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Tuber and Tuberous Root Development

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Keywords

potato, sweetpotato, cassava, tuber, storage root, development

Abstract

Root and tuber crops have been an important part of human nutrition since the early days of humanity, providing us with essential carbohydrates, proteins, and vitamins. Today, they are especially important in tropical and subtropical regions of the world, where they help to feed an ever-growing population. Early induction and storage organ size are important agricultural traits, as they determine yield over time. During potato tuberization, environmental and metabolic status are sensed, ensuring proper timing of tuberization mediated by phloem-mobile signals. Coordinated cellular restructuring and expansion growth, as well as controlled storage metabolism in the tuber, are executed. This review summarizes our current understanding of potato tuber development and highlights similarities and differences to important tuberous root crop species like sweetpotato and cassava. Finally, we point out knowledge gaps that need to be filled before a complete picture of storage organ development can emerge.

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BIOLOGY AND AGRICULTURAL IMPORTANCE OF ROOT AND TUBER CROPS

Root and Tuber Crops Are Botanically Diverse and Indispensable for Human Nutrition

Plant organogenesis can create fascinating shapes and sizes. This is especially true for root and tuber crops, which can form all kinds of underground storage structures like tubers (e.g., potato), taproots (e.g., yam, carrot), tuberous roots (e.g., cassava, sweetpotato), hypocotyl/root transition structures (e.g., turnip), rhizomes (e.g., ginger, topinambur), corms (e.g., taro), and many more

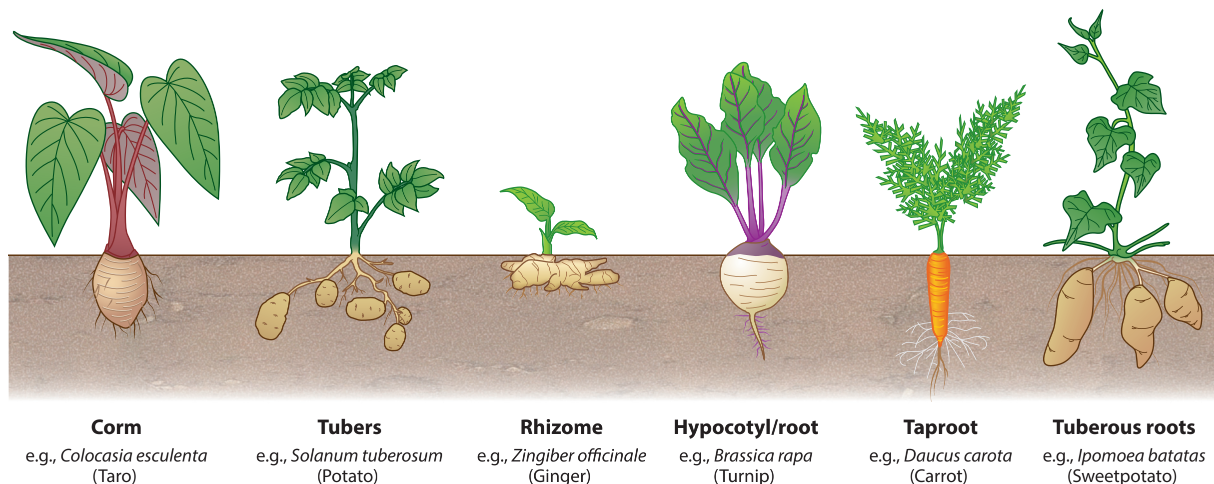


Figure 1

Examples of different storage organs within root and tuber crops. Thickening of the stem base results in corms in plants like *Colocasia esculenta* (taro). Tubers are formed on stolons, a modified stem structure found in plants like *Solanum tuberosum* (potato). Rhizomes are horizontally growing underground stems found in plants like *Zingiber officinale* (ginger). Beets and turnips, like *Brassica rapa*, develop from thickening hypocotyls and/or roots. Plants like *Daucus carota* (carrot) enlarge their roots to form a single taproot. Several tuberous roots can develop from thickening filamentous roots in plants like *Ipomoea batatas* (sweetpotato).

(**Figure 1**). Despite their morphological diversity, root and tuber crops have one thing in common: They contain high amounts of water and carbohydrates as well as varying levels of protein and vitamins. This fact makes root and tuber crops indispensable for human nutrition. In particular, potato (*Solanum tuberosum*), sweetpotato (*Ipomoea batatas*), and cassava (*Manihot esculenta*) are consumed by billions of people and are among the most important food crops worldwide. The global production in 2018 for potato, sweetpotato, and cassava was approximately 368, 91, and 277 megatons, respectively.[1] Sweetpotatoes are very nutritious with high levels of carbohydrates, proteins, and fibers. They are an excellent source of vitamin C, vitamin E, and pantothenic acid, as well as provitamin A (beta-carotene), which gives sweetpotato its bright orange color. Potato tubers are rich in carbohydrates and proteins, as well as minerals and vitamins (B6 and C). Cassava roots contain less protein and vitamins but are an excellent source of energy as they are extremely rich in starch. Cassava storage roots can contain up to 85% starch based on root dry weight (15).

The potato plant belongs to the nightshade family *Solanaceae*, and the vegetable is grown as an annual crop. Potato plants can be very productive, yielding more than 40 tons per hectare within 4 months after planting, if grown in a temperate climate and with proper irrigation.[2] However, potato suffers from heat-induced reduction in tuber yield (92). In tropical and subtropical regions of the world, sweetpotato and cassava are grown more widely than potato. Sweetpotato and cassava are tropical perennial plants that are often cultivated as annual crops. While cassava only grows in tropical climates, sweetpotato is also grown in climates that are more temperate. Cassava belongs to the family *Euphorbiaceae* and is a rather undemanding plant with respect to soil

[1]This information was taken from the FAOSTAT database (47) using the following search parameters: "All Countries", "Yield", "Potato", "Sweetpotato", "Cassava", and "2018".
[2]This information was taken from the FAOSTAT database (47) using the following search parameters: "All Countries", "Yield", "Potato", and "2019+2018+2017".

quality and supply of fertilizer. Yet, it can be extremely productive under favorable growth conditions. The woody shrub can grow up to 5 meters in height and form several starchy storage roots with a total root yield of up to 80 tons per hectare within approximately 12 month of planting (59). Sweetpotato shares a taxonomic order with potato, the *Solanales*, but belongs to the *Convolvulaceae* rather than the nightshade family. Under optimal agronomic conditions and irrigation, sweetpotato reaches similar levels of productivity as potato (approximately 40 tons per hectare within 4 months after planting).[3]

While potato and sweetpotato storage organs look similar at first glance, they are botanically very different. In contrast to the tuber-forming potato, sweetpotato produces a tuberous root (also known as storage root) that develops from fibrous roots. Potato and sweetpotato plants can reproduce sexually through flowering and seed production or asexually through storage organ formation, as both potato tubers and sweetpotato storage roots are able to regrow a new shoot that eventually develops into a new plant. Plants have evolved vegetative reproduction strategies to bridge adverse conditions, like winter or extended periods of heat and drought. Like sweetpotato, the storage root of cassava develops from its fibrous roots. In contrast to potato and sweetpotato, the storage root of cassava is unable to produce a new plant by itself. However, it also serves as an organ to withstand adverse conditions. During the tropical dry season, the plant sheds its leaves to conserve water. With the onset of the subsequent rainy season, the plant stem sprouts new leaves. The storage root remobilizes energy reserves from starch to support the new growth.

Morphological Changes During Storage Organ Formation

Storage root and tuber formation is initiated in an underground precursor organ. Potato tubers are formed from a specialized shoot, termed stolon. Hence, they are modified stems originating from the plants' main stem in response to endogenous and environmental signals. The development of a potato tuber undergoes different phases: (*a*) stolon induction and initiation, (*b*) stolon elongation and branching, (*c*) cessation of the longitudinal stolon growth, (*d*) tuber induction by swelling of the stolon subapical region, and (*e*) tuber growth and enlargement (141). These growth processes can be observed similarly in vivo and in vitro, yet with a different timing and final growth potential (154). In vitro tuberization assays showed continued stolon elongation for approximately 4 days by cell division of meristem-like cell files along their transversal axis in the stolon tip. After 5 days in vitro, cell divisions in the stolon tip stopped and stolon swelling was initiated in the subapical region of the stolon tip. Cell divisions now occurred along the longitudinal axis of pith and cortex cells up to a diameter of approximately 8 mm, the size at which in vitro tuberization ceases (154).

In vivo tuberization also starts from a hooked and unswollen stolon (154) (**Figure 2*a***). The central pith tissue in the subapical region slightly swells, resulting in arc-shaped vascular bundles in this region (154) (**Figure 2*b***). At this early stage, a regular circle of xylem tissue with external and internal phloem is observed (154) (**Figure 2*e*,*f***). Further tuber expansion is mostly driven by expansion of the perimedullary zone (154) (**Figure 2*c*,*d***), which establishes around the vasculature. With increasing thickness of this zone, the vascular tissue becomes more irregular and the xylem and phloem cells are scattered in the whole perimedullary region (154) (**Figure 2*b*–*d***). Groups of meristem-like, isodiametric cells form in the perimedullary region with a few xylem and

[3]This information was taken from the FAOSTAT database (47) using the following search parameters: "All Countries", "Yield", "Sweetpotato", and "2019+2018+2017".

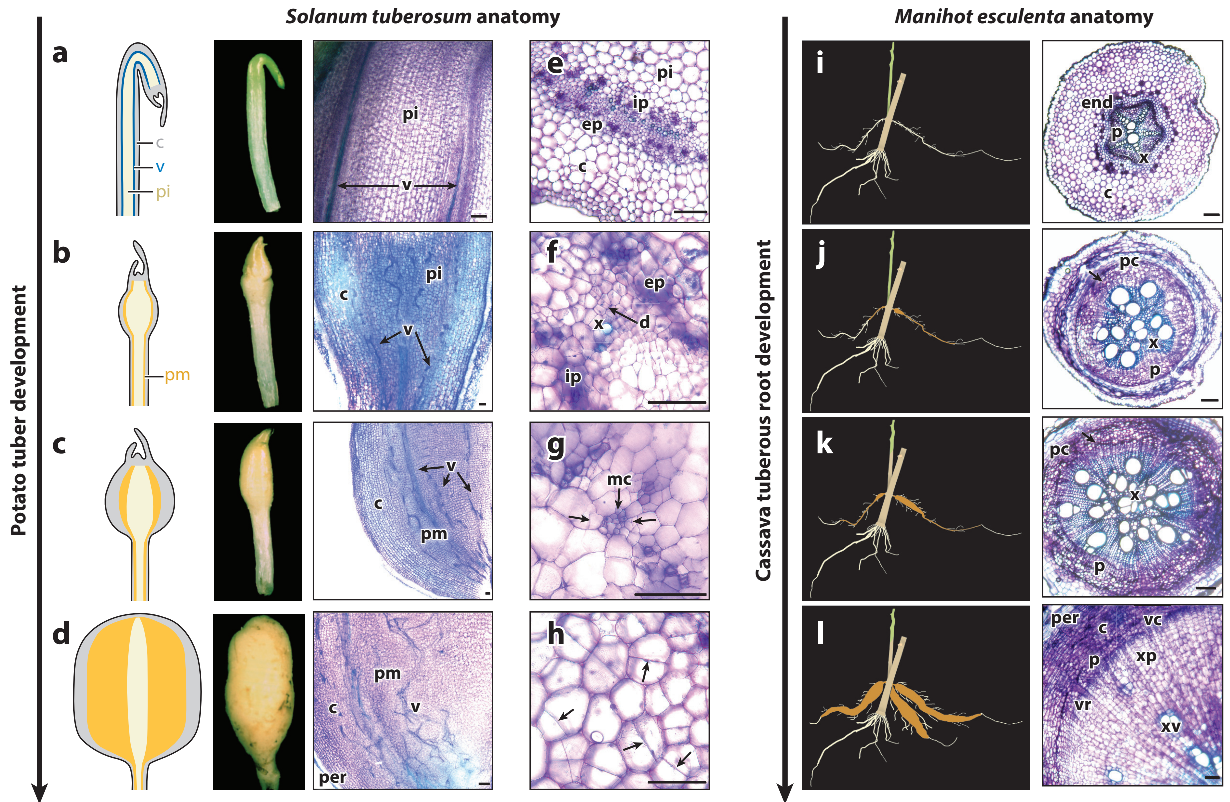


Figure 2

Storage organ formation in potato and cassava. (*a–d*) Potato tuberization stages and corresponding longitudinal sections: (*a*) Hooked stolon prior to stolon swelling: Central pith tissue and regular shaped vasculature can be observed. (*b*) Initial stolon swelling in the subapical region: Beginning extension of the central pith tissue, resulting in arc-shaped vascular bundles (*arrows*), and limited extension of the outer cortex tissue and first signs of vascular tearing can be observed. (*c*) Progressing stolon swelling: Further stolon swelling with an establishing perimedullary zone and increasing vascular tearing (*arrows*) can be observed. (*d*) Small tuber forming on the distal end of the stolon: An extended perimedullary zone with scattered vasculature and an established periderm can be observed. (*e–h*) Cross sections of different stolon/tuber stages: (*e*) Stolon prior to swelling displaying ring-shaped vasculature with external and internal phloem. (*f*) Vasculature enlargement of panel *e* showing external/internal phloem, xylem, and dividing cells. (*g*) Enlargement of the perimedullary zone showing meristematic clusters (*arrows*). (*h*) Randomly orientated cell division planes (*arrows*) occurring in the swollen stolon/early tuber. (*i–l*) Different stages of storage organ formation in cassava and corresponding cross sections: (*i*) Basal- and nodal-derived fibrous roots emerging from a stem cutting: A star-shaped central vascular cylinder containing alternating phloem and xylem areas surrounded by an intact endodermis can be observed. (*j*) Brown coloring, stiffening, and first signs of root swelling: An extending central xylem pushing cells toward the yet intact endodermis and a layer of procambial cells (*arrow*) surrounding the primary xylem and phloem cells can be observed. (*k*) Progressive tuberous root filling from the proximal end of the root: The expanding central xylem has torn the surrounding endodermis, and the procambium has established as a ring-shaped structure. (*l*) Enlarging storage roots with fully established secondary growth anatomy: A protective periderm surrounds the cortex area containing the secondary phloem, followed by the vascular cambium, which creates new secondary phloem and xylem cells. Vascular rays bridge the phloem and the root core, ensuring continuous connection of the phloem and xylem systems. The root core consists almost exclusively of starch-storing xylem parenchyma cells and water-transporting xylem vessels. All scale bars indicate 100 μm. Abbreviations: c, cortex; d, dividing cells; end, endodermis; ep, external phloem; ip, internal phloem; mc, meristematic cluster; p, phloem; pc, procambium; per, periderm; pi, pith; pm, perimedullary region; v, vasculature; vc, vascular cambium; vr, vascular ray; x, xylem; xp, xylem parenchyma cells; xv, xylem vessel.

phloem elements in the center (154) (**Figure 2*g***). Several layers of enlarging parenchyma cells are surrounding them. The outermost layer consists of mature parenchyma cells filled with starch granules. When the tuber diameter has reached approximately 8 mm, further tuber enlargement is boosted by growth in the perimedullary zone until the tuber reaches its final size, although some tangential cell divisions still occur in the cortical cells to enable further expansion of the tuber. Cell divisions in the meristematic cells, in the enlarging cells, and in the mature cells now appear randomly oriented (154) (**Figure 2*h***). Potato also develops a protective periderm on the tuber surface (**Figure 2*d***). The periderm is formed through a secondary meristem cork cambium or phellogen. Recent reports indicate that the potato phellogen is similar to the vascular or cork cambium of tree species (142).

Since sweetpotato and cassava are often planted from stem cuttings, the development of sweetpotato and cassava tuberous roots starts from stem nodal–derived adventitious roots that enlarge and form starch-containing storage roots (26, 86) (**Figure 2*i–l***). They are characterized by a central vascular cylinder containing star-shaped xylem, with alternating phloem and parenchyma cells (**Figure 2*i***), and the vascular cylinder is confined by an endodermis (9, 26, 90) (**Figure 2*i,j***). Upon induction of tuberous root formation, central parenchyma cells start to divide and enlarge, forcing protoxylem cells outward (**Figure 2*j,k***). A procambium is established between the phloem and xylem cells, which gradually forms a complete cylinder (**Figure 2*j,k***). With increasing rates of cell division and expansion within the vascular cylinder, the endodermis of the cylinder becomes stretched and disorganized over time (**Figure 2*k***). Cells in the root cortex increase in number to accommodate the widening circumference of the growing organ. The fully grown storage roots of sweetpotato and cassava show a comparatively narrow cortex region, which is protected by a periderm. The periderm increases in thickness by a phellogen, which remains active throughout the season, forming new cells to replace those sloughed off as the surface of the fleshy root expands. A ring-shaped vascular cambium (built from the former procambium) follows the cortex area and separates it from the central core of storage parenchyma (**Figure 2*l***). These morphological changes were described in several studies (9, 26, 90, 97). However, there are also some notable differences between both species: Sweetpotatoes not only grow from their vascular cambium but also develop many secondary, circular cambia. These first appear close to the vascular cambium, only one cell wide, but subsequently the number of cell rows of this new cambium increases rapidly and forms a tangential band around it. During later development of the storage root, circular cambia can be observed throughout the storage root and produce xylem toward the center and phloem toward the periphery. An adult sweetpotato may contain hundreds of these small circular cambia (9). Cassava, in contrast, grows only from its vascular cambium. On the inward-facing side of the cambium, mostly xylem parenchyma and no phloem cells are formed. However, cassava displays a large number of vascular rays, connecting the outer phloem area of the root with the central xylem area (90). No vascular rays have been reported in sweetpotato, indicating that the vascular cells formed from the secondary cambia contribute to support the central root areas.

Taken together, potato is a stem-derived tuber that mostly grows from scattered meristematic clusters in a specific region of a former vasculature in the stolon tip by producing large parenchyma cells. Sweetpotato and cassava are fibrous root-derived tuberous roots, which establish a vascular cambium ring in the root. While cassava anatomy appears highly organized and the root continuously grows from its vascular cambium ring by building starch-storing xylem parenchyma cells, sweetpotato additionally forms a circular secondary cambium distributed within the root. All three root and tuber crops possess a phellogen, building a layer of protective periderm at their surface.

Common Physiological and Biochemical Changes During Storage Organ Development

The cellular restructuring occurring during the different stages of storage organ formation is also accompanied by physiological and biochemical alterations. Changes in the mode of phloem unloading seem to be a common change occurring during storage organ formation. Noninduced potato stolons and the fibrous roots of sweetpotato and cassava are initially characterized by the mode of apoplasmic unloading, in which sucrose and other assimilates have to be exported into and reimported from the apoplast by carrier proteins (84, 90, 140). However, at very early stages of tuberization and storage root formation, the apoplasmic mode switches to a symplasmic unloading transport mode mediated by plasmodesmata (PD). This switch could be demonstrated through fluorescent tracer studies for potato, sweetpotato, and cassava (84, 90, 140). This transition is accompanied by reduced cell wall invertase and increased sucrose synthase activities (8, 81, 90). The increase in sucrose synthase activity correlated with the accumulation of starch in storage organs of many plant species, indicating that it is an important determinant of sink strength (129, 161). Enhancing sucrose synthase activity in transgenic potato increased tuber starch levels and yield (12). Concurrently with the activation of sucrose synthase activity, genes involved in starch biosynthesis are transcriptionally activated (44, 139). It is well known that expression of starch biosynthesis genes is regulated by sugars and the circadian clock (19). A comparative transcriptome analysis in potato tubers revealed that starch genes, such as the granule-bound starch synthase, also show a diurnal rhythm that correlates with the sucrose supply from the leaves (44). Similarly, expression of starch biosynthetic genes is increased early during storage root initiation in sweetpotato and cassava, which is most likely fueled by an increased sucrose supply (45, 155).

Apoplasmic unloading: the export of assimilates from the phloem system into the surrounding cell wall space is achieved actively through transport proteins

Symplasmic unloading: the export of assimilates from the phloem system into adjacent cells is achieved passively via diffusion through plasmodesmata

Plasmodesmata (PD): nanoscale pores that connect the intracellular space of neighboring cells, facilitating exchange and transfer of macromolecules and signals

Source organs: organs that produce an excess of assimilates during photosynthesis, which can be exported to supply non-photosynthetic organs

RELATIVE SOURCE AND SINK STRENGTH AND NUTRIENT RATIOS INFLUENCE STORAGE ORGAN FORMATION

Control of Storage Organ Initiation Is Crucial for Plant Development

As sessile organisms, plants have evolved strategies to outlast unfavorable environmental conditions. While annual plants complete their life cycle from seed to seed within a single growing season, perennials have developed specialized storage organs to survive growth restrictions caused by conditions such as cold, drought, or heat. Storage organs are formed under favorable growth conditions and provide building blocks and energy for future growth and defense (24). During formation, storage organs represent strong sink tissues and compete with overall plant growth. Sink tissues, such as young leaves, roots, developing seeds, or storage organs, are net importers of assimilates. Assimilates are derived from source organs, such as mature leaves, which produce an excess of assimilates. In an elegant grafting experiment, Rapoport & Loomis (110) nicely demonstrated that sugar beet root stocks, having a high sink capacity, limit growth of grafted chard leaves, while chard root stocks, with a rather low sink strength, did not impair growth of grafted sugar beet leaves. This result suggests that sink strength of storage organs can override source demand and hence limit shoot growth. Sink-to-source relations are not static but change during development. Storage organs represent strong sinks during formation but turn into source tissues during mobilization of the stored reserves (112a). Under natural conditions, reduced shoot growth could impair assimilate acquisition and restrict storage organ growth due to reduced resource availability. Conversely, in the absence of storage sinks, photosynthesis is inhibited by end product accumulation. In this case, limitation of triose phosphate utilization results in a downregulation of photosynthesis to prevent over-reduction of chloroplasts and photooxidative damage. Under these conditions, plants cannot realize their full photosynthetic potential and may

not achieve their maximum biomass production and reproductive success (35). Based on these two considerations, proper timing of storage organ formation is important for overall plant performance. To determine the right timing, plants continuously monitor their environment and determine available time and resources for growth and storage organ and/or seed formation. This is achieved by integrating environmental signals including day length, light quality and intensity, water availability, and temperature and nutrient supply. In the last years, significant progress has been made in understanding signal perception and transduction of many environmental stimuli [recently reviewed by Lamers et al. (77)], and a central player for the integration of nutrient, environmental, and hormonal signals, TARGET OF RAPAMYCIN (TOR), has been described [recently reviewed by Wu et al. (150)]. One breakthrough in understanding the link between light and temperature sensing in leaves was the discovery that PHYTOCHROME B (PHYB) serves as a sensor for not only light but also temperature (67, 79). Deciphering this convergent signal transduction pathway provided the first mechanistic explanation for the observed similarities in growth responses to light and temperature signals. Environmental cues not only provide external signals to adjust plant growth but also directly influence plant metabolism. Solar energy together with atmospheric carbon dioxide provide energy and precursors for synthesis of organic carbon (C), which is used to fuel cellular processes in mesophyll cells. Converted into sucrose, excess C is allocated to other parts of the plant to provide building blocks for growth, defense, or storage. Sucrose serves not only as a nutrient but also as a signaling molecule in various developmental processes.

PHYTOCHROME B (PHYB): red light–absorbing photoreceptors involved in day-length and temperature perception

SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTER (SWEET): protein family that facilitates transport of sucrose and other sugars

SUCROSE TRANSPORTER (SUT): protein family that acts as H^+/sucrose symporters and that plays a prominent role in regulating source-to-sink sucrose transport; also abbreviated as SUC

Sink organs: organs dependent on assimilate import, as they are unable to produce a sufficient amount of assimilates themselves (e.g., roots, tubers)

Sugars Regulate Plant Growth and Development

Sucrose is the primary transport form of photoassimilates in most plants. In apoplasmic phloem loaders (such as *Arabidopsis thaliana*, potato, sweetpotato, and cassava), sucrose is produced in the cytosol of mesophyll cells and moves symplasmically from cell to cell via PD until it reaches the phloem parenchyma–companion cell border. Here, sucrose efflux carriers of the SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTER (SWEET) family are thought to facilitate efflux of sucrose into the apoplasm (29). From there, sucrose is actively transported into companion cells by the activity of the sucrose/H^+ symporter [SUCROSE TRANSPORTER (SUT, also abbreviated elsewhere as SUC)] (21, 112). This activity allows the generation of a concentration gradient and long-distance transport of sucrose via mass flow through the sieve elements to sink tissues. In potato, there are three SUT proteins (30). The high-affinity sucrose/H^+-symporter StSUT1 is mainly expressed in the loading phloem of mature leaves and is essential for long-distance transport of sucrose (111, 112). Moreover, StSUT1 is also expressed in sink tubers, where it most likely plays an important role during early stages of tuber development (75). StSUT2 and StSUT4 are more prominently expressed in sink organs and transport sucrose with low affinity (30). Strikingly, RNAi-mediated suppression of *StSUT4* in potato (ssp. *andigena*) resulted in shorter plants that flowered earlier and tuberized under noninductive conditions. This effect on potato development was accompanied by increased sucrose efflux and a higher expression of phloem-mobile tuberization signals (see the section titled Photoperiodic Control of Tuberization). As a possible mechanism to explain the observed molecular changes, a direct inhibition of StSUT1 activity by StSUT4 at the plasma membrane has been discussed (30). This inhibition would require colocalization of both transporters, which has recently been questioned (38, 120). While the underlying molecular details need to be deciphered, perturbation of *SUT* expression might cause changes in the subcellular distribution and signaling of sucrose. Sucrose signaling has been associated with flowering in several species (14, 31). In potato, external application of sucrose induces tuberization (153).

Plants Sense the C:N Ratio to Align Developmental Programs with the Environment

Besides C fixation, nutrient availability is a crucial regulator of plant development. In nonfertilized ecosystems (34), nitrogen (N) represents the most limiting nutrient. Given the crucial function of cellular C and N, it is not surprising that availability of both is sensed. As nonmotile organisms, plants sense C and N nutrient availability in their surroundings and adjust their developmental programs accordingly. C and N metabolism are tightly linked, and both nutrients are needed in balanced quantities. Therefore, plants have evolved systems monitoring C:N ratios. High C:N ratios in leaves indicate an imbalance in photosynthesis and N availability. This imbalance leads to an increased allocation of C from shoots to roots to support root growth and nutrient acquisition (48). At the same time, plants switch from vegetative growth to storage and reproduction, which is accompanied by leaf senescence (33). In contrast, low C:N ratios indicate sufficient N supply but limited photosynthesis. Under those conditions, shoot rather than root growth is supported, leading to a higher photosynthetic capacity (40, 105). The correlation between C:N ratios and tuberization dates back almost a century, when Wellensiek (148) observed that low C:N ratios delay tuberization. Thereafter, several studies have confirmed this observation [Zheng et al. (159) and references therein]. A link between N status and phytohormones in potato was established by Krauss & Marschner (74) in hydroponic cultures. Continuous supply of N abolished potato tuberization, which coincided with high gibberellin (GA) levels. Depleting N from hydroponic cultures resulted in low GA levels and stimulated tuberization. In subsequent studies, application of bioactive GA species substantiated the inhibitory role of GA during tuberization (104, 125). The role of GA was further supported by dwarf potato (ssp. *andigena*) mutants blocked in GA biosynthesis. These mutants form tubers under noninductive conditions, even though they were formed only after several months (138). Subsequent studies elucidated the role of the GA pathway in the tuberization pathway, as further discussed below and summarized elsewhere (113, 130).

C: carbon

N: nitrogen

GA: gibberellin

LEAF-DERIVED SIGNALS INITIATING STORAGE ORGAN FORMATION

Potato Tuber Formation as a Model to Study Storage Organ Development

Despite their importance as a food source, comparatively little is known about the development of root and tuber crops compared with cereal crops and about the signals that control storage organ formation (95). What little information we have on tuber crops comes from potato, which has become an important model for studying the development of storage organs (4, 42, 43, 52, 55, 113). During the last few decades, particular attention was given to processes related to tuberization, as maturity determines the potential yield of potato cultivars. In general, late-maturing cultivars have high yield potentials compared with early maturing ones. In light of expected climate change, however, drought and heat waves may negatively affect tuber quality and yield of late-maturing cultivars, providing advantages for early maturity cultivars that are able to escape adverse environmental conditions. Studying tuberization of potato plants not only will help to secure potato production under climate change conditions but also will drive a better understanding of storage organ formation in other plants (95).

More than 60 years ago, the first evidence for a leaf-derived tuber-forming stimulus (tuberigen) that is produced under inductive conditions and transported to the site of tuber formation was presented (25, 52). This finding raised the hypothesis that tuberization, similar to flowering, is controlled by the photoperiod (5, 63, 113). Further support for a mobile tuber-inducing signal came from experiments described by Chailakhyan et al. (23), demonstrating that grafting flowering tobacco scions onto nontuberizing potato rootstocks induced tuberization.

Potato Tuberization Is Day-Length Dependent

***Andigena* (*Solanum tuberosum* ssp. *andigena*):** wild relative strictly dependent on short day conditions for tuberization

LD: long day

SD: short day

Tuber formation is controlled by an interplay between environmental and endogenous signals and is orchestrated by transcriptional, metabolic, and structural changes. Day length, light quality, temperature, and the nutrient supply are the most important environmental cues that trigger signals in leaves that are transmitted to stolons to initiate the developmental program of tuber formation (62). Day length and temperature control ensures that tuber formation is completed at the end of the vegetation period to outlive adverse conditions during winter. Wild potatoes were domesticated approximately 8,000 years ago and were mainly cultivated in the Andes of South Peru in altitudes 2,000–4,000 m; these are regions characterized by (short) day lengths close to 12 h, high light intensities, and cool temperatures. Potato plants later spread to the southern latitudes of Argentina and Chile with longer summer days. This migration was accompanied by introgression and polyploidization and resulted in a long-day-adapted subgroup (*S. tuberosum* Chilotanum), which contributed much to the genetic background of all commercial genotypes (53, 56, 128). Taxonomically, the *S. tuberosum* group is divided into two cultivar groups based on morphological and genetic markers: *andigena* of upland Andean genotypes (*S. tuberosum* ssp. *andigena*) and *Chilotanum* (*S. tuberosum* ssp. *chilotanum*) representing lowland Chilean landraces (128). Modern tetraploid cultivars were selected to grow under moderate temperatures and to form tubers under long day (LD) conditions, but tuber formation is still accelerated under short day (SD) conditions (5, 53). Adaptation to LD conditions is considered to be the most important adaptation of European potato cultivars, as tuber formation in wild relatives such as *andigena* is strictly dependent on SD conditions (e.g., a photoperiod <12 h). *Andigena* species do not form tubers under LD or under SD interrupted by a light pulse during the dark period [also called night break (NB)] (76, 113). Based on its strict day-length dependence, *andigena* became the most prominent model to study (photoperiodic) tuberization signals (42, 113).

Photoperiodic Control of Tuberization

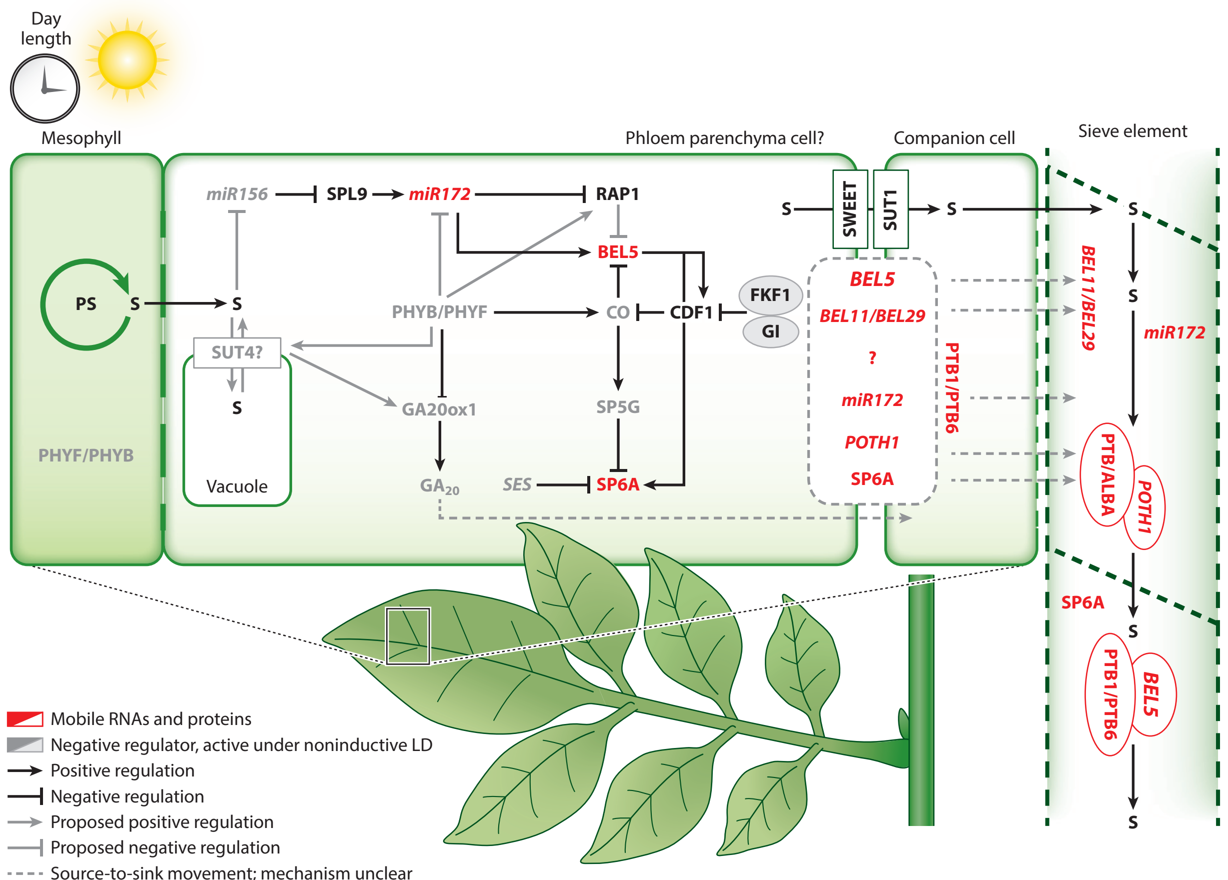
The photoperiod controls many aspects of plant development (63). Plants sense changes in day length as a seasonal indicator to regulate developmental transitions, such as induction of flowering, onset of bud dormancy, and outgrowth in trees as well as tuber formation in potatoes (10, 63, 123). The sensing mechanisms integrate light information in leaves with the circadian clock to produce a signal that is transmitted through the plant to stimulate a developmental transition. Among the examples mentioned, flower induction is the best studied, and the elucidation of the flowering pathway in *A. thaliana* paved the way for the identification of orthologous genes and signaling molecules involved in regulation of developmental transitions in other species. Analysis in *A. thaliana* placed the CONSTANS/FLOWERING LOCUS T (CO/FT) module at the center of a pathway that promotes flowering in response to changes in day length (60, 127, 137). FT was identified as florigen in *A. thaliana*. It is produced in leaves under inductive conditions and moves through the phloem to the shoot apex to induce flowering. To date, FT and FT-like proteins have been described in many different species. They appear to be conserved elements of flower induction and many other developmental processes, including storage organ formation (see section titled FT Proteins as Important Regulators of Storage Organ Formation). Activation of FT in response to photoperiod occurs via CO, a key transcription factor integrating information from the circadian clock and light perception.

Light signals are perceived by photoreceptors, and plants deploy multiple receptors, such as phytochromes, cryptochromes, phototropins, and members of the Zeitlupe family, to detect and respond to changes in light quality and duration (49). Phytochromes that respond to red

(R)/far-red (FR) light were the first molecular components identified, suggesting that tuberization is photoperiodically controlled. Thus, tuberization was diminished when long nights were interrupted by R light, and this effect was partially reversed by subsequent exposure to FR light (13). Further work revealed that *StPHYB* controls the photoperiod-dependent tuberization (64). Downregulation of *StPHYB* expression using an antisense approach induced tuberization in transgenic potato (ssp. *andigena*) plants under LD and SD+NB conditions. These results suggested that the tuberization pathway is activated in transgenic plants with reduced PHYB level. This conclusion was further substantiated by grafting experiments in which *PHYB* antisense plants triggered tuberization of wild-type stocks (65). This groundwork laid the first puzzle piece of the current tuberization model and demonstrated that PHYB acts as inhibitor of tuberization upstream of a SD-dependent regulatory pathway.

The understanding of the underlying processes has increased progressively, and the progress was continuously summarized in excellent review articles (4, 37, 42, 43, 55, 72, 113, 130). Here, we update the model by recently identified components and players (**Figure 3**).

Work by Zhou et al. (160) showed that potato harbors five phytochrome genes (named *StPHYA*, *StPHYB1*, *StPHYB2*, *StPHYE*, *StPHYF*) and that, in addition to StPHYB (= StPHYB1), StPHYF plays an essential role in the LD-mediated suppression of tuberization, most likely by forming a



(*Caption appears on following page*)

Figure 3 (*Figure appears on preceding page*)

Model depicting the regulation of potato tuber induction by leaf-derived mobile signals. The FT homolog SP6A and the *BEL5* mRNA are the two main mobile signals that are produced in the leaf and translocated via the sieve elements to stimulate tuberization. Their expression is regulated by environmental signals, such as day length, which is perceived by the endogenous clock and is induced by inductive SD conditions. Expression of SP6A is negatively controlled by CO, which transcriptionally activates the SP6A antagonist SP5G under noninductive LDs. Under these conditions, CO protein is stabilized by PHYB and PHYF, while CO transcription is increased through proteolytic degradation of CDF1, mediated by the FKF1/GI complex. Under SD, CDF1 evades degradation by FKF1, thereby inhibiting CO expression and indirectly activating SP6A. SP6A transcript abundance is also surveilled by the small RNA *SES*. Both SP6A and CDF are transcriptionally activated by BEL5, which acts in tandem with POTH1. BEL5 mRNA accumulation is under control of *miR172* (via RAP1) and PHYB. The mRNAs of *POTH1*, *BEL11*, *BEL29*, and *miR172* were also shown to be phloem mobile. *BEL5* and *POTH1* mRNA transport is facilitated by RNA-binding proteins such as PTB1/PTB6 or ALBA, while it is not yet known how the transport of SP6A is mediated. Sucrose is the primary transport form of photoassimilates, which not only serves as a substrate to fuel growth and starch production in the developing tuber but also signals a sufficient source capacity. This signal might be integrated via the *miR156*/SPL module into the photoperiodic pathway. Sugar transporters like SWEET and SUT1 and SUT4 regulate the sucrose availability. In addition, movement of GA_{20} as direct precursor of active GA has been proposed. Expression of many players of the pathway was assigned to the vasculature based on promoter reporter studies. However, the exact subcellular localization and how they reach the sieve elements remain unresolved, as illustrated by the faint dotted box and the question mark between phloem parenchyma cells and companion cells. Abbreviations: ALBA, ALBA-DOMAIN PROTEIN; BEL5, BELLRINGER-1 like 5; BEL11, BELLRINGER-1 like 11; BEL29, BELLRINGER-1 like 29; CDF1, CYCLING DOF FACTOR 1; CO, CONSTANS; FKF1, FLAVIN-BINDING KELCH REPEAT F-BOX PROTEIN 1; FT, FLOWERING LOCUS T; GA_{20}, gibberellin 20; GA20ox1, gibberellin 20-oxidase 1; GI, GIGANTEA; LD, long day; PHYB, PHYTOCHROME B; PHYF, PHYTOCHROME F; POTH1, POTATO HOMEOBOX 1; PS, photosynthesis; PTB1, POLYPYRIMIDINE TRACT-BINDING PROTEIN 1; PTB6, POLYPYRIMIDINE TRACT-BINDING PROTEIN 6; RAP1, RELATED TO APETALA2 1; S, sucrose; SD, short day; SES, SUPPRESSING EXPRESSION OF SP6A; SP5G, SELF PRUNING 5G; SP6A, SELF PRUNING 6A; SPL9, SQUAMOSA PROMOTER BINDING-LIKE 9; SUT1, SUCROSE TRANSPORTER 1; SUT4, SUCROSE TRANSPORTER 4; SWEET, SUGARS WILL EVENTUALLY BE EXPORTED.

heterodimer with PHYB. Both proteins may contribute to stabilize CONSTANS (CO/StCOL1) under LD conditions (3, 160).

In potato, *StCOL1* transcript peaks at dawn in LD and the protein accumulates to high levels (due to StPHYB and StPHYF activity), while under SD the transcript reaches its highest level in the dark and the protein is rapidly degraded (3, 51). This pattern regulates the expression of (at least) two downstream *FT* paralogs, namely SELF PRUNING 5G (*StSP5G*) and SELF PRUNING 6A (*StSP6A*). They belong to a small gene family consisting of five members in potato (96). According to the current model, StCOL1 directly activates expression of *StSP5G* by binding to a *CO* response element present in its promoter (3). In fact, the *SP5G* expression pattern in the leaves strongly correlates with that of *StCOL1*, and functional studies using transgenic plants with increased or decreased expression showed that both repress the expression of the mobile tuberization signal (3, 51, 96). In a breakthrough study by Navarro et al. (96), the mobile FT paralog StSP6A was identified as the key tuberization signal in potato. StSP6A is strongly expressed under inductive (SD) conditions in the vascular bundles of leaves and is transported through the phloem to stolons to induce tuberization (96, 122) (**Figure 3**). Under noninductive conditions, its expression is inhibited via StCOL1/SP5G. In addition, expression of *StSP6A* in the leaf is regulated by other factors. One of those is a small RNA, termed *SUPPRESSING EXPRESSION OF SP6A* (*SES*), which is highly expressed in juvenile stages of development and during heat stress and targets *StSP6A* mRNA for posttranscriptional degradation (80).

Another factor is the Zinc finger DOF family protein CYCLING DOF FACTOR 1 (StCDF1), which transcriptionally represses *StCOL1* under inductive conditions and thereby indirectly activates *StSP6A* (68). StCDF1 protein accumulation itself is controlled by the two clock proteins GIGANTEA (StGI) and FLAVIN-BINDING KELCH REPEAT F-BOX PROTEIN 1 (StFKF1), which bind to StCDF1 and mediate its proteolytic degradation in darkness (68) (**Figure 3**). Thereby, StCDF1 acts as mediator between the circadian clock and

the CO/FT module. Interestingly, allelic variation in the coding sequence of *StCDF1* allowed LD adaptation of European potato cultivars (53, 56, 68, 94). Modern European cultivars (Neotuberosum group) harbor allelic variants of the ancestral *StCDF1* (referred to as *StCDF1.1*) that evade binding of StFKF1 and their subsequent proteolytic degradation. Thus, these variants are expressed constantly during the day, allowing accumulation of StSP6A even under LD.

FT Proteins as Important Regulators of Storage Organ Formation

FT encodes the florigen that moves from leaves to the shoot apex to induced flowering as initially uncovered in *Arabidopsis* [reviewed by Turck et al. (137)]. Further work placed FT orthologs as universal regulators of flowering (108, 127, 149). These studies revealed that often several FT-like genes control flowering, which have overlapping or antagonistic function, e.g., in sugar beet and tobacco (57, 106). FT are small globular proteins that belong to the family of PHOSPHATIDYLETHANOLAMINE BINDING PROTEINS (PEBP) that is divided into three subfamilies: FT-like, TERMINAL FLOWER 1-like (TFL)/CENTRORADIALIS (CEN), and MOTHER OF FT (MFT)-like (5, 147). Besides flowering, FT-like proteins influence a wide range of developmental processes, such as vegetative growth, fruit set, bud dormancy, and storage organ formation (5, 107, 149). These findings suggest that FT plays a wider role in plant growth and development. Navarro et al. (96) first used the FT paralog from rice (HEADING DATE 3A) to demonstrate that FT-like proteins control not only flowering but also tuberization in potato and provided evidence that two different FT proteins in potato control tuberization and flowering. While a gene, *SELF PRUNING 3D* (*StSP3D*), stimulated flowering, StSP6A was shown to be the mobile signal that stimulates tuberization. In addition, evidence accumulated that StSP6A and other FT proteins control source-sink balance. Overexpression of a codon-optimized *StSP6A* gene in potato resulted in impaired shoot growth but accelerated tuberization (80). Moreover, tubers of these plants promoted the formation of new daughter tubers instead of sprouts, indicating a strong sink-forming capacity of StSP6A (80). Similarly, overexpression of tomato florigen (SlSFT) in transgenic tomato or tobacco was accompanied by early flowering, indicated by fewer leaflets with thinner stems and a reduced plant height at time of flowering (82). In these plants, sink organ formation (here the flower) was initiated before the source capacity was fully developed. The balance between SlSFT and SlSP3D, a TFL-like protein that acts as potent inhibitor of SlSFT, was subsequently shown to regulate flowering and growth by altering source-sink relations (121). These studies indicate that expression of FT and its transport is tightly controlled and adjusted to resource availability to determine the best time point for a developmental switch.

In addition to tuberization, FT-like proteins were recently shown to play a role in formation of other storage organs such as onion bulbs (78) and pseudobulbs in orchids (145). FT-like genes were identified in the genomes of sweetpotato and cassava (6, 95). Expression studies in cassava indicated that *MeFT1* is expressed in leaves without a clear-cut photoperiod response, while *MeFT2* is expressed in a photoperiod-dependent manner (6). Overexpression of MeFT1 induced early flowering but negatively affected storage root formation in grafting studies, indicating preferential sucrose flux toward reproductive organs (100). Transcriptome studies indicated a function of an FT homolog during tuberous root formation in *Calleria speciosa* (152). However, no functional evidence for the involvement of FT or FT-like genes in the formation of storage roots has been obtained until now.

Remarkably, a direct upregulation of the potato tuberization signal StSP6A by sucrose was reported by Abelenda et al. (2), and sucrose was also shown to promote flowering in different species (31). Recent work in the ornamental plant *Chrysanthemum morifolium* revealed that spraying leaves with sucrose accelerated flowering (131). Exogenous application of sucrose also complemented the

late flowering phenotype of *Arabidopsis* mutants such as *co* and *gi* but did not restore flowering time of the *ft* mutant (31, 101). This finding suggests that FT acts downstream of sucrose. Interestingly, the sugar transporter AtSWEET10 was found to be induced by FT in *Arabidopsis*, and ectopic expression of AtSWEET10 led to early flowering (7). Based on this finding, it can be speculated that sucrose serves as a metabolic signal linking FT expression to photosynthetic output. Subsequently, FT influences sucrose allocation by manipulating sucrose efflux into sink organs (31, 101).

BELL: BEL1-like homeodomain proteins

Mobile RNAs Contribute to Storage Organ Formation

The transcription factor BEL5 (BELLRINGER-1 like) is another player that serves as a signal in the tuberization pathway in potato. BEL5 was first identified as an interaction partner of the POTATO HOMEBOX1 (POTH1) transcription factor (28). Subsequent studies revealed that expression of *BEL5* mRNA increases in leaves under SD conditions and its mRNA moves long distances via the phloem through underground stolons and roots (11, 28, 83). *BEL5* is expressed in phloem parenchyma cells as shown by in situ hybridization and *promoter*::*GUS* fusion, as well as detection of its mRNA in laser dissected phloem parenchyma cells (11, 83). Movement was confirmed by both RNA analyses of different plant parts and heterografting experiments. The transport of the *BEL5* mRNA is facilitated by RNA-binding proteins of the POLYPYRIMIDINE TRACT-BINDING PROTEIN (PTB) family, which bind to the 3′ UTR (untranslated region) of the mRNA (32). This binding allows its movement and increases RNA stability. The movement of *BEL5* from leaves to distal organs was correlated with increased tuber yield (11) and, interestingly, also with increased root growth (83). The expression of the two PTB proteins important for *BEL5* binding, PTB1 and PTB6, is also induced by SD in leaves, and their expression was found to be restricted to phloem companion cells (32). Moreover, overexpression of either or both resulted in increased tuber yields, while downregulation reduced tuber formation (32). Two more members of the BELL transcription factor family of potato, StBEL11 and StBEL29, were recently described to be phloem mobile as well (50). Their RNA is produced in the vasculature of leaves, petioles, and stems and is translocated to stolons and roots, where they most likely negatively regulate StBEL5 targets (50). However, in stolons, both are also activated by StBEL5 (122), arguing against an important role as a long-distance signal. Likewise, POTH1 was shown to be expressed in phloem cells and to be phloem mobile (83, 87, 116). The *POTH1* mRNA is also stabilized and transported by RNA-binding proteins, and its movement is associated with stolon-to-tuber transition.

In addition to being translocated, it was postulated that *StBEL5* and *POTH1* mRNA is translated in leaves, where they together activate expression of StSP6A and StCDF1 by binding to specific elements in their promoters (72, 73, 122). In leaves, *BEL5* expression was also proposed to be regulated by PHYB via upregulation of *miR172* and its target, RELATED TO APETALA2 1 (RAP1) (88). The study by Martin et al. (88) proposed that RAP1 may repress *BEL5* and that, after upregulation of *miR172* under SD conditions, this suppression is released. An additional layer of control is imposed by an *miR172*-independent upregulation of RAP1 by PHYB directly that may allow fine-tuning of the tuberization signals via a feedback loop (88). Strikingly, *miR172*, as found in other plants, is controlled by the *miR156*/SQUAMOSA PROMOTER BINDING-LIKE (SPL) network, which determines the transition from juvenile to adult developmental stages (16, 143).

Both *miR172* and *miR156* were also reported to be phloem mobile (16, 88). While overexpression of *miR172* enabled transgenic potato (ssp. *andigena*) lines to form tubers under LD and accelerated tuberization under SD+NB (88), overexpression of *miR156* caused severe morphological alterations but did not support underground tuber formation (16). Instead, these transgenic plants formed aerial tubers only under SD (16, 41). Moreover, the typical reciprocal expression

pattern of both miRNAs as observed in *A. thaliana* and other species was seen in potato leaves but not in stolons. Thus, in leaves, *miR172* RNA levels increased under SD, while *miR156* RNA levels decreased with age and under SD conditions. In contrast, both miRNAs were reported to accumulate in stolons during tuber induction (16, 88). These results led to the hypothesis that *miR156* acts as a negative regulator of tuberization in leaves by suppressing *miR172* during juvenile stages of plant development but may have an additional function in stolons.

An interesting link between sugars and the juvenile-to-adult transition was recently provided by Yu et al. (156), who showed that expression of *miR156* was reduced by application of sucrose, glucose, or maltose, while sugar starvation increased its abundance. The authors demonstrated that sugars act as a signal to suppress *miR156* and progressively trigger the phase transitions, which seems to be an evolutionary conserved mechanism. The regulation of *miR156* by sugars appears as a developmental timer to ensure that a phase transition occurs under favorable conditions (157). This finding is consistent with reports that exogenous application of sucrose promotes flowering, while low sucrose levels result in a prolonged juvenile phase of tobacco plants (136). Similar to flowering, storage organ formation is coupled to sugar levels. The described activation of SP6A by sucrose in potato leaves might be initiated by decreased accumulation of *miRNA156* (**Figure 3**). These studies are in agreement with the hypothesis that developmental transitions require both metabolic competence and mobile protein and mRNA signals.

MOLECULAR MECHANISMS OF POTATO TUBER DEVELOPMENT

Potato Tuber Formation Is Associated with Changes in Sugar and Hormone Levels

Changes in the content of phytohormones are largely involved in the transition from an elongating stolon into a swelling stolon and finally in the formation of the tuber as a starchy storage organ. These changes are required to alter the pattern of cell division and to stimulate cell enlargement and metabolism to facilitate storage of starch and proteins.

GA is a key factor controlling different aspects of tuber formation, and its stimulating effect on potato stolon elongation was demonstrated more than 50 years ago (102–104). Exogenously applied GA stimulates potato stolon elongation but inhibits tuber formation, an effect that could be overcome by high concentrations of sucrose in vitro (153). The inhibitory effect of GA on tuberization was validated in transgenic potato plants with elevated or suppressed expression of the GA biosynthetic enzyme GIBBERELLIN 20-OXIDASE 1 (GA20ox1). Plants overexpressing *StGA20ox1* developed shoots with elongated internodes and displayed delayed tuberization, while plants with reduced expression of *StGA20ox1* had decreased internodes and tuberized earlier than control plants, demonstrating that shoot-derived GA inhibits tuber formation (22) **(Figure 3**). In contrast, transgenic potato (ssp. *andigena*) plants with increased expression of another biosynthesis gene, *StGA3ox2*, tuberized earlier under SD conditions (20). Both *StGA3ox2* and *StGA20ox1* contained high levels of GA_1 (the main bioactive GA species in potato) in the shoots but different levels of GA_{20}, the direct precursor of GA_1 and substrate of GA3ox2. To explain the conflicting results, it was proposed that GA_{20} might be mobile and is preferentially translocated from source leaves to aerial sinks, where it stimulates elongation, while less GA_1 is produced in the stolons by overexpression of GA3ox2 and thereby tuberization is favored. In addition to varying levels of shoot-derived GA, the hormone is also regulated in the stolon directly. StGA2ox1, a GA catabolizing enzyme, is upregulated in the stolon prior to visible swelling and is preferentially expressed in the subapical region of stolons and developing tubers. Its activity was proposed to decrease GA_1 levels in the subapical regions, which results in a stop of stolon elongation, a reorientation of the

plane of cell division, and a subsequent radial swelling of the subapical part of the stolon (70, 154). Overexpression of StGA2ox1 resulted in earlier tuberization, while downregulation of StGA2ox1 delayed tuberization (70). The *GA2ox* gene is therefore considered to be a primary tuber identity gene.

CK: cytokinin

Using an in vitro tuberization system, Xu et al. (153) demonstrated that the addition of auxin indole acetic acid (IAA) to a tuber-inducing medium led to earlier tuber initiation, while the addition of IAA together with GA led to retarded stolon growth under noninductive conditions. This result suggests the involvement of auxin in the transition from longitudinal growth to expansion growth occurring in early tuber stages. Consistent with this hypothesis, many genes related to auxin transport (PIN-FORMED, or PIN proteins), signaling, and response were differentially expressed during early tuber development (69). Further studies demonstrated that, upon the shift to tuber-inducing SD conditions, the basipetal auxin flux from the plant apex to the stolon is strongly reduced and that local auxin synthesis is initiated in the stolon apical meristem, leading to an accumulation of auxin in the stolon tip. Auxin transporting PIN proteins, which are subsequently activated, were thought to mediate the redistribution of auxins in the swelling stolon and allow the development of a new organ (117, 118). An additional hint for the tuberization promoting effect of auxins comes from another study, in which tuber-specific overexpression of an auxin synthesis enzyme stimulated tuber initiation in potato (71).

Auxins interact with cytokinin (CK), known for its stimulating effect on cell division and regulating meristematic activity (18). While auxin improved tuber growth, kinetin application mainly initiated new tubers, resulting in an increased tuber number (114). Likewise, expression of the CK biosynthesis gene *ISOPENTYL TRANSFERASE* (*IPT*) induced aerial stolons, promoted growth of underground stolons, and increased tuber number but reduced tuber weight and N content (133). Ectopic expression of the CK synthesis enzyme LONELY GUY 1 (LOG1) in tomato resulted in the formation of aerial minitubers, proving that CK promotes the expansion of meristematic tissues and may function as a universal regulator during storage organ formation (41).

While important, phytohormones alone are not sufficient to facilitate efficient development of storage organs. In vitro studies demonstrated that phytohormone action is influenced by assimilates, primarily sucrose. In fact, sucrose is the most abundant sugar in both the unswollen and swollen stolon, with a significantly higher concentration found in the latter, particularly close to the stolon tip (140). Thus, sucrose may act as a signal for tuber initiation, provide the main source of energy for tuber growth, and serve as a substrate for starch synthesis.

Simultaneous Regulation of SP6A and the KNOX/BELL Module Couples Sugars and Hormones

StSP6A and StBEL5 are most likely the two main phloem-mobile signals that are translocated from leaves to stimulate stolon swelling. As described above, tuber formation is associated with altered content of phytohormones. Strikingly, modulating the levels of StBEL5 and its interaction partner POTH1 caused an alteration in GA and CK levels (26, 110). A subsequent study confirmed binding of the StBEL5/StPOTH1 complex to the promoter of *GA20ox1*, which inhibits its expression and results in reduced GA levels in the stolon (27). To identify additional downstream target genes of StBEL5, Sharma et al. (122) utilized an ethanol-inducible expression system to induce StBEL5 in stolons and performed an RNA-Seq analysis. In particular, genes involved in hormonal regulation were found to be upregulated—for instance, the CK synthesis genes *LOG1–LOG3*, the GA-degrading gene *GA2ox1*, and genes coding for auxin-transporting *PINs* and signaling proteins [*AUXIN RESPONSE FACTOR8* (*ARF8*)]. In addition, the MADS-box gene *AGAMOUS-LIKE 8* (*AGL8*) and genes involved in cell division were stimulated. Notably, StBEL5 upregulated its own

expression, as well as the expression of *StSP6A* and *StCDF1* (73, 122). The promoter regions of both genes contain numerous TTGAC motifs that allow binding of the StBEL5/StPOTH1 complex, and mutations in the motifs rendered the promotors inactive. Based on this, the authors proposed that StBEL5 acts upstream of StSP6A and StCDF1 to regulate potato stolon-to-tuber transition. In addition, StBEL5 activates two further members of the *BELL* gene family, *StBEL11* and *StBEL29*, which were implemented as negative regulators of stolon-to-tuber development. All three BELL factors may act in concert to regulate a network leading to hormonal changes that facilitate altered cell division and growth during tuber formation (51).

TAC: tuberigen activation complex

Induction of StSP6A in stolons via an ethanol-inducible promotor activated a largely overlapping set of genes found during stolon-specific ethanol induction of StBEL5. These include *PIN*s, *ARF8*, *GA2ox1*, and *AGL8* (96). While StBEL5 and StPOTH1 directly act as transcriptional regulators, StSP6A appeared to be part of a functional tuberigen activation complex (TAC) that regulates a set of target genes. The formation of such a complex was proposed in analogy to the florigen activation complex (FAC). The FAC is formed in specific cells of the shoot apical meristem, where FT (arriving there as a mobile signal from leaves) interacts with the basic leucine Zipper transcription factor bZIP14, also called FD (FLOWERING LOCUS D) via 14-3-3 (134). The FT-FD complex functions as a transient flowering stimulus and activates floral identity genes, such as multiple MADS-box genes, to initiate an inflorescence meristem and to induce flowering (1, 115). Following the idea of an analogous TAC that initiates tuberization, Teo et al. (135) identified FD-like clones in potato and showed that StSP6A interacts with StFDL1 via St14-3-3 proteins. Functional studies in transgenic plants showed that RNAi-mediated inhibition of StFDL1 delayed tuberization, while early tuberization caused by StSP6A is dependent on binding to St14-3-3 proteins (135). Very recently, another player was identified, explaining further details of the mode of action of the TAC (158). Zhang et al. (158) demonstrated that, in addition to SP6A, a TFL1/CEN protein interacts with StFDL1 via 14-3-3 proteins and proposed that TFL1/CEN competes with SP6A in the TAC to antagonize the activation of tuber identity genes. Consequently, RNAi-mediated inhibition of TFL1/CEN accelerated tuberization. Using the SP6A promoter fused to a luciferase reporter, evidence was provided that SP6A itself is a target of the TAC complex. In addition to early tuber identity genes, such as MADS-box genes, a number of genes coding for germin-like proteins were upregulated in CEN-RNAi lines and are potential TAC targets (158). Germin-like proteins were described to locate at PD (among others) and to modulate assimilate allocation (54). Because during tuber development the mode of assimilate unloading switches toward PD-mediated symplasmic unloading, upregulation of genes with putative functions in regulating size exclusion of PD fits with these structural changes, but further studies are necessary to validate their function. Additional evidence for a role of StSP6A in regulating assimilate allocation toward the developing tubers comes from a study by Abelenda et al. (2). RNAi-mediated downregulation of sugar transporter StSWEET11 delayed tuberization, and constitutive overexpression of StSWEET11 resulted in aerial tubers and reduced tuberization. More importantly, StSP6A was shown to interact with StSWEET11, and its expression is induced by sucrose. Binding of StSWEET11 by StSP6A in phloem companion cells of stem and stolon blocks sucrose efflux into the apoplasm and thereby contributes to increased sucrose delivery toward the stolon (2) (**Figure 4**). This binding and the resulting block of sucrose efflux promote the switch of assimilate unloading toward the symplasmic pathway in the swelling stolon and place the FT protein StSP6A at a central position in controlling assimilate distribution. In contrast, the main function of StBEL5 might be to modulate expression of genes that change the hormonal homeostasis, which subsequently alters the mode of cell division (**Figure 4**). How StBEL5 and SP6A signaling pathways converge and how they affect each other remains to be elucidated.

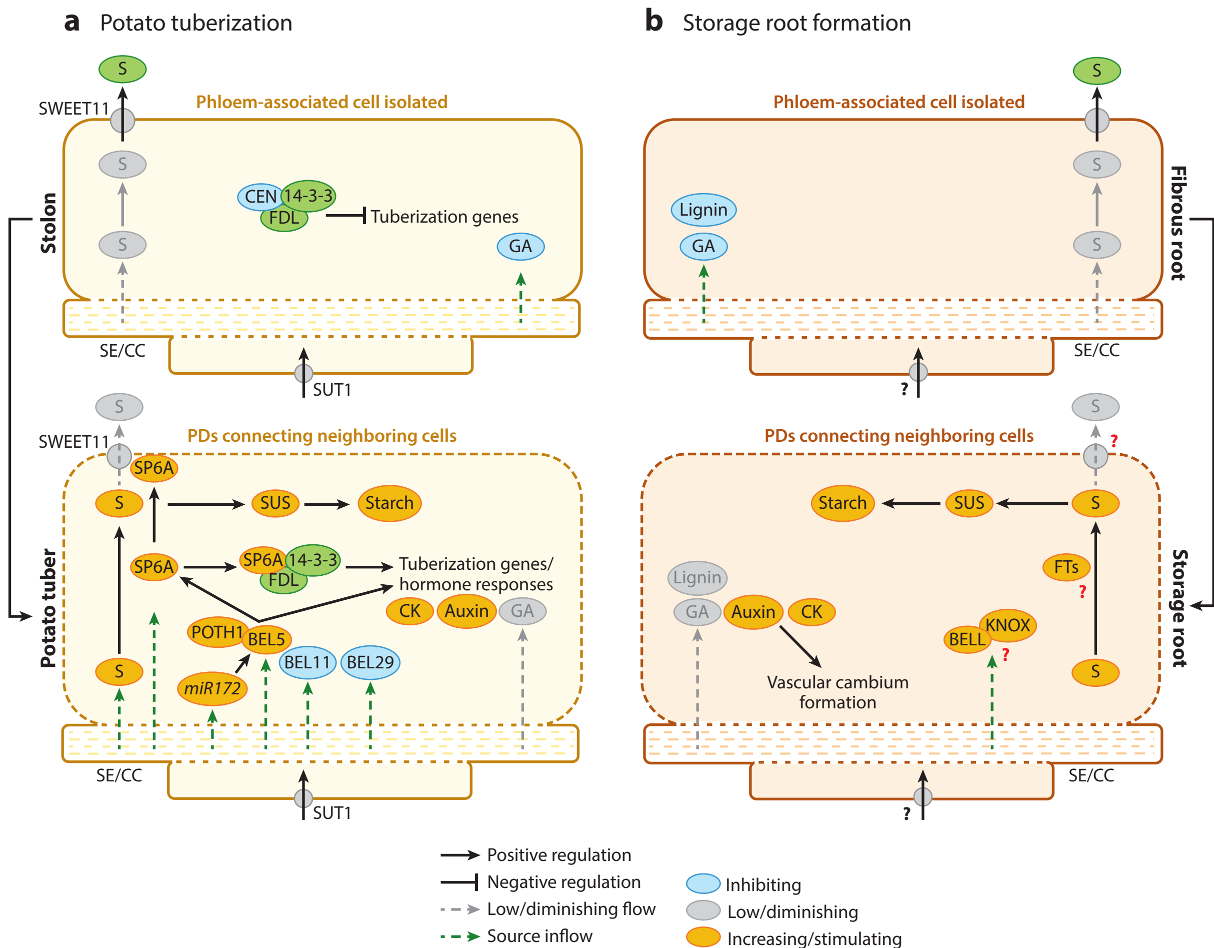


Figure 4

Overview of core regulation modules for storage organ formation. (*a*) Model of potato tuberization. The upper panel represents a potato stolon: Sucrose is exported into the apoplast by SWEET proteins, keeping a moderate intracellular sucrose concentration in the stolon. The CEN/FDL/14-3-3 protein complex suppresses expression of tuber identity genes. High levels of GA promote stolon elongation growth and inhibit tuberization in a phloem-associated cell. The lower panel represents a tuberizing stolon: Mobile RNAs (e.g., *miR172*, *POTH1*, *BEL5*, *BEL11*, *BEL29*) and mobile proteins (e.g., SP6A) arrive in phloem-associated cells near the stolon tip. SP6A binds to SWEET proteins in the stolon tip, thereby blocking the apoplasmic sucrose export and increasing the intracellular concentration. SP6A also replaces CEN, forming the tuber activation complex. Expression of BEL5 is stimulated by *miR172*, and the POTH1/BEL5 protein complex is formed. The tuber activation complex and the POTH1/BEL5 protein complex both activate similar sets of tuberization genes, resulting in reductions in GA levels, increased auxin, and increased CK signaling. The sum of these actions triggers cell division and expansion in the stolon tip, resulting in increasing amounts of symplasmically connected and starch-storing parenchyma cells. (*b*) Rudimentary model of storage root formation. The upper panel represents a fibrous root: Apoplasmic transport creates moderate sucrose levels in fibrous roots, and GA stimulates elongation growth and lignification. The lower panel represents a storage root: Storage root formation is triggered by yet unknown mechanisms, and the unloading mode switches to symplasmic transport that increases sucrose concentration and promotes starch accumulation via sucrose synthase. Reductions in GA levels and transient increases in auxin levels likely trigger vascular cambium formation. Subsequently, expansion growth is stimulated by increasing levels of CK. Abbreviations: BEL5, BELLRINGER-1 like 5; BEL11, BELLRINGER-1 like 11; BEL29, BELLRINGER-1 like 29; BELL, BELLRINGER-1 like homeodomain family; CC, companion cell; CEN, CENTRORADIALIS; CK, cytokinin; FDL, FD-like; FT, FLOWERING LOCUS T; GA, gibberellin; KNOX, KNOTTED1-LIKE HOMEOBOX; PD, plasmodesmata; POTH1, POTATO HOMEOBOX1; S, sucrose; SE, sieve element; SP6A, SELF PRUNING 6A; SUS, SUCROSE SYNTHASE; SUT1, SUCROSE TRANSPORTER1; SWEET11, SUGARS WILL EVENTUALLY BE EXPORTED 11.

REGULATORY MECHANISMS DURING STORAGE ROOT FORMATION

The development of tuberous roots (e.g., sweetpotatoes and cassava) starts with the transition of water- and nutrient-transporting fibrous roots to a bulky storage structure containing high amounts of starch-storing parenchyma cells. In contrast to potato tuberization, in which meristematic cells in the stolon undergo a transition to rather unorganized meristematic clusters, the root procambium develops toward a highly organized vascular cambium in root crop species. Cell division in the vascular cambium drives the lateral expansion of the storage root. The formation, patterning, and maintenance of the vascular cambium is regulated by phytohormones (especially auxin and CK) and ligand/receptor signaling, as well as various transcription factors. Briefly, the sum of these crosstalking and often noncell autonomous regulations specifies different root domains: vascular cambium stem cells maintain a pluripotent status to create transient amplifying daughter cells, which can differentiate into either phloem cells or xylem cell types. To date, developmental studies on the vascular cambium have mostly focused on *Arabidopsis* and poplar, and the knowledge achieved so far has been recently described in excellent reviews (46, 109).

Auxin Signaling Mediates Early Swelling and Cellular Restructuring in Storage Roots

One of the first key players in vascular cambium development is the phytohormone auxin. Auxin is transported rootward from the shoot via polar transport mechanisms governed by PIN proteins. Hormone distribution analyses in *Populus trichocarpa* stem cross sections demonstrated a peak of auxin in the vascular cambium (61). The resulting auxin gradient is believed to provide spatial information to cambial stem cells and their daughters, with high concentrations signaling cell division, intermediate concentrations signaling cell expansion, and low concentrations signaling secondary wall formation (46). Gene expression studies provided indications that early and transient auxin signaling are also involved in the fibrous root-to-storage root transition in root crop species, as genes involved in auxin transport and signaling are transiently upregulated in early stages of storage root formation (126, 146). An auxin-responsive MADS-box transcription factor *IbSRD1* was identified in sweetpotato, enhancing the proliferation of metaxylem and cambium cells. The transcript was barely expressed in fibrous roots but strongly upregulated in the actively dividing cells in the early stages of storage root development. Overexpression of *IbSRD1* resulted in earlier thickening of storage roots, suggesting that the gene is involved in initial growth regulation of storage roots in an auxin-dependent manner (97). A subsequent study demonstrated that the *IbSRD1* promotor is auxin responsive (98). Auxin likely triggers vascular cambium formation in storage roots in a similar manner as that described in *Arabidopsis* and poplar (119a).

Storage Root Formation Is Accompanied by Reductions in Gibberellin Signaling and Lignification

While the principal regulatory mechanisms of vascular cambium formation are likely transferable between different species, differentiation of cambial daughter cells displays striking differences. Tree species, for instance, form predominantly xylem fiber cells and lignified xylem vessels, while root crop species mainly form starch-storing xylem parenchyma cells. In woody species, a peak of GA is observed on the xylem side of the cambium. GA promotes lignification and secondary wall formation as shown in several studies. This feature is already utilized in biotechnology to either increase or decrease the levels of woody tissue in the target species (17, 39, 151). Several findings from sweetpotato and cassava indicate that storage root formation is accompanied by marked reductions in GA signaling, an early prominent response that also occurs during potato

tuberization (see above). In addition, reductions in the root lignification response are reported, and in contrast to secondary growth in tree species, high levels of lignification appear to be detrimental to storage organ formation. Constitutive overexpression of a maize *LEAF COLOR* (*LC*) gene in sweetpotato stimulated lignin biosynthesis, which resulted in enhanced lignification of vascular cells in the early storage root, severely reducing storage root expansion (144). Genes involved in lignification are strongly downregulated in early stages of the transition from fibrous roots to storage roots in sweetpotato and cassava (45, 126). Exogenous application of GA to sweetpotato shoots stimulated stem elongation and increased root GA levels. Consequently, starch biosynthesis genes were downregulated, while lignin biosynthesis genes were upregulated. Root lignification was enhanced, resulting in reduced storage root expansion (124). Noh et al. (99) investigated the sweetpotato expansin gene *IbEXP1*, which is strongly downregulated during early stages of the fibrous root-to-storage root transition. *IbEXP1* antisense plants displayed reduced elongation of epidermal cells, thicker and shorter fibrous roots, and a marked reduction in lignification. Soil-cultured *IbEXP1* antisense plants displayed a larger number of storage roots and increased root weight compared with controls. Unfortunately, the GA response was not directly tested in this study; however, reduced elongation and lignification point toward a reduction in GA signaling. Together, these studies illustrate the importance of reduced GA signaling during storage organ formation (**Figure 4**).

KNOTTED1-LIKE HOMEOBOX (KNOX): proteins that are members of the plant-specific TALE family of transcription factors

KNOX/BELL Genes as Potential Mediators of Hormonal Shifts in Storage Roots

One proposed explanation for the GA gradient on the xylem side of the vascular cambium in *P. trichocarpa* is the action of class I KNOTTED1-LIKE HOMEOBOX (KNOX) proteins depleting the cambium of GA to prevent premature differentiation of stem cells and derivatives (46). KNOX proteins and their interacting BELL proteins are versatile regulators of plant development. *KNOX* genes were initially described as central regulators of the shoot apical meristem, where they specify subdomains for meristem maintenance and further differentiation. Their expression domain has pronounced effects on leaf morphology. The module could serve a similar role in storage root differentiation. The interaction between KNOX and BELL transcription factors is required for high-affinity DNA binding in promoter regions of their target genes, and the protein complex can bind to the promotors of GA20ox1, G2ox1, and lignin biosynthetic genes, as well as IPT7. The module readout is a repression of GA synthesizing GA20ox1, activation of GA catabolizing GA2ox1, downregulation of lignin biosynthesis, and activation of CK synthesis via IPT7 [reviewed by Hay & Tsiantis (58)]. A KNOX/BELL module (POTH1/BEL5) also plays a very central role in the potato tuberization process, in which similar shifts in hormone regulation occur (as described above). It was proposed that KNOX proteins act as general orchestrators of growth-regulation homeostasis by simultaneously repressing GA and activating CK, thus promoting meristem activity. It is tempting to speculate that the KNOX/BELL module has an extended expression domain in storage roots compared with *Arabidopsis* and tree species, which also repress GA signaling in phloem and xylem parenchyma cells, resulting in increased amounts of these nonlignified cells (**Figure 4**).

Transcriptome studies investigating storage root formation have highlighted spatiotemporal regulation of *KNOX* or *BELL* genes in both cassava and sweetpotato. Tanaka et al. (132) identified homologs of the *KNOX* genes *SHOOT MERISTEMLESS* (*Ibkn1*) and *BREVIDICELLUS/KNAT1* (*Ibkn2/Ibkn3*) in sweetpotato and demonstrated their upregulation in storage roots compared with fibrous roots. Homologs of *KNAT1* and *BEL1* were upregulated 60-fold and 40-fold, respectively, in early storage root stages compared with fibrous roots during transcriptome studies in sweetpotato (36, 45).

Cytokinin Promotes Cell Division and Organ Swelling in Storage Roots

CK is known for its role in stimulating cell division, and the hormone has been demonstrated as a central regulator of cambium activity in *Arabidopsis* and poplar (61, 89). Cambial activity is also key in root crop species (i.e., cassava, sweetpotato), as the process drives storage root expansion. Cell proliferation activities in the cambium of radish roots were positively correlated with radish root yield and were linked to CK-dependent secondary growth (66). During transcriptome comparisons between the rootless pak choi and turnips, the *trans*-zeatin synthesis enzyme CYP735A2 was found both in a QTL region and as a selective sweep, indicating a key function in hypocotyl/root expansion in turnip (85).

FT/SP6A: FLOWERING LOCUS T/SELF PRUNING 6A

Hormone profiling on different transition stages of sweetpotato storage roots showed down-regulation of GA levels, an initial increase in auxin levels, and steadily increasing CK concentrations over the course of storage root development (36, 132). The CK distribution gradient displayed highest levels on the proximal end of the storage root with decreasing concentrations toward the distal end and slightly diminishing but still high levels of *trans*-zeatin from the phloem area toward the xylem area in root cross sections. *Ibkn1* expression was highest in the proximal, unswollen part of the root and associated with the vascular cambium. *Ibkn2* and *Ibkn3* were preferentially expressed in the proximal and thickening parts of the storage root but less toward the distal end. Overall, the CK levels mirrored KNOX expression in this study (132). *Trans*-ribosylzeatin, dihydrozeatin, and *trans*-zeatin are the major CK forms in the cassava storage root, and high concentrations were reported in the phloem, cambium, and outer xylem area in cassava (91). Interestingly, these areas were also reported to display the highest levels of sucrose, sucrose synthase, and starch in cassava, indicating areas of active storage metabolism (90). In addition to its role in stimulating cambium activity, CK also might play a role in stimulating storage metabolism in parenchyma cells. Interestingly, auxin and CK were reported to exert opposing effects on amyloplast development and starch storage in tobacco cells, with auxin inhibiting and CK stimulating the process (93).

Although direct genetic studies on storage root formation are yet scarce, a few hormonal responses appear to be common during their formation: (*a*) early auxin signaling, (*b*) reduction in GA signaling and reduced lignin levels, and (*c*) increasing levels of CK. These observations likely correspond to formation and stimulation of the vascular cambium as well as inhibition of parenchyma differentiation, ensuring a high number of starch-storing cells. It will be very informative to investigate hormone distributions between different cell types and during development more closely, e.g., with the help of hormone-responsive fluorescent reporters.

The formation of a high number of parenchyma cells is accompanied by a shift in the sucrose transport mode. Apolasmic transport in fibrous roots is shifted toward symplasmic sucrose transport, which is believed to represent an adaptive strategy for low oxygen levels in bulky tissues such as seeds, tubers, and roots, because sucrose synthase–mediated sucrose cleavage is more energy efficient compared with invertase-mediated sucrose cleavage (119). In contrast to potato, the regulation of this shift is unknown, and it is unclear if FT/SP6A homologous proteins play a role in the regulation of sucrose allocation in storage root crops (**Figure 4**). It will be very interesting to learn more about the regulation of resource allocation and developmental processes in root crop species in the future.

CONCLUSION AND FUTURE CHALLENGES

The organogenesis of storage organs is a complex process that integrates endogenous and environmental signals to ensure proper timing of organ formation. For instance, in potato, the timing of tuber formation is ensured by day-length sensing mechanisms and constant monitoring of the resource status. Induction of potato tuber formation is mediated by several phloem-mobile

signaling factors, consisting of both mobile RNAs and proteins (**Figure 3**). These factors induce the coordinated execution of cellular restructuring, starting in the procambium or other phloem-associated meristematic cells. Changes in hormone levels and responses together with changes in sugar transport mechanisms represent prominent and common events during both root and tuber formation (**Figure 4**). Storage organs of potato, sweetpotato, or cassava contain large amounts of nondifferentiated parenchyma cells that have an active ongoing metabolism and store large quantities of starch. Therefore, storage organs execute only limited parenchyma cell differentiation but activate sugar and starch metabolism. Storage metabolism in these cells is generally characterized by symplasmic assimilate unloading and sucrose synthase–mediated sucrose cleavage, most likely due to the more energy-efficient mode of operation of sucrose synthase in tissues with low levels of oxygen.

While a number of regulatory protein–protein interactions regulating potato tuberization have been described, a detailed spatial and temporal analysis of their cell and tissue specificity is missing. Cellular processes, occurring in phloem-associated meristematic regions very early during storage organ initiation, remain especially elusive and need further investigations. This lack of knowledge, together with limited knowledge about the downstream target genes affected by these regulatory complexes, prevents a deeper understanding of the tuberization process.

To generate a detailed picture of storage organ formation as a whole, much more research outside of the potato system is needed. For instance, it is unclear how the timing of storage organ formation is regulated in other root and tuber crops, like sweetpotato or cassava. Is the formation of storage roots in tropical crops like sweetpotato and cassava also linked to day-length sensing, or are signals, like the plant's water status, more important? Are mobile RNAs and/or proteins involved in mediating the storage organ induction in these systems, or is it a purely metabolic regulation? Are FT-like proteins involved in the changes in sucrose allocation similar to those in potato? What is the mode of action of FT-like proteins mediating sucrose allocation? How are these structural and metabolic adaptations synchronized? Future research should seek to address these questions in important root crop species.

SUMMARY POINTS

1. Plants utilize storage organs with diverse origins and morphology to survive adverse growth conditions.
2. Storage organs are strong assimilate sinks, which greatly impact overall plant growth.
3. A complex leaf signaling network, centered around photoreceptors and clock genes, senses and integrates day length, light quality, temperature, and other signals to ensure proper timing of tuber induction in potato.
4. This information is relayed from source to sink through phloem-mobile proteins and RNAs, as well as through metabolic and hormonal signals, coupling the plant's resource status and its organ development.
5. The mode of assimilate unloading in sink organs commonly switches from apoplasmic to symplasmic during root and tuber formation.
6. FT proteins can form regulatory complexes and interact with sugar transporters during tuber formation in potato.
7. In addition, KNOX/BEL modules seem to play an important role in storage organ formation in both root and tuber crops.

8. Changes in auxin, gibberellin, and cytokinin signaling are typical events observed during root and tuber crop development, regulating the increased cell division activity, the necessary shift from elongation growth to expansion growth, and the production of parenchyma cells.

DISCLOSURE STATEMENT

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