature conditions. Interestingly, in another report, the authors applied DNA methylation inhibitor - zebularine (40 μ M) to the single node (stem) cuttings under *in vitro* conditions and evaluated its effects on photoperiodic tuberization, along with comparison of whole-genome DNA methylation between photoperiod-sensitive, and photoperiod-insensitive potato genotypes^[50]. This study revealed that photoperiod-sensitive potato genotypes are the most affected by the DNA methylation inhibitor compared to the photoperiod insensitive (day-neutral) potato genotypes. Further, the authors found that the DNA methylation inhibitor promoted tuber initiation in the strict SD potato genotypes, possibly by modulating the methylation status of photoperiod and GA pathway genes or their promoter sequences. Moreover, the differential epigenome status of potato genotypes and their effect on the expression of key tuberization marker genes could be important factors deciding the photoperiod-dependency of potato genotypes. Among 52 candidate genes which were found to be the targets of DNA methylation and differentially expressed during tuberization process, nine genes

were related to the GA pathways (biosynthesis: *StGA3ox* and *StGA20ox*; catabolism: *StGA2ox*, and signalling: *GID1* GA receptor), one gene encoded ethylene biosynthesis enzyme - ACO, and two genes encoded auxin signalling pathway components (AUX/IAA, a repressor protein, and SAUR, a positive regulator)^[50] (Fig. 4). Of these 12 genes which were methylated, four genes showed downregulation, and the remaining eight genes exhibited upregulation (Supplementary Tables S1 and S2), suggesting that DNA methylation does not necessarily always result in gene silencing, and the ultimate gene expression would be the cumulative effects of epigenetic modifications by DNA methylation and other mechanisms like histone modification and post-transcriptional gene silencing.

Histone modifications

Gene transcription primarily depends on chromatin accessibility within the nucleosomes, which is regulated by histone modifiers. Chromatin re-modelling leads to spatio-temporal regulation of genes involved in various developmental processes in animals and plants^[59,60]. Plants possess two important sets of chromatin modifiers, mainly the Polycomb repressive complex (PRC), and Trithorax group (TrxG) proteins that regulate target gene expression through H3K27me3 (repressive) and H3K4me3 (activation) histone modifications, respectively. A previous report on potato showed that two PRC members *MULTICOPY SUPPRESSOR OF IRA 1* (*StMSI1*) and *StBMI1* (*B-CELL-SPECIFIC MOLONEY MURINE LEUKEMIA VIRUS INTEGRATION SITE 1*) play an important role in tuberization^[52]. Both *StMSI1* and *StBMI1* are differentially expressed in stolons under tuber-inducing SD conditions. Further, *StMSI1* overexpression or *StBMI1* knockdown in potato reduced belowground tuber yield, but induced aerial stolon and tubers under SD conditions. Key genes related to phytohormone regulation and tuber development were differentially expressed in *StMSI* overexpression lines^[52]. Further study revealed that ENHANCER OF ZESTE 2 (*StE(z)2*), a core subunit

of the PRC2 complex, can target several tuberization related genes and is thus involved in tuberization^[53]. The methyltransferase activity of *StE(z)2* catalyzes H3K27me3 modifications on target gene chromatin; thereby repressing their activity. An important subset of *StE(z)2* targets include genes involved in phytohormone metabolism, transport, and signalling were observed. Chromatin immunoprecipitation sequencing of stolons under short-day conditions revealed increased H3K4me3 activation marks on key tuberization genes. Phytohormone genes were also identified as common targets of both H3K27me3 modifications and *StE(z)2* binding sites suggesting that these genes may be repressed during tuber development^[3,53]. A comparative analysis of target genes of *StBEL5* and *POTH15* with H3K27me3 targets, revealed an overlap of key tuberization and several hormone-related genes^[3], suggesting an interactive network of important tuberization TFs (*StBEL5* and *POTH15*), and histone modifiers that govern phytohormone metabolism, transport, and signalling during tuber development.

Reanalysis of the target genes of *StE(z)2*, H3K4me3, and H3K27me3 modifications in the stolons^[53] revealed about 350 hormone-related target genes being regulated by these histone modifications, which include auxin (94), CK (81), GA (37), ABA (29), ethylene (84), BR (21), SL (2), and JA (2), highlighting their importance during tuber development (Fig. 4, Supplementary Table S2). Almost all genes of the auxin pathway e.g., biosynthesis (INDOLE-3-ACETIC ACID [IAA] AMINO ACID HYDROLASE, IAA HYDROLASE), transport (*PIN*, *PIL*, *LAX*, *WAT1*, *ABCB/PGP*), and signalling (*TIR1*, *ARF*, *AUX/IAA* and *SAUR*) are found to have H3K4me3 activation histone marks (Supplementary Table S2), which is consistent with their upregulation from stolon to tuber developmental transitions (Supplementary Table S1). Similarly, CK biosynthesis (*LOG*, *ZOGT*, and *IPT*), signalling (*CRF*, *HK*, *HPT*, type-B *ARRs*) and transport (*PURINE PERMEASE* and *AZG1*) genes are upregulated, and also identified as

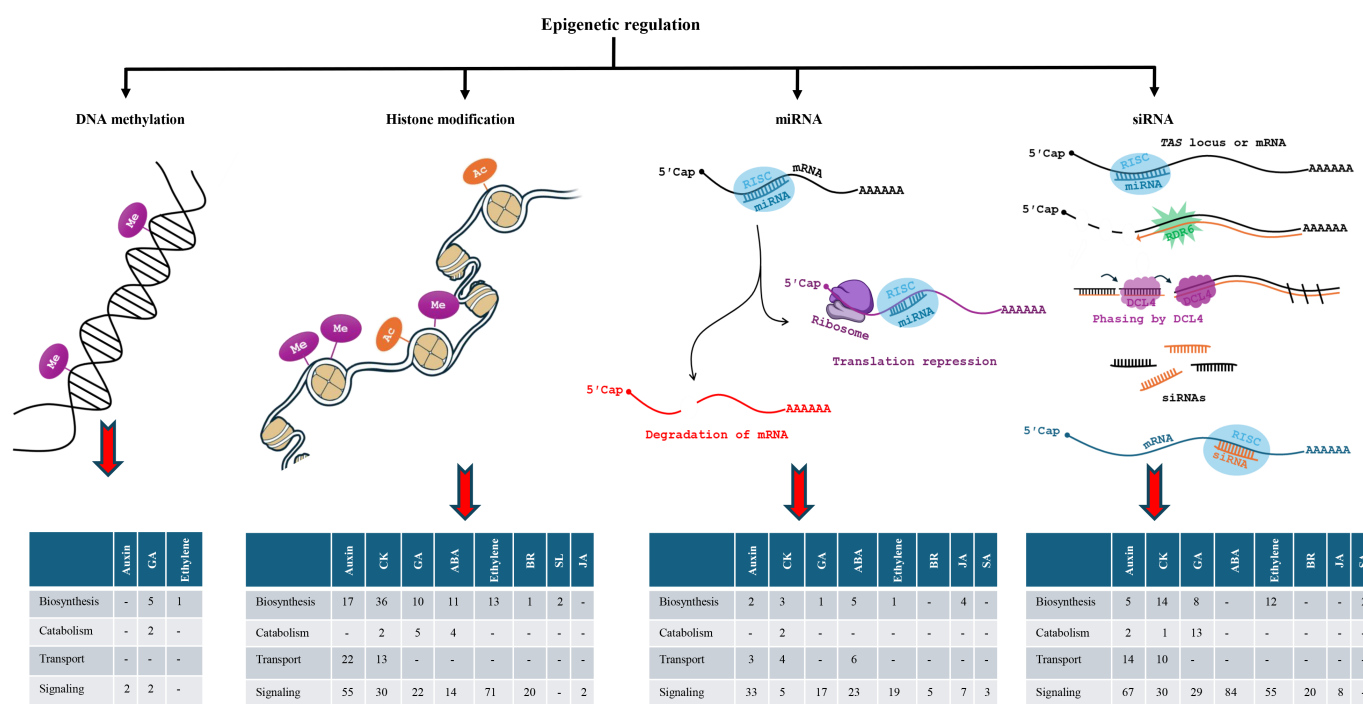


Fig. 4 Epigenetic regulation of phytohormone genes during tuberization in potato. Four types of epigenetic mechanisms, such as: DNA methylation; histone modifications, especially H3K4me3, H3K27me3 modifications and targets of a histone methyltransferase *StE(z)2*; microRNA (miRNA); and phased short-interfering RNA (phasiRNA) mediated regulation, are reported in potato that could control the expression of numerous tuberization pathway genes. In this figure, the number of genes from various phytohormone pathways (biosynthesis, catabolism, transport and signalling) that are potentially regulated by these epigenetic mechanisms are summarized. The number of genes represented are from various reports e.g. DNA methylation^[50], histone modifications^[3,52,53], microRNAs^[57,58,66], and siRNAs^[3,11,57], and their details are provided in Supplementary Table S2.

H3K4me3 targets. The same is the case with a BR biosynthesis gene (*BR hydroxylase*) and various signalling components (*BRI*, *BRIK1*, *BZR1*, *LRR*, and *THESEUS1 KINASE* receptors), suggesting that the BR pathway is active during tuberization and it could function as a positive regulator of tuber development, matching with the functions of *StBRI1* and *StBIN2* (Table 1). ABA increases during tuber development, and its catabolism gene, such as *ABA8'H*, is found as the *StE(z)2* target, consistent with their downregulation during tuber transition stages. Furthermore, ABA biosynthesis genes (*NCED1/2* and *AAO*), receptors (*ABI1B*, *PYL4*, and *PP2C*) and a responsive gene (*ABRE*) have H3K4me3 activation marks, and this could contribute to their enhanced gene expression, high ABA levels, and pronounced ABA response (Supplementary Tables S1 and S2).

GGPP SYNTHASE, *ENT-KAURENE OXIDASE*, *GA20ox*, *GA2ox*, *GID1*, and *DELLA* are identified as *E(z)2* targets, suggesting that *StE(z)2* catalyzed H3K27me3 modification could contribute to the modulation of GA biosynthesis, catabolism, and signalling genes, in such a way that collectively it can cause reduced GA levels, a pre-requisite for stolon-to-tuber transition. Moreover, *StGA3ox*, in addition to the *StE(z)2* targets mentioned earlier, have H3K4me3 activation marks, suggesting that the cumulative effect of both activation and repressive histone modifications could decide the final effect on the gene expression, and if H3K4me3 modifications are more abundant, genes would be upregulated, whereas the prevalence of H3K27me3 marks could cause downregulation of gene expression. SL is a branching inhibitor and its key biosynthesis genes *CCD4* and *MAX1* are found as *StE(z)2* or H3K27me3 targets, and both are downregulated during tuber transition stages (Supplementary Tables S1 and S2). This could lead to reduced SL levels during tuber initiation, which may cause reduced stolon branching so that the majority of the sugar resources are possibly being used for stolon-to-tuber formation.

miRNAs

Small non-coding RNAs have been shown to regulate various biological processes in plants and animals^[61,62]. Especially, microRNAs (miRNAs) participate in nearly all physiological events, such as shoot-apical meristem development and maintenance, leaf morphogenesis, juvenile-to-adult phase transition, flowering, and root development by regulating various hormonal networks via targeting mRNAs based on the complementary sequence and direct them to degradations^[62]. A few small RNAs, such as miR172, miR156, miR390, and SES (Suppressing Expression of SP6A) have been demonstrated to regulate tuber development. miR172 acts as a positive regulator of tuberization^[54], whereas miR156 is known to regulate miR172 expression. Interestingly, overexpression lines of miR156 showed profuse stem branching and aerial stolons that formed tubers under inductive conditions by enhancing CK levels in the axillary meristems^[55]. These lines also exhibited reduced levels of SL (e.g., orobanchyl acetate) that aid stem branching, suggesting a crucial role of miR156 in regulating CK and SL metabolism. Further, miR390 was demonstrated to target CALCIUM-DEPENDENT PROTEIN KINASE 1 (*StCDPK1*) that can phosphorylate *StPIN4* (auxin efflux transporter), *in vitro*^[56]. A study demonstrated the role of a small RNA, SES, that targets *StSP6A* mRNA to inhibit tuberization at high temperatures^[63]. These reports indicate that small RNAs regulate phytohormone-related genes associated with tuberization. Previous studies have profiled miRNA populations from potato^[64,65]. Specifically, two reports identified several conserved and potato-specific miRNAs from early stolon stages, and revealed unique small RNAs that might be potentially involved in stolon-to-tuber transitions in potato^[57,66]. Two conserved miRNAs, such as *Stu-miR479* and *Stu-miR319b*, with their confirmed targets *StGRAS* and

StGAMYB (GA-responsive TFs), showed complementary expression patterns across the stolon stages^[57]. A total of 143 phytohormone-related genes are predicted to be the targets of miRNAs identified from stolon stages^[57,65,66]. While the majority of target genes belonged to the auxin (38) and ABA (34) pathways, GA (18) pathway genes were also targeted by miRNAs identified in these studies (Fig. 4). Among the 143 potential targets, 112 genes were related to the phytohormone signalling pathways, including ARFs, ETHYLENE RESPONSE FACTORS (ERFs), PP2C, and GRAS/GAMYB TFs (Supplementary Table S2). These findings suggest that miRNAs may act as key regulators in the gene regulatory networks operating during tuber development in potato.

siRNAs

Phased secondary short-interfering RNAs (PhasiRNAs) represent a key class of small RNAs that regulate gene expression through post-transcriptional gene silencing mechanisms, similar to miRNAs. PhasiRNAs can target both self- and non-self-transcripts, with those targeting non-self mRNAs referred as trans-acting siRNAs (tasiRNAs). *TAS/PHAS* loci produce transcripts that are specifically cleaved by certain miRNAs to generate phasiRNAs^[61]. PhasiRNAs were also demonstrated to regulate hormone metabolism genes. For example, a wheat-specific miRNA, miR9678, targets a lncRNA - WSGAR and produces phasiRNAs that could regulate the germination process in wheat by controlling the expression of GA metabolism genes^[67]. A report in 2018, was the first to report 830 potential *TAS/PHAS* loci that produced tasiRNAs^[57] during stolon-to-tuber transition stages of potato grown under long-day and SD photoperiods. Further, target analysis revealed a total of 374 phytohormone related genes to be targets of these phasiRNAs^[3] with major categories as auxin (88), GA (50), CK (55), BR (20), ABA (84), ethylene (67), JA (eight), and SA (two) (Fig. 4, Supplementary Table S2). One of the phasiRNAs, referred to as siRD29(-), was shown to target a GA biosynthesis gene, *StGA3ox3*^[11]. Additionally, *StGA3ox3* is tightly regulated by *StBEL5* protein, indicating a dual regulatory control to maintain its expression levels. This finding serves as a good example of how phasiRNAs contribute to the regulation of key phytohormone-related genes. Thus, phasiRNAs possess potential to control hormonal networks like miRNAs; thereby fine-tuning tuber developmental transitions. Future research can delve into other phasiRNA-mediated phytohormone regulatory modules for their roles in tuber development.

Role of phytohormones in storage root development of sweetpotato

Physiological changes during SR initiation in sweetpotato

Sweetpotato is a vegetatively propagated crop *via* vine cuttings or through sprouting of SRs. One of the important physiological changes in sweetpotato is SR formation. Three types of developmental stages are classified for adventitious roots (ARs) of sweetpotato: (i) initiated SR; (ii) pencil root (PR); and (iii) lignified root (LG)^[68]. ARs are said to be initiated with the formation of anomalous cambium. In 2009, a report showed that ARs emerging within the first week of planting account for SR development^[69]. Several anatomical changes happen in the ARs that lead to SR development. Initially, vascular cambium begins to form undifferentiated procambium cells between the primary xylem and phloem, resulting in root thickening. Further, the formation of primary and anomalous cambium leads to the development of thin-walled parenchyma cells in the swelling roots. This is the first developmental sign of ARs

transitioning into SRs. The formation of intermediate root structures, known as PRs, results from the halting of normal SR development^[69]. Whereas, heavy lignification of the parenchyma cell walls of the pith in ARs form LGs^[68]; thus, inhibiting SR development in sweetpotato. Transcriptome analysis showed that the expression of lignin biosynthesis genes, including *CAFFEYL-CoA 3 O-METHYLTRANSFERASE* (*CCoAoMT*) and *CINNAMYL ALCOHOL DEHYDROGENASE* (*CAD*), was lower in young SRs compared to fibrous roots (FRs)^[70]. Lignin biosynthesis and stress-related proteins are exclusively expressed and upregulated during young SR formation. Moreover, PRs in comparison to SRs contain significantly higher levels of the total phenolic compounds, which are mostly the lignin precursors^[71].

Understanding the molecular mechanism of SR development can help in developing genome-edited sweetpotato varieties with enhanced traits, especially yield, starch content, and disease-resistance capacity, which normally requires a laborious and time-consuming process with conventional breeding programs^[72]. Recent advancements in the field, such as the availability of genome sequences of sweetpotato and its close ancestors - *Ipomoea trifida* and *Ipomoea triloba* (<https://sweetpotato.uga.edu>), tissue-culture free cut-dip-budding (CDB) delivery method for *Agrobacterium*-based sweetpotato transformation^[73], and the multi-omics dataset of FRs and SR developmental stages^[74,75], have enabled researchers to investigate the molecular mechanism of SR development in sweetpotato. For example, the transgenic sweetpotato plants overexpressing *SRF1* gene (encodes for a DOF protein) increased dry matter and starch content of SRs compared to wild-type (WT) plants. This increase resulted from the suppression of the *VACUOLAR INVERTASE* gene by *SRF1*, which alters the carbohydrate metabolism in sweetpotato SRs^[76]. Further, auxin-dependent and root-specific expression of *MADS-BOX* gene (*SRD1*) enhanced proliferation of cambium and metaxylem cells in FRs^[77]. Sweetpotato plants overexpressing *SRD1* showed thicker and shorter FRs compared to WT. Field-grown knock-down sweetpotato lines of *lbEXP1* (*EXPANSIN*) produced shorter and thicker FRs due to reduced lignin content in the central stele regions of FRs compared to WT plants, suggesting the *lbEXP1* gene negatively regulates SR development^[78]. Using dynamic network biomarker (DNB) analysis, *lbNAC083* was identified as a key regulator of earliness for SR initiation in sweetpotato^[79]. SR formation is associated with starch accumulation in FRs. In 2024, it was shown that the overexpression of *lbSUT1* plasma membrane sucrose transporter inhibits SR formation in sweetpotato^[80], possibly due to high lignin deposition and sucrose accumulation in the roots, reduced ZR levels, and enhanced GA₃ levels. This is consistent with earlier reports, suggesting that the endogenous phytohormones influence SR development^[74,81].

Overall, few studies have explored the role of molecular factors in regulating SR development in sweetpotato. Phytohormones appear to be the crucial factors that not only integrate various extrinsic cues with intrinsic molecular pathways, but also control the dynamic physiological changes occurring during SR developmental stages. In this review, the role of differentially expressed phytohormone-related genes (Fig. 5) and miRNAs-mediated regulation of these genes are the main focus (Fig. 6), which could be associated with sweetpotato SR development.

Effect of endogenous phytohormone levels and their exogenous applications on sweetpotato SR development

Thickening of sweetpotato SRs appears to be a collective action of various phytohormones. An earlier report quantified the endogenous phytohormones, such as auxin (IAA), CKs (like zeatin riboside [ZR], dihydro-zeatin riboside [DHZR], and isopentenyl adenine [IPA]),

and ABA from sweetpotato genotypes and one of the closely-related ancestral species - *Ipomoea trifida*^[82]. The ZR, DHZR, and ABA had a positive correlation with the initial thickening of SRs and the final yield of sweetpotato^[82]. Later, another study investigated the distribution of endogenous trans-zeatin riboside (t-ZR) in developing and mature SRs of sweetpotato^[83]. As compared to FRs, developing and mature SRs exhibited 2.8- and 3.6-folds increase in t-ZR levels, suggesting its role in SR development^[84]. Another study quantified five phytohormones, such as IAA, CK, GA, JA, and ABA in FRs and SRs of sweetpotato^[74] (Fig. 2c, d). The levels of IAA and ABA were significantly induced in SRs at the initial stage, compared to FRs (Fig. 2c, d), followed by a drastic reduction in mature SRs, suggesting that IAA and ABA are possibly required for the SR initiation from FRs, whereas CK increased steadily during SR development, as CK is required for the proliferation of cambium cells. GA and JA levels reduced steadily during the FR to SR developmental stages (Fig. 2c, d). Moreover, RNA-seq data suggested that phytohormone-related genes are differentially expressed during the SR developmental stages of sweetpotato^[74]. This includes upregulation of IAA, CK, and ABA biosynthesis genes, whereas GA and JA biosynthesis-related genes were downregulated in SR compared to FR, suggesting that phytohormones could play major roles during SR thickening and subsequent growth stages of sweetpotato.

Application of GA₃ caused a reduction in SR number, size, and fresh weight of sweetpotato possibly due to reduced starch content of ARs and high lignin deposition^[81]. These observations were further supported by upregulation of lignin biosynthesis genes (*lbPAL*, *lbC4H*, *lb4CL*, *lbCCoAoMT*, and *lbCAD*), and downregulation of starch biosynthesis genes (*lbAGPase* and *lbGBSS*) in GA₃-treated roots, suggesting the potential negative role of GA in sweetpotato SR development. Another study showed that a CK treatment (6-BA) significantly increased sweetpotato SR yield, whereas ABA had no effect^[85].

Role of ABA in SR formation

ABA plays various roles in sweetpotato SR development. It regulates sporamin, a major storage protein in SRs. Beyond regulation of storage protein, ABA has a positive correlation with SR thickening and the overall yield, mostly by enhancing starch synthase activity^[82], and the regulation of secondary meristem growth in the xylem. During SR development, the ABA levels change dynamically, wherein ABA significantly increases from FR to the initiating SR stage, followed by its drastic reduction during the subsequent stages of SR maturation^[74]. Moreover, expression patterns of the ABA biosynthesis pathway genes, *AAO* and *lbZEP*, as well as ABA signalling genes like *ABA-INSENSITIVE* (*lbABI*), *PYRABACTIN RESISTANCE 1-LIKE* (*lbPYL4*), *ABRE-BINDING FACTOR* (*lbABF3*), *lbABF4*, *DOF-TYPE PROLINE-RICH BASIC LEUCINE ZIPPER FACTOR* (*lbDPBF3*, *lbDPBF4*), *lbSnRK2.1* (*SUCROSE NON-FERMENTING 1-RELATED KINASE*), and *lbSnRK2.2* (Fig. 5a; Supplementary Table S3) correlated with endogenous ABA levels in SRs^[74,86], suggesting that ABA might have a role during the initial stages of SR development. These findings suggest that ABA is essential for sweetpotato SR initiation and bulking; however, it is unclear how the ABA signalling components contribute to these processes.

Role of GA in SR development

In sweetpotato, GA levels reduce steadily from FR to SR. The reduced GA levels are associated with the downregulation of GA biosynthesis genes^[74]. GA causes lignin deposition and reduces starch accumulation in sweetpotato roots^[81]. All seven *lbGA2ox* genes from the sweetpotato genome (*lbGA2ox-1* to *lbGA2ox-7*)^[87], *lbGA3ox*, and signalling components (*lbGID* and *lbGRP*) were

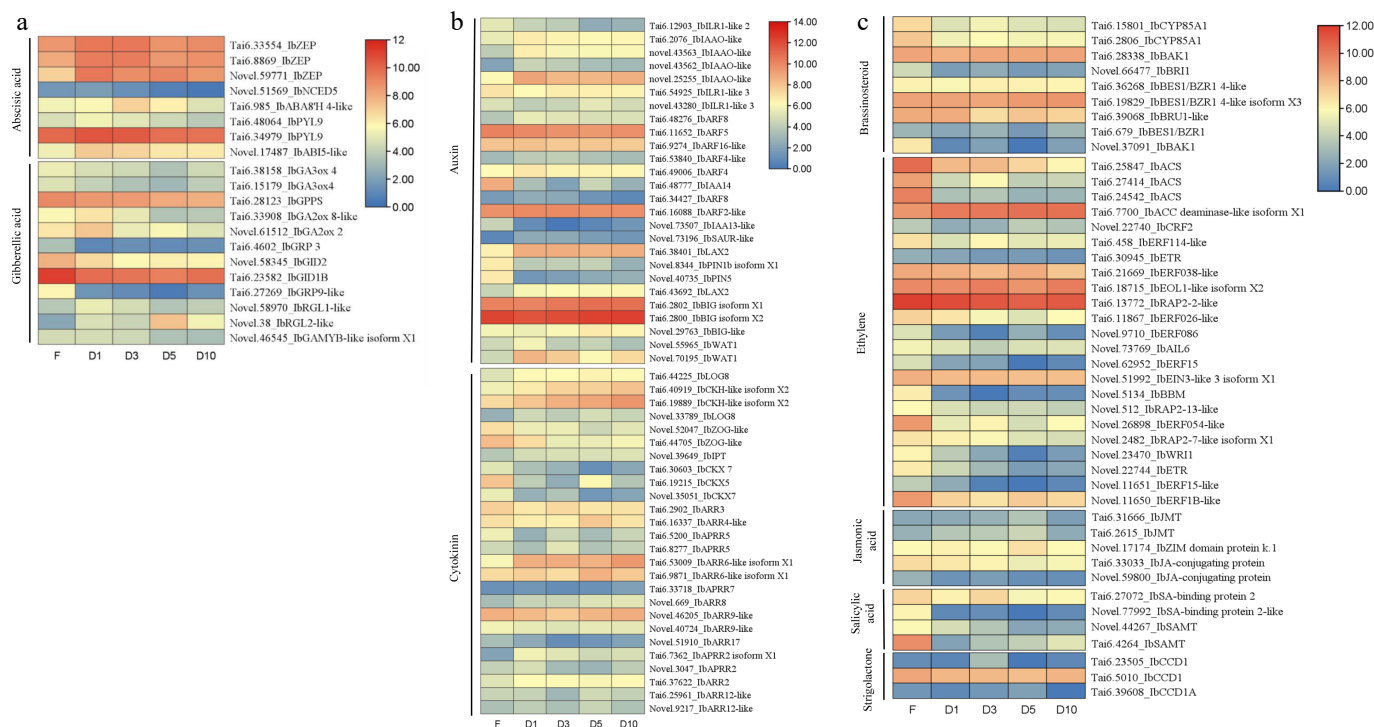


Fig. 5 Heat maps showing differentially expressed phytohormone-related genes during different stages of storage root formation in sweetpotato. (a) Differentially expressed abscissic acid and gibberellic acid related genes. (b) Auxin and cytokinin genes differentially expressed during storage root development. (c) Differentially expressed genes related to brassinosteroid, ethylene, jasmonic acid, salicylic acid, and strigolactone. The expression of genes from various root developmental tissue types, such as F-fibrous root with diameter 1 mm; D1-initiating storage root with diameter 1 cm; D3-storage root with diameter 3 cm; D5-storage root with diameter 5 cm, D10-storage root with diameter 10 cm. The scale bar represents normalized read counts (log2 values). The gene expression values are retrieved from Dong et al.^[74] and also provided in [Supplementary Table S3](#). TBtool^[102] was used to prepare heat maps. Abbreviations: ABA8'H: ABSCISIC ACID HYDROXYLASE 8; ABI: ABSCISIC ACID INSENSITIVE; ACS: 1-AMINOCYCLOPROPANE-1-CARBOXYLATE OXIDASE, AP2-LIKE: APETALA2-LIKE; APRR: TWO-COMPONENT RESPONSE REGULATOR-LIKE APRR; ARF: AUXIN RESPONSE FACTOR; BBM: BABY BOOM; BIG: AUXIN TRANSPORT PROTEIN BIG; BAK: BRASSINOSTEROID INSENSITIVE RECEPTOR KINASE; CCD: CAROTENOID CLEAVAGE DIOXYGENASE; CKX: CYTOKININ HYDROXYLASE; CKX: CYTOKININ OXIDASE/DEHYDROGENASE; CRF: CYTOKININ RESPONSE FACTOR; CYP84A1: CYTOCHROME P450 CYP85A1; EIN: ETHYLENE INSENSITIVE LIKE; EOL: ETHYLENE-OVERPRODUCTION PROTEIN; ERF: ETHYLENE RESPONSIVE FACTOR; ETR: ETHYLENE RECEPTOR; GAMYB: GA-RESPONSIVE MYB TRANSCRIPTION FACTOR; GA2ox: GIBBERELLIN 2 OXIDASE; GA3ox: GIBBERELLIN 3- β -DIOXYGENASE; GPPS: GERANYL PYROPHOSPHATE SYNTHASE; GRP10_LIKE: GIBBERELLIN REGULATED PROTEIN 10-LIKE; IAA: INDOLE-3-ACETIC ACID INDUCIBLE PROTEIN; IAAO: INDOLE-3-ACETALDEHYDE OXIDASE-LIKE; Ib: *Ipomoea batatas*; IPT: ISOPENTENYL TRANSFERASE; IRL: IAA-AMINO ACID HYDROLASE; JMT: JASMONATE O-METHYLTRANSFERASE; LAX: LIKE-AUX1; LOG: LONELY GUY; NCED: 9-CIS-EPOXYCAROTENOID DIOXYGENASE; PCNT115: AUXIN-INDUCED PROTEIN PCNT115; PIN: PIN-FORMED; PP2C: PROTEIN PHOSPHATASE 2C; PYL: PYRABACTIN RESISTANCE ABA RECEPTOR; RGL: RGA-LIKE; RAP: RELATED TO APETALA; SA-binding protein: SALICYLIC ACID-BINDING PROTEIN; SAMT: SALICYLATE O-METHYLTRANSFERASE; SAUR: SMALL AUXIN-UP RNA; WAT1: WALLS ARE THIN1; WRI: WRINKLED; ZEP: ZEAXANTHIN EPOXIDASE; ZIM: ZINC-FINGER EXPRESSED IN INFLORESCENCE MERISTEM; ZOG: ZEATIN O-GLUCOSYLTRANSFERASE.

downregulated in developing SRs compared to FR (Fig. 5a; [Supplementary Table S3](#)). Recently, a gene *IbCYP714A1* encoding cytochrome P450 monooxygenase was identified as a GA inactivation enzyme, and its overexpression lines prevented SR formation (Table 1), but resulted in a greater number of FRs compared to WT sweetpotato plants^[88]. These results suggest that *IbGA2ox* enzymes inactivate bioactive gibberellins (GAs) to reduce bioactive GA levels during SR initiation, that may promote FR-to-SR transition. However, it appears that optimal GA levels are possibly required to initiate SR formation, and continuous low GA levels in FRs can lead to the complete inhibition of SR formation.

Role of auxin in SR development

In sweetpotato, endogenous IAA levels were significantly induced during the initial stage of SR development, and decreased sharply during SR maturation stages^[74]. Both high or low levels of IAA adversely affect sweetpotato root growth^[74]; however, various reports suggest that the auxin negatively regulates SR development (Table 1). For instance, heterologous expression of *AtYUCCA6* in sweetpotato reduced SR yield^[89]. Furthermore, expression of

IbYUCCA4 under auxin-inducible *IbNF-YA1* promoter enhanced IAA biosynthesis, and thereby reduced SR weight^[90]. Recently, it has been shown that an IAA-inducible auxin-repressed domain protein—*IbDRM1* is positively regulated by *IbARF11L* and *IbMYB52*, and *IbDRM1* overexpression inhibits root development by lowering auxin concentrations of sweetpotato roots^[91]. Auxin response factors, *IbARF5*, *IbARF8*, and *IbARF18*, showed a significant upregulation in SR compared to stem or leaf^[92,93]. Furthermore, genes involved in auxin signalling and transport (*IbARF*, *IbPIN*, *IbWAT1*) were downregulated in the mature SR stage compared to the initial SR stage (Fig. 5b; [Supplementary Table S3](#)). The differential expression patterns of these genes suggest their potential roles during the early stage of SR development.

Role of CK in SR development

The levels of active CKs (like ZR and DHZR) have a positive correlation with the SR thickening and the final yield of sweetpotato^[82]. An earlier study showed that the exogenous application of *t*-ZR causes enhanced SR thickness. The CK levels increase gradually from FR to SR stages^[74] (Fig. 2d). Consistent with this observation, it was found

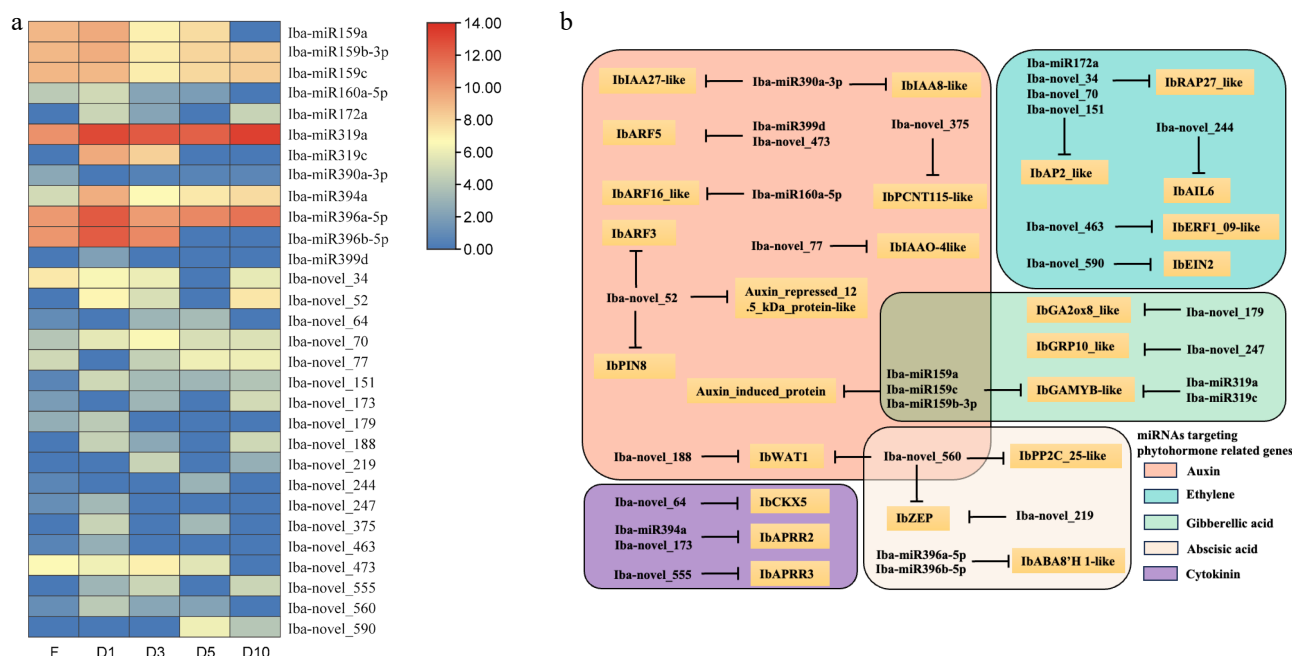


Fig. 6 Differentially expressed miRNAs targeting phytohormone-related genes during storage root developmental stages of sweetpotato. (a) Heat map showing differently expressed miRNAs in storage root developmental tissue types, such as F-fibrous root with diameter 1 mm; D1-initiating storage root with diameter 1 cm; D3-storage root with diameter 3 cm; D5-storage root with diameter 5 cm, D10-storage root with diameter 10 cm. The scale bar represents normalized read counts (log2 values). The expression values of miRNAs are retrieved from the study by Tang et al.^[75]. (b) Depiction of selective differentially expressed miRNAs targeting phytohormone-related genes. Target prediction analysis was performed using psRNAtarget analysis tool^[103], with cleavage efficiency (E) value < 3.0 and sweetpotato cDNA library (<http://public-genomes-ngs.molgen.mpg.de/sweetpotato>). Detailed information is available in [Supplementary Table S4](#). Abbreviations: ABA8'H: ABSCISIC ACID HYDROXYLASE 8; AIL6: AINTEGUMENTA-LIKE PROTEIN 6; EIN2: ETHYLENE INSENSITIVE 2; AP2-LIKE: APETALA2-LIKE; APRR: TWO-COMPONENT RESPONSE REGULATOR-LIKE APRR; ARF: AUXIN RESPONSE FACTOR; CKX: CYTOKININ OXIDASE/DEHYDROGENASE; ERF: ETHYLENE RESPONSIVE FACTOR; GAMYB: GA-RESPONSIVE MYB TRANSCRIPTION FACTOR; GA2ox: GIBBERELLIN 2 OXIDASE; GRP10_LIKE: GIBBERELLIN REGULATED PROTEIN 10-LIKE; IAA: INDOLE-3-ACETIC ACID INDUCIBLE PROTEIN; IAAO: INDOLE-3-ACETALDEHYDE OXIDASE-LIKE; Iba: *Ipomoea batatas*; miR: MicroRNA; PCNT115: AUXIN-INDUCED PROTEIN PCNT115; PIN: PIN-FORMED; PP2C: PROTEIN PHOSPHATASE 2C; RAP: RELATED TO APETALA; WAT1: WALLS ARE THIN1; ZEP: ZEAXANTHIN EPOXIDASE.

that CK biosynthesis genes (*IbLOG*, *IbCKH*, *IbIPT*) were upregulated throughout the SR stages as compared to FR (Fig. 5b; [Supplementary Table S3](#)). Conversely, the CK catabolism gene, *IbCKX* showed the opposite expression pattern. Furthermore, an increase in CK levels during SR development correlates with high expression of *KNOX-I* genes^[83]. In Arabidopsis, it has been shown that KNOX proteins, along with BELL partners, activate the expression of the CK biosynthetic gene—*IPT*, and thereby increase CK levels. CK's role is proposed in the proliferation of cambium cells, which contributes to SR bulking^[74]. Additionally, the increase in CK levels is positively correlated with the expression of the *APRT* gene (*ADENINE PHOSPHORIBOSYL TRANSFERASE*) during SR stages^[74]. Overall, CKs appear to stimulate cell division, and act as positive regulators of SR development.

Roles of JA, ethylene, SA, BR, and SL during SR development

JA content gradually decreases as FRs transition into SRs, but then it recovers at the D10 developmental stage (Fig. 2d). The JA biosynthesis gene, *IbOPR3* (*OPDA REDUCTASE 3*), exhibited a similar expression pattern, suggesting a potential role of JA in SR development^[74]. Consistent with this, another study showed that JA signaling genes, such as *IbJAZ1.1* and *IbJAZ8.1* were downregulated in SR compared to FR^[94]. Moreover, *IbBBX24* has been shown to activate *IbMYC2* by binding to *IbJAZ10*, and causes activation of JA-responsive genes that help to accumulate JA, which ultimately leads to an increase in sweetpotato yield^[95]. It is hypothesized that the *IbBBX24* effect on SR yield could not be a direct consequence of activated JA

signaling; rather, altered expression of other phytohormone-associated genes, could be a contributing factor for this SR phenotype^[95]. However, it is intriguing to note why JA levels decrease in the early stages of SR development, before they peak at the final maturation stage.

Ethylene negatively regulates root growth by stimulating auxin biosynthesis and transport^[96]. During the FR to SR transition (D1), and later SR maturation stages (D3, D5, D10), most ethylene biosynthesis and signaling genes were downregulated, while the ethylene catabolism gene *ACC DEAMINASE* was upregulated (Fig. 5c; [Supplementary Table S3](#)), suggesting that ethylene might negatively regulate SR development. Moreover, four SA-related genes, such as two *SA-BINDING PROTEINS* and two *SA CARBOXYL METHYLTRANSFERASE* (*SAMT*), were downregulated during the transition from FR to the subsequent SR developmental stages - D1, D3, D5, and D10 (Fig. 5c). However, to date, there are no reports regarding how ethylene or SA pathway genes influence SR development in sweetpotato.

SL biosynthesis gene, *CCD* remains unchanged during the transition from FR to the subsequent SR developmental stages - D1, D3, D5, and D10 (Fig. 5c), suggesting that SL may not have a direct effect on SR development. BR biosynthesis (*CYP85A1*) and various signalling genes (*BRI1*, *BAK1*, *BS1/BZR1*, and *BRU1*) remain either unchanged or downregulated during the transition from FR to the subsequent SR developmental stages - D1, D3, D5, and D10 (Fig. 5c; [Supplementary Table S3](#)), indicating a possible negative role of BR during SR formation process. Only future research will infer if there is a role of SL or BR in SR development.

MicroRNA-mediated regulation of phytohormone genes during SR development of sweetpotato

There are no reports on the epigenetic regulation of SR development in sweetpotato, except the one focused on miRNA identification from FR and developmental stages of SRs^[75]. Nevertheless, not a single miRNA has so far been characterized for its role in SR development. Here, small RNA datasets from a previous report were utilized to highlight those differentially expressed (DE) miRNAs which are likely to target phytohormone-related genes and could influence SR development^[75]. This study identified 61 conserved and 471 novel miRNAs. Of which, more than 145 miRNAs were differentially expressed between FR and various SR stages- D1, D3, D5, and D10^[75]. The expression patterns of miRNAs that are differentially expressed during SR development and predicted to target phytohormone-related genes are shown in Fig. 6a. While seven conserved, and nine novel miRNAs were highly expressed in the D1 stage of SR compared to FR, miRNAs, such as lba-miR390a-3p, lba-novel_77, lba-novel_173, and lba-novel_244 were downregulated, suggesting that these miRNAs may regulate SR initiation by targeting phytohormone-related genes.

Several auxin-related genes were identified as targets of DE miRNAs during SR development (Fig. 6b; Supplementary Table S4). These include auxin biosynthesis gene - *INDOLE-3-ACETALDEHYDE OXIDASE-LIKE* (IAAO-LIKE), signaling components (*ARF3*, *ARF5*, *ARF16-LIKE*, and *IAA-INDUCIBLE proteins* - *IAA8*, *IAA27*), transporters (auxin efflux carrier *PIN8* and *WALLS ARE THIN1* [*WAT1*]), and *AUXIN-INDUCED proteins*, including *PCNT115-like* (Fig. 6b). CK-related genes that are targets of DE miRNAs, include a catabolism gene-*CKX5* and signaling components, such as *RESPONSE REGULATORS APRR2* and *APRR3*. ABA-related genes, such as *ZEAXANTHIN EPOXIDASE* (*ZEP*; a biosynthesis gene), *ABA HYDROXYLASE 8* (*ABA8'H*; a catabolism gene), and the signaling gene - *PP2C-25-LIKE* as well as GA catabolism gene - *GA2ox8*, and GA signalling components like *GAMYB-LIKE TF*, and *GA-REGULATED PROTEIN 10-LIKE* (*GRP10-LIKE*) were also found as targets of DE miRNAs (Fig. 6b). Further, DE miRNAs' target genes include ethylene signaling pathway component - *ETHYLENE INSENSITIVE 2* (*EIN2*), and TFs, such as *AINTEGUMENTA-LIKE protein 6* (*AIL6*), *APETALA2-LIKE* (*AP2-LIKE*), *ERF*, and *RELATED TO APETALA2* (*RAP2*) (Fig. 6b; Supplementary Table S4). Considering the negative roles of auxin and GA during SR development, it would be interesting to investigate the regulatory roles of many of these DE miRNAs and their proposed targets (e.g. lba-miR160-lbaARF16, lba-miR319a/c-lbGAMYB-LIKE, etc.) during SR initiation (Fig. 6b; Supplementary Table S4). Thus, miRNA-mediated regulation of phytohormone genes could be one of the crucial mechanisms that control phytohormone dynamics and signaling pathways to fine-tune SR developmental transitions in sweetpotato.

Differences and similarities in tuber formation in potato vs SR development in sweetpotato with respect to phytohormones levels and their roles

Both the crops, potato (*Solanaceae* family) and sweetpotato (*Convolvulaceae* family), have polyploid genomes, with the most cultivated potatoes being tetraploid whereas sweetpotatoes are hexaploid. Tuberization in potato and SR formation in sweetpotato require substantial investment of nutrients and energy, and it appears that both these complex processes could be regulated by multiple parallel pathways of various phytohormones, TFs, and sRNAs^[97,98]. Considering the difference in terms of their origin of storage organ (tissue type) for potato (stem) vs sweetpotato (AR), there is a possibility to have unique pathway(s) to fine-tune the

tuber or SR development process. However, both being below-ground storage organs, and also involving similar physiological processes (e.g. halting of the longitudinal growth of the stolon tip in potato or AR in sweetpotato, radial growth after the change in orientation of cell growth from elongation to expansion, and the rapid thickening growth following the initiation of cell division and biochemical changes during their development^[77]), a few common pathways are likely to be present. There are also environmental and endogenous factors' analogues (e.g. high cytokinin and low nitrogen levels) that similarly help during tuber formation in potato and SR development in sweetpotato. A hypothesis of the 'orthologs of potato mobile RNAs and proteins including RNA-binding proteins regulating SR formation in sweetpotato^[99,100]' supports the existence of a common pathway for belowground storage organ formation. Furthermore, similar and distinct patterns of gene expression profiles for several phytohormone signaling pathway genes during potato tuberization stages (Fig. 3), and sweetpotato SR formation stages (Fig. 5), suggest the existence of common as well as unique gene regulatory hubs contributing to tuber or SR development. For instance, among these phytohormones, auxin, CK, and GA show similar patterns of endogenous levels during stolon-to-tuber transitions of potato and fibrous to developing SR stages of sweetpotato, supporting their conserved roles during storage organ initiation (Fig. 2b, d). Particularly, GA levels decrease rapidly from stolon to tuber, or from fibrous to SR maturation stages. In contrast, CK shows a continuous increase during these stages, except in potato, wherein CK levels decrease in the last stage (i.e., from the mini-tuber to the tuber formation stage). Auxin shows a rapid increase at the tuber or SR initiation stage (Fig. 2b, d), but the levels then decrease gradually until maturation stages; except the last stage transition from D5 to D10 in sweetpotato, where there is a slight increase in auxin levels at the D10 stage. During potato tuber development, ABA keeps increasing from stolon to tuber stages (Fig. 2b), whereas in sweetpotato, ABA levels increase drastically from FR to SR initiation stage (D1), but then the levels decrease rapidly in the subsequent SR maturation stages (D3 and D5), before increasing slightly at the D10 stage (Fig. 2d). To date, there is no data available for the levels of other phytohormones (BR, SL, ethylene, JA, SA) during the tuber or SR stages; except JA levels in sweetpotato.

In potato, auxin is crucial for swollen stolon formation (the tuber induction process). It is shown to positively regulate tuber numbers, but it has a negative effect on tuber weights, especially when auxin pathway genes are constitutively expressed throughout the plant (Fig. 7a; Table 1). In sweetpotato, constitutive expression of auxin biosynthesis, or signalling genes throughout the plant has a strong negative effect on SR formation (Fig. 7b; Table 1). Thus, further investigations should test the effects of SR specific expression of auxin genes, as well as exploring negative regulators of auxin signalling (e.g., *AUX/IAA*) through genome-editing to enhance SR yield. In both potato and sweetpotato, GA has negative effects on tuberization or SR formation (Fig. 7b; Table 1). In contrast, other phytohormones, such as ABA, CK, SL, and BR, are shown to function as positive regulators of potato tuber development (Fig. 7a; Table 1). Based on the gene expression analysis during stolon-to-tuber transitions of potato (Fig. 3), JA, SA, and ethylene are proposed to have a positive effect on tuber formation (Fig. 7a). Similarly, in sweetpotato, based on the gene expression profiling data (Fig. 5), it appears that ABA, CK, and JA could have a positive effect on SR formation, whereas other phytohormones like BR, SA, and ethylene may have negative effects (Fig. 7b). However, the precise role of differentially expressed genes involved in the metabolism, transport, and signalling pathways of these six phytohormones require further research. Detailed comparative studies involving co-expression analysis of

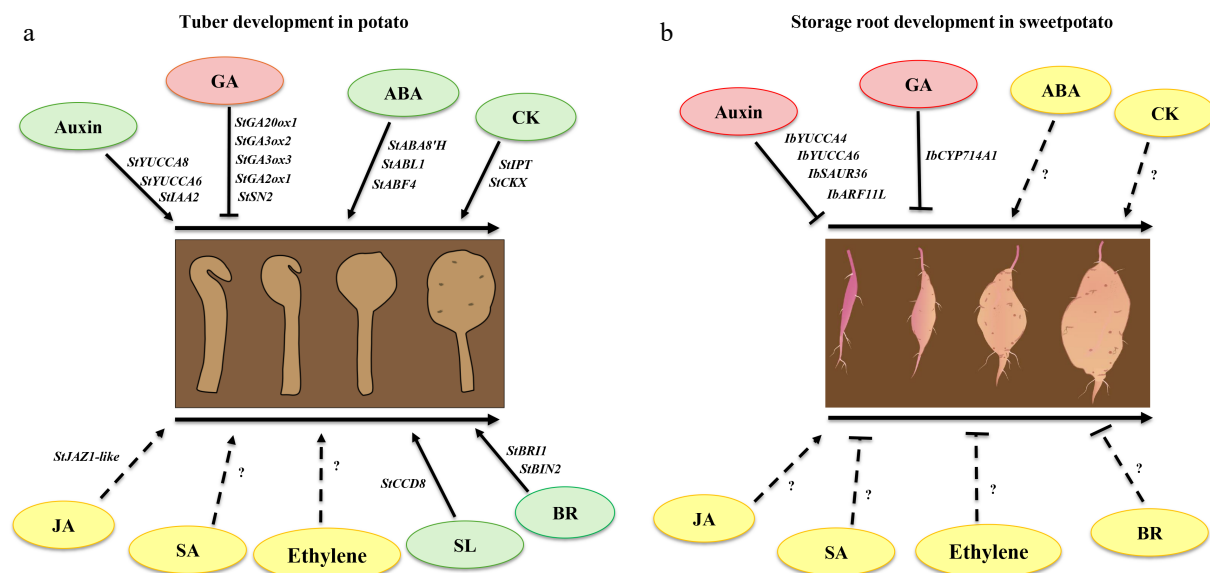


Fig. 7 Model for phytohormones' role in tuber and storage root development. The overall phytohormones' role in (a) potato tuber developmental stages, and (b) sweetpotato storage root developmental stages are depicted. Thick line arrow (→) indicate known positive effect on tuber or storage root development; dotted line arrow (--->) indicate proposed positive effect on tuber or storage root development, and symbol (?) indicate phytohormone-related genes not been characterized yet to assign their function.

various phytohormone signaling genes, and the functional characterization of key phytohormone associated genes, would unravel unique and common phytohormone gene regulatory networks involved in the belowground storage organ formation in potato and sweetpotato.

Conclusions and future perspectives

Understanding the molecular mechanisms of tuber and SR development is important for enhancing their yield potential. Among various factors involved in tuber or SR development, phytohormones are emerging as crucial regulators of tuber or SR development. With the rapid progress in technologies for genome sequencing, the genomic datasets of a tuber crop - potato and few storage root crops (e.g. sweetpotato, cassava) have become available. Furthermore, the protocols for *Agrobacterium tumefaciens* and *Agrobacterium rhizogenes* mediated plant transformation and subsequent regeneration methods, as well as the multi-omics datasets of the developmental stages of tuber and SRs, has opened up avenues for characterizing the functions of candidate genes in these staple crops. Here, the emerging insights about phytohormones' roles in tuber and SR development are summarized, as well as emphasizing the candidate genes identified from the latest gene expression studies for future functional studies. Thus, this information can serve as an ideal platform to further investigate tuber and SR development mechanisms, so that advanced biotechnological and genome-editing strategies can be designed to enhance their yield.

This emerging area of research raises several important questions which will help to better understand how modulating phytohormone pathway genes could influence tuber development in potato or SR formation in sweetpotato. These include the role of CKs in promoting early cell divisions in stolons during tuber formation; the influence of hormonal interactions, such as auxin-CK and auxin-CK-BR crosstalk, on the stolon-to-tuber transition in potato; and the regulatory function of StBEL5-KNOX and Tuberigen Activation Complexes (TAC/aTAC) in controlling phytohormone-related gene expression during tuber development. Additionally, novel techniques for phytohormone quantification in stolons are expected to

improve knowledge of hormonal dynamics during tuber transitions. In sweetpotato, the molecular factors that govern the fate of ARs to differentiate into PRs or SRs remains to be explored. The mechanistic basis by which phytohormone levels are regulated during SR development, the identification of downstream genes regulated by phytohormones, and the role of non-coding RNAs in regulating phytohormone pathway genes during both tuberization and SR development also represent critical areas for future research.

Author contributions

The authors confirm contribution to the manuscript as follows: study conception: Kondhare KR; study design, data collection, analysis and interpretation of results, manuscript draft preparation: Malankar NN, Vyawahare AB, Kondhare KR. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data generated or analyzed during this study are included in this manuscript and its supplementary tables.

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Conflict of interest

The authors declare that they have no conflict of interest.

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References

- Chandrasekara A, Kumar TJ. 2016. Roots and tuber crops as functional foods: a review on phytochemical constituents and their potential health benefits. *International Journal of Food Science* 2016:3631647
- Zierer W, Rüschler D, Sonnewald U, Sonnewald S. 2021. Tuber and tuberous root development. *Annual Review of Plant Biology* 72:551–80
- Kondhare KR, Kumar A, Patil NS, Malankar NN, Saha K, et al. 2021. Development of aerial and belowground tubers in potato is governed by photoperiod and epigenetic mechanism. *Plant Physiology* 187(3):1071–86
- Ravi V, Naskar SK, Makesh Kumar T, Babu B, Krishnan BSP. 2009. Molecular physiology of storage root formation and development in sweet potato [*Ipomoea batatas* (L.) Lam.]. *Journal of Root Crops* 35:1–27
- Roumeliotis E, Visser RGF, Bachem CWB. 2012. A crosstalk of auxin and GA during tuber development. *Plant Signaling & Behavior* 7:1360–63
- Carrera E, Bou J, García-Martínez JL, Prat S. 2000. Changes in GA 20-oxidase gene expression strongly affect stem length, tuber induction and tuber yield of potato plants. *The Plant Journal* 22(3):247–56
- Kloosterman B, Navarro C, Bijsterbosch G, Lange T, Prat S, et al. 2007. StGA2ox1 is induced prior to stolon swelling and controls GA levels during potato tuber development. *The Plant Journal* 52(2):362–73
- Bou-Torrent J, Martínez-García JF, García-Martínez JL, Prat S. 2011. Gibberellin A₁ metabolism contributes to the control of photoperiod-mediated tuberization in potato. *PLoS One* 6(9):e24458
- Roumeliotis E, Kloosterman B, Oortwijn M, Lange T, Visser RGF, et al. 2013. Down regulation of StGA3ox genes in potato results in altered GA content and affect plant and tuber growth characteristics. *Journal of Plant Physiology* 170:1228–34
- Roumeliotis E, Kloosterman B, Oortwijn M, Kohlen W, Bouwmeester HJ, et al. 2012. The effects of auxin and strigolactones on tuber initiation and stolon architecture in potato. *Journal of Experimental Botany* 63(12):4539–47
- Malankar NN, Kondhare KR, Saha K, Mantri M, Banerjee AK. 2023. The phased short-interfering RNA siRD29(–) regulates GIBBERELLIN 3-OXIDASE 3 during stolon-to-tuber transitions in potato. *Plant Physiology* 193(4):2555–72
- Roumeliotis E, Kloosterman B, Oortwijn M, Visser RGF, Bachem CWB. 2013. The PIN family of proteins in potato and their putative role in tuberization. *Frontiers in Plant Science* 4:524
- Roumeliotis E, Kloosterman B, Oortwijn M, Kohlen W, Bouwmeester HJ, et al. 2023. Over-expression of a YUCCA-like gene results in altered shoot and stolon branching and reduced potato tuber size. *Potato Research* 66:67–84
- Hartmann A, Senning M, Hedden P, Sonnewald U, Sonnewald S. 2011. Reactivation of meristem activity and sprout growth in potato tubers require both cytokinin and gibberellin. *Plant Physiology* 155(2):776–96
- Eviatar-Ribak T, Shalit-Kaneh A, Chappell-Maor L, Amsellem Z, Eshed Y, et al. 2013. A cytokinin-activating enzyme promotes tuber formation in tomato. *Current Biology* 23(12):1057–64
- Ohashi-Ito K, Fukuda H. 2020. Transcriptional networks regulating root vascular development. *Current Opinion in Plant Biology* 57:118–23
- Muñiz García MN, Cortezzi JI, Fumagalli M, Capiati DA. 2018. Expression of the *Arabidopsis* ABF4 gene in potato increases tuber yield, improves tuber quality and enhances salt and drought tolerance. *Plant Molecular Biology* 98:137–52
- Liu L, Zhang RJ, Zhu WJ, Liu XR, Shi K, et al. 2017. Inhibitory effect of StCYP707A1 gene on tuberization in transgenic potato. *Plant Biotechnology Reports* 11:219–28
- Jing S, Sun X, Yu L, Wang E, Cheng Z, et al. 2022. Transcription factor StAB1-like 1 binding to the FLOWERING LOCUS T homologs promotes early maturity in potato. *Plant Physiology* 189(3):1677–93
- Liu T, Dong L, Wang E, Liu S, Cheng Y, et al. 2023. StHAB1, a negative regulatory factor in abscisic acid signaling, plays crucial roles in potato drought tolerance and shoot branching. *Journal of Experimental Botany* 74(21):6708–21
- Zhu W, Jiao D, Zhang J, Xue C, Chen M, et al. 2020. Genome-wide identification and analysis of BES1/BZR1 transcription factor family in potato (*Solanum tuberosum* L.). *Plant Growth Regulation* 92:375–87
- Huang S, Zheng C, Zhao Y, Li Q, Liu J, et al. 2021. RNA interference knockdown of the brassinosteroid receptor BRI1 in potato (*Solanum tuberosum* L.) reveals novel functions for brassinosteroid signaling in controlling tuberization. *Scientia Horticulturae* 290:110516
- Liu S, Cai C, Li L, Yu L, Wang Q, et al. 2024. Transcriptome analysis reveals the molecular mechanisms of BR negative regulatory factor StBIN2 maintaining tuber dormancy. *International Journal of Molecular Sciences* 25(4):2244
- Deng R, Huang S, Du J, Luo D, Liu J, et al. 2024. The brassinosteroid receptor StBRI1 promotes tuber development by enhancing plasma membrane H⁺-ATPase activity in potato. *The Plant Cell* 36(9):3498–520
- Alder A, Jamil M, Marzorati M, Bruno M, Vermathen M, et al. 2012. The path from β -carotene to carlactone, a strigolactone-like plant hormone. *Science* 335(6074):1348–51
- Pasare SA, Ducreux LJM, Morris WL, Campbell R, Sharma SK, et al. 2013. The role of the potato (*Solanum tuberosum*) CCD8 gene in stolon and tuber development. *New Phytologist* 198(4):1108–20
- Brewer PB, Dun EA, Ferguson BJ, Rameau C, Beveridge CA. 2009. Strigolactone acts downstream of auxin to regulate bud outgrowth in pea and *Arabidopsis*. *Plant Physiology* 150(1):482–93
- Cenzano A, Vigliocco A, Kraus T, Abdala G. 2003. Exogenously applied jasmonic acid induces changes in apical meristem morphology of potato stolons. *Annals of Botany* 91(7):915–19
- Begum S, Jing S, Yu L, Sun X, Wang E, et al. 2022. Modulation of JA signalling reveals the influence of StJAZ1-like on tuber initiation and tuber bulking in potato. *The Plant Journal* 109(4):952–64
- Koda Y, Takahashi K, Kikuta Y. 1992. Potato tuber-inducing activities of salicylic acid and related compounds. *Journal of Plant Growth Regulation* 11:215–19
- Khilji SA, Rafique A, Ahmad Sajid Z, Rauf M, Ali Shah A, et al. 2024. Foliar application of salicylic acid improved morpho-anatomical features of potato by irrigating with wastewater. *BMC Plant Biology* 24(1):754
- Catchpole AH, Hillman J. 1969. Effect of ethylene on tuber initiation in *Solanum tuberosum* L. *Nature* 223:1387
- Vreugdenhil D, Van Dijk W. 1989. Effects of ethylene on the tuberization of potato (*Solanum tuberosum*) cuttings. *Plant Growth Regulation* 8:31–39
- Saidi A, Hajibarat Z. 2021. Phytohormones: plant switchers in developmental and growth stages in potato. *Journal of Genetic Engineering and Biotechnology* 19(1):89
- Mathura SR, Sutton F, Rouse-Miller J, Bowrin V. 2024. The molecular coordination of tuberization: current status and future directions. *Current Opinion in Plant Biology* 82:102655
- Chen P, Yang R, Bartels D, Dong T, Duan H. 2022. Roles of abscisic acid and gibberellins in stem/root tuber development. *International Journal of Molecular Sciences* 23(9):4955
- Zhang M, Jian H, Shang L, Wang K, Wen S, et al. 2024. Transcriptome analysis reveals novel genes potentially involved in tuberization in potato. *Plants* 13(6):795
- Guo C, Huang Z, Luo S, Wang X, Li J, et al. 2025. Cell fate determination of the potato shoot apex and stolon tips revealed by single-cell transcriptome analysis. *Plant, Cell & Environment* 48(7):4838–58
- Wang X, Zheng K, Na T, Ye G, Han S, et al. 2025. Transcriptomic profiles reveal hormonal regulation of sugar-induced stolon initiation in potato. *Scientific Reports* 15:19122

40. Li T, Kang X, Lei W, Yao X, Zou L, et al. 2020. SHY2 as a node in the regulation of root meristem development by auxin, brassinosteroids, and cytokinin. *Journal of Integrative Plant Biology* 62(10):1500–17
41. González-Schain ND, Díaz-Mendoza M, Żurczak M, Suárez-López P. 2012. Potato CONSTANS is involved in photoperiodic tuberization in a graft-transmissible manner. *The Plant Journal* 70(4):678–90
42. Zhou T, Song B, Liu T, Shen Y, Dong L, et al. 2019. Phytochrome F plays critical roles in potato photoperiodic tuberization. *The Plant Journal* 98(1):42–54
43. Abelenda JA, Cruz-Oró E, Franco-Zorrilla JM, Prat S. 2016. Potato StCONSTANS-like1 suppresses storage organ formation by directly activating the FT-like StSP5G repressor. *Current Biology* 26(7):872–81
44. Teo CJ, Takahashi K, Shimizu K, Shimamoto K, Taoka KI. 2017. Potato tuber induction is regulated by interactions between components of a tuberigen complex. *Plant and Cell Physiology* 58(2):365–74
45. Banerjee AK, Chatterjee M, Yu Y, Suh SG, Miller WA, et al. 2006. Dynamics of a mobile RNA of potato involved in a long-distance signaling pathway. *The Plant Cell* 18(12):3443–57
46. Mahajan A, Bhogale S, Kang IH, Hannapel DJ, Banerjee AK. 2012. The mRNA of a Knotted1-like transcription factor of potato is phloem mobile. *Plant Molecular Biology* 79:595–08
47. Sharma P, Lin T, Hannapel DJ. 2016. Targets of the StBEL5 transcription factor include the FT ortholog StSP6A. *Plant Physiology* 170(1):310–24
48. Zhang X, Campbell R, Ducreux LJM, Morris J, Hedley PE, et al. 2020. TERMINAL FLOWER-1/CENTRORADIALIS inhibits tuberisation via protein interaction with the tuberigen activation complex. *The Plant Journal* 103(6):2263–78
49. Nicolas M, Torres-Pérez R, Wahl V, Cruz-Oró E, Rodríguez-Buey ML, et al. 2022. Spatial control of potato tuberization by the TCP transcription factor BRANCHED1b. *Nature Plants* 8:281–94
50. Ai Y, Jing S, Cheng Z, Song B, Xie C, et al. 2021. DNA methylation affects photoperiodic tuberization in potato (*Solanum tuberosum* L.) by mediating the expression of genes related to the photoperiod and GA pathways. *Horticulture Research* 8:181
51. Dutta M, Raturi V, Gahlaut V, Kumar A, Sharma P, et al. 2022. The interplay of DNA methyltransferases and demethylases with tuberization genes in potato (*Solanum tuberosum* L.) genotypes under high temperature. *Frontiers in Plant Science* 13:933740
52. Kumar A, Kondhare KR, Vetal PV, Banerjee AK. 2020. PcG proteins MSI1 and BMI1 function upstream of miR156 to regulate aerial tuber formation in potato. *Plant Physiology* 182:185–203
53. Kumar A, Kondhare KR, Malankar NN, Banerjee AK. 2021. The Polycomb group methyltransferase StE(z)2 and deposition of H3K27me3 and H3K4me3 regulate the expression of tuberization genes in potato. *Journal of Experimental Botany* 72:426–44
54. Martin A, Adam H, Díaz-Mendoza M, Żurczak M, González-Schain ND, et al. 2009. Graft-transmissible induction of potato tuberization by the microRNA miR172. *Development* 136:2873–81
55. Bhogale S, Mahajan AS, Natarajan B, Rajabhoj M, Thulasiram HV, et al. 2014. MicroRNA156: a potential graft-transmissible microRNA that modulates plant architecture and tuberization in *Solanum tuberosum* ssp. *andigena*. *Plant Physiology* 164:1011–27
56. Santin F, Bhogale S, Fantino E, Grandellis C, Banerjee AK, et al. 2017. *Solanum tuberosum* StCDPK1 is regulated by miR390 at the posttranscriptional level and phosphorylates the auxin efflux carrier StPIN4 *in vitro*, a potential downstream target in potato development. *Plant Physiology* 159:244–61
57. Kondhare KR, Malankar NN, Devani RS, Banerjee AK. 2018. Genome-wide transcriptome analysis reveals small RNA profiles involved in early stages of stolon-to-tuber transitions in potato under photoperiodic conditions. *BMC Plant Biology* 18:284
58. Zhang H, Lang Z, Zhu JK. 2018. Dynamics and function of DNA methylation in plants. *Nature Reviews Molecular Cell Biology* 19:489–06
59. Feng S, Jacobsen SE, Reik W. 2010. Epigenetic reprogramming in plant and animal development. *Science* 330(6004):622–27
60. Le H, Simmons CH, Zhong X. 2025. Functions and mechanisms of histone modifications in plants. *Annual Review of Plant Biology* 76:551–78
61. Liu Y, Teng C, Xia R, Meyers BC. 2020. PhasiRNAs in plants: their biogenesis, genic sources, and roles in stress responses, development, and reproduction. *The Plant Cell* 32(10):3059–80
62. Dong Q, Hu B, Zhang C. 2022. microRNAs and their roles in plant development. *Frontiers in Plant Science* 13:824240
63. Lehretz GG, Sonnewald S, Hornyik C, Corral JM, Sonnewald U. 2019. Post-transcriptional regulation of FLOWERING LOCUS T modulates heat-dependent source-sink development in potato. *Current Biology* 29(10):1614–24
64. Xie F, Frazier TP, Zhang B. 2011. Identification, characterization and expression analysis of microRNAs and their targets in the potato (*Solanum tuberosum*). *Gene* 473(1):8–22
65. Zhang R, Marshall D, Bryan GJ, Hornyik C. 2013. Identification and characterization of miRNA transcriptome in potato by high-throughput sequencing. *PLoS One* 8(2):e57233
66. Lakhota N, Joshi G, Bhardwaj AR, Katiyar-Agarwal S, Agarwal M, et al. 2014. Identification and characterization of miRNAome in root stem leaf and tuber developmental stages of potato (*Solanum tuberosum* L.) by high-throughput sequencing. *BMC Plant Biology* 14:6
67. Guo G, Liu X, Sun F, Cao J, Huo N, et al. 2018. Wheat miR9678 affects seed germination by generating phased siRNAs and modulating abscisic acid/gibberellin signaling. *The Plant Cell* 30(4):796–814
68. Villordon A, LaBonte D, Solis J, Firon N. 2012. Characterization of lateral root development at the onset of storage root initiation in 'Beauregard'sweetpotato adventitious roots. *HortScience* 47(7):961–68
69. Villordon AQ, La Bonte DR, Firon N, Kfir Y, Pressman E, et al. 2009. Characterization of adventitious root development in sweetpotato. *HortScience* 44(3):651–55
70. Firon N, LaBonte D, Villordon A, Kfir Y, Solis J, et al. 2013. Transcriptional profiling of sweetpotato (*Ipomoea batatas*) roots indicates down-regulation of lignin biosynthesis and up-regulation of starch biosynthesis at an early stage of storage root formation. *BMC Genomics* 14:460
71. Lee JJ, Kim YH, Kwak YS, An JY, Kim PJ, et al. 2015. A comparative study of proteomic differences between pencil and storage roots of sweetpotato (*Ipomoea batatas* (L.) Lam.). *Plant Physiology and Biochemistry* 87:92–101
72. Morales A, Ma P, Jia Z, Rodríguez D, Vargas IJP, et al. 2025. Evolution of sweet potato (*Ipomoea batatas* [L.] Lam.) Breeding in Cuba. *Plants* 14(13):1911
73. Cao X, Xie H, Song M, Lu J, Ma P, et al. 2023. Cut–dip–budding delivery system enables genetic modifications in plants without tissue culture. *The Innovation* 4(1):100345
74. Dong T, Zhu M, Yu J, Han R, Tang C, et al. 2019. RNA-Seq and iTRAQ reveal multiple pathways involved in storage root formation and development in sweet potato (*Ipomoea batatas* L.). *BMC Plant Biology* 19:136
75. Tang C, Han R, Zhou Z, Yang Y, Zhu M, et al. 2020. Identification of candidate miRNAs related in storage root development of sweet potato by high throughput sequencing. *Journal of Plant Physiology* 251:153224
76. Tanaka M, Takahata Y, Nakayama H, Nakatani M, Tahara M. 2009. Altered carbohydrate metabolism in the storage roots of sweetpotato plants overexpressing the SRF1 gene, which encodes a Dof zinc finger transcription factor. *Planta* 230:737–46
77. Noh SA, Lee HS, Huh EJ, Huh GH, Paek KH, et al. 2010. SRD1 is involved in the auxin-mediated initial thickening growth of storage root by enhancing proliferation of metaxylem and cambium cells in sweetpotato (*Ipomoea batatas*). *Journal of Experimental Botany* 61(5):1337–49
78. Noh SA, Lee HS, Kim YS, Paek KH, Shin JS, et al. 2013. Down-regulation of the *lEXPT1* gene enhanced storage root development in sweetpotato. *Journal of Experimental Botany* 64(1):129–42
79. He S, Wang H, Hao X, Wu Y, Bian X, et al. 2021. Dynamic network biomarker analysis discovers lbnAC083 in the initiation and regulation of sweet potato root tuberization. *The Plant Journal* 108(3):793–813
80. Wang D, Li C, Liu H, Song W, Shi C, et al. 2024. Sweetpotato sucrose transporter *lBSUT1* alters storage roots formation by regulating

- sucrose transport and lignin biosynthesis. *The Plant Journal* 120(3):950–65
81. Singh V, Sergeeva L, Ligterink W, Aloni R, Zemach H, et al. 2019. Gibberellin promotes sweetpotato root vascular lignification and reduces storage-root formation. *Frontiers in Plant Science* 10:1320
 82. Wang QM, Zhang LM, Guan YA, Wang ZL. 2006. Endogenous hormone concentration in developing tuberous roots of different sweet potato genotypes. *Agricultural Sciences in China* 5(12):919–27
 83. Tanaka M, Kato N, Nakayama H, Nakatani M, Takahata Y. 2008. Expression of class I *knotted1*-like homeobox genes in the storage roots of sweetpotato (*Ipomoea batatas*). *Journal of plant physiology* 165(16):1726–35
 84. Matsuo T, Mitsuzono H, Okada R, Ito S. 1988. Variations in the levels of major free cytokinins and free abscisic acid during tuber development of sweet potato. *Journal of Plant Growth Regulation* 7:249–58
 85. Li H, Wang JQ, Liu Q. 2020. Photosynthesis product allocation and yield in sweet potato with spraying exogenous hormones under drought stress. *Journal of Plant Physiology* 253:153265
 86. Mathura SR, Sutton F, Bowrin V. 2023. Characterization and expression analysis of *SnRK2*, *PYL*, and *ABF/AREB/ABI5* gene families in sweet potato. *PLoS One* 18(11):e0288481
 87. Wan H, Ren L, Ma J, Li Y, Xu H, et al. 2023. Sweet potato gibberellin 2-oxidase genes in the dwarf phenotype. *Scientia Horticulturae* 313:111921
 88. Xing M, He M, Deng S, Zhang Y, Zhu H. 2025. Identification and functional characterisation of the gibberellin-inactivating enzyme, *IbCYP714A1*, in sweetpotato. *Plant Physiology and Biochemistry* 226:109973
 89. Park SC, Kim HS, Lee HU, Kim YH, Kwak SS. 2019. Overexpression of *Arabidopsis YUCCA6* enhances environment stress tolerance and inhibits storage root formation in sweetpotato. *Plant Biotechnology Reports* 13:345–52
 90. Xue L, Wang Y, Fan Y, Jiang Z, Wei Z, et al. 2024. *IbNF-YA1* is a key factor in the storage root development of sweet potato. *The Plant Journal* 118(6):1991–2002
 91. Li C, Song W, Wang D, Li C, Tang W, et al. 2025. The *IbMYB52/IbARF11L-IbDRM1* module negatively regulates the root development of sweetpotato. *Plant Physiology and Biochemistry* 14:110250
 92. Kang C, He S, Zhai H, Li R, Zhao N, et al. 2018. A sweetpotato auxin response factor gene (*IbARF5*) is involved in carotenoid biosynthesis and salt and drought tolerance in transgenic *Arabidopsis*. *Frontiers in Plant Science* 9:1307
 93. Mathura SR, Sutton F, Bowrin V. 2023. Genome-wide identification, characterization, and expression analysis of the sweet potato (*Ipomoea batatas* [L.] Lam.) *ARF*, *Aux/IAA*, *GH3*, and *SAUR* gene families. *BMC Plant Biology* 23:622
 94. Huang Z, Wang Z, Li X, He S, Liu Q, et al. 2021. Genome-wide identification and expression analysis of *JAZ* family involved in hormone and abiotic stress in sweet potato and its two diploid relatives. *International Journal of Molecular Sciences* 22:9786
 95. Zhang H, Zhang Q, Zhai H, Gao S, Yang L, et al. 2020. *IbBBX24* promotes the jasmonic acid pathway and enhances fusarium wilt resistance in sweet potato. *The Plant Cell* 32(4):1102–23
 96. Ružička K, Ljung K, Vanneste S, Podhorská R, Beeckman T, et al. 2007. Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. *The Plant Cell* 19(7):2197–212
 97. Hannapel DJ. 2013. A perspective on photoperiodic phloem-mobile signals that control development. *Frontiers in Plant Science* 4:295
 98. Mathura SR. 2023. Deciphering the hormone regulatory mechanisms of storage root initiation in sweet potato: challenges and future prospects. *AoB Plants* 15(3):plad027
 99. Kondhare KR, Kumar A, Hannapel DJ, Banerjee AK. 2018. Conservation of polypyrimidine tract binding proteins and their putative target RNAs in several storage root crops. *BMC Genomics* 19:124
 100. Natarajan B, Kondhare KR, Hannapel DJ, Banerjee AK. 2019. Mobile RNAs and proteins: Prospects in storage organ development of tuber and root crops. *Plant Science* 284:73–81
 101. Koda Y, Okazawa Y. 1983. Characteristic changes in the levels of endogenous plant hormones in relation to the onset of potato tuberization. *Japanese Journal of Crop Science* 52(4):592–97
 102. Chen C, Chen H, Zhang Y, Thomas HR, Frank MH, et al. 2020. TBtools: an integrative toolkit developed for interactive analyses of big biological data. *Molecular Plant* 13(8):1194–202
 103. Dai X, Zhao PX. 2011. psRNATarget: a plant small RNA target analysis server. *Nucleic Acids Research* 39:w155–w159
 104. Fladung M. 1993. Influence of the indoleacetic acid-lysine synthetase gene (*iaaL*) of *Pseudomonas syringae* subsp. *savastanoi* on yield attributes of potatoes. *Plant Breeding* 111:242–45
 105. Kim JI, Baek D, Park HC, Chun HJ, Oh DH, et al. 2013. Overexpression of *Arabidopsis YUCCA6* in potato results in high-auxin developmental phenotypes and enhanced resistance to water deficit. *Molecular Plant* 6(2):337–49
 106. Kolachevskaya OO, Sergeeva LI, Floková K, Getman IA, Lomin SN, et al. 2017. Auxin synthesis gene *tms1* driven by tuber-specific promoter alters hormonal status of transgenic potato plants and their responses to exogenous phytohormones. *Plant Cell Report* 36:419–35
 107. Kloosterman B, Visser RGF, Bachem CWB. 2006. Isolation and characterization of a novel potato *Auxin/Indole-3-Acetic Acid* family member (*StIAA2*) that is involved in petiole hyponasty and shoot morphogenesis. *Plant Physiology and Biochemistry* 44(11–12):766–75
 108. Gális I, Macas J, Vlasák J, Ondřej M, Van Onckelen HA. 1995. The effects of an elevated cytokinin level using the *ipt* gene and *N*⁶-benzyladenine on single node and intact potato plant tuberization *in vitro*. *Journal of Plant Growth Regulation* 14:143–50
 109. Liu S, Wang Y, Li L, Yan L, Wang X, et al. 2025. *StSN2* enhances tuber formation in potato via upregulating of the ABA signaling pathway. *Frontiers in Plant Science* 16:1566237



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