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REVIEWS

Regulation of Potato Tuber Dormancy and Sprouting

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Abstract—Dormancy is the final stage of tuber life serving to preserve tubers as organs of vegetative reproduction under unfavorable growth conditions. Since the duration of potato tuber dormancy and their sprouting time have significant economic importance, much attention is given to the study of the regulation of these processes. This review considers metabolite, genetic, and hormonal aspects of regulation of potato (*Solanum tuberosum* L.) tuber dormancy and sprouting. Particular attention is paid to the relationship between processes occurring in different parts of the tuber: its storage tissues and buds. The interaction of hormonal and metabolite (carbohydrate) regulation of dormancy and sprouting is discussed.

Keywords: Solanum tuberosum, tuber, dormancy, sprouting, carbohydrate metabolism, phytohormones

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INTRODUCTION

Tuber is the organ of potato vegetative propagation. Tuber formation and further functioning is based on the whole complex of physiological processes and can be divided into several successive stages [1, 2]. The issues of hormonal regulation of the basic stages of tuber formation – the development of stolons, induction of tuberization, and tuber initiation and growth – have been discussed by us earlier [3]. The present review is devoted to the final stages of tuber life, e.g., dormancy and sprouting; the regulation of these stages and the role of phytohormones are considered.

Tuber growth is determinated one. In temperate latitudes, tubers grow mainly in the late summer and early autumn. After maturation when tubers attain their final sizes, they transit to deep (internal) dormancy. Dormancy lasts during winter and serves to protect tubers as organs of vegetative reproduction under conditions unfavorable for growth. During dormancy period tubers are highly resistant to pathogen attacks, thus keeping reserves of starch and protein for future sprouts [4, 5]. Overall, tuber dormancy is an adaptation of potato ontogeny providing for the successful reproduction of *Solanum tuberosum* species [6]. Upon a dormancy period, tuber buds awakes and sprouts start to grow intensively with the formation of roots at their bases. At this time, tubers convert from the storage organ into the source of nutrients and energy to sustain developing sprouts [7]. Here the cycle of potato vegetative propagation is completed and a young plant, which is a new clone of the original parent organism, arises.

According to the current terminology [8], dormancy is a temporary growth arrest of any plant structure containing a meristem. Dormancy is divided into three categories based on how growth is arrested. During deep dormancy (endodormancy), growth is stopped under the influence of internal physiological factors. During forced or induced dormancy, growth is arrested by unfavorable external factors (ecodormancy) or physiological causes external to this meristem (paradormancy). This terminology has been developed for the dormancy of stem vegetative buds [9], but it is also used for potato tuber dormancy [6].

Tuber buds pass through all three dormancy phases. Immediately after harvest, tuber buds are in the state of deep dormancy: they can not sprout even under environmental conditions most favorable for growth. After the termination of the deep dormancy phase, tuber buds can sprout, but they remain at rest under unfavorable external conditions, for example, at a temperature from 0 to 4°C. In the beginning of sprouting, lateral buds are in the state of forced dormancy (depending on internal physiological factors) because they experience a correlative inhibition from the api-

Abbreviations: AGPase—ADP-glucose pyrophosphorylase; BA—benzyladenine; BS—brassinosteroids; CF—carboxyfluoresceine; CK—cytokinins; JA—jasmonic acid; SP—starch phosphorylase; T6P—trehalose-6-phosphate; TDF—transcriptionally derived fragments.

cal bud sprouting earlier [6, 10]. The present review focuses on processes related to deep dormancy of tubers.

There are different opinions concerning the time of dormancy beginning. The start of tuberization results in the growth cessation of the stolon developing a tuber, and the former stolon apical meristem converts into a central dormant bud, the eye, which, like other eyes, did not outgrow until tuber dormancy release [11]. Therefore, some researchers consider the earliest periods of young tuber initiation and growth as the beginning of dormancy [12, 13]. During this period intense mitoses occur in both cortex and pith tissues of young tubers with subsequent increase in the size of cells and the whole tuber [14]. A noticeable increase in the cell number was observed even in large 120-g tubers, especially in the cortex parenchyma; a substantial increase in the cell volume (expansion growth) in the pith parenchyma occurred as well [15]. In this connection, many researchers consider the beginning of deep dormancy as the time when mature tubers attain their final size, i.e., the time of tuber harvesting [6]. As the tuber is an integral organ with the cooperation of all its parts, in this review, we also consider what happens under deep dormancy not only in buds but also in other tuber tissues. The beginning of visible bud outgrowth is considered the termination of deep dormancy.

The duration of tuber dormancy period depends primarily on potato cultivar properties (genotype) and also on conditions of tuber growing and storage. Tuber storage at the elevated (up to 30°C) temperature and humidity (up to 90% of water capacity) and also changed atmosphere composition (hypoxia, anoxia, increased content of CO_2) favor dormancy breaking and premature bud outgrowth. At the same time, definite seasonal environmental changes, which would serve cues for the start or termination of tuber deep dormancy, are not found [6, 12]. The development of approaches to the regulation of tuber dormancy duration is of great practical value. Premature tuber sprouting during their long-term storage accounts for economic losses. In contrast, early potato planting requires dormancy breaking. To this end, numerous ways for chemical regulation of dormancy duration were developed. For example, tuber treatment with ethylene chlorohydrin, ethanol, or bromoethane favors dormancy breaking [12, 16, 17]. Maleic hydrazide and some contemporary inhibitors of potato sprouting, such as CIPC (chlorpropham), DMN (dimethylnaphthalene) [12, 18], and also volatile components of caraway and peppermint oils are applied for tuber dormancy induction and prolongation [19].

GROWTH, METABOLISM, AND GENE EXPRESSION

Potato buds, eyes, did not usually outgrow during many months after tuber formation. Such long absence of eye growth has evidently adaptive nature, because it allows vegetative buds to be kept as a tuber part during intense storage metabolite accumulation as well as in the subsequent period of an unfavorable season.

The specific mechanisms for bud growth blocking and removing this blockage at the end of tuber dormancy were not fully elucidated, but some of their essential characteristics are disclosed. It was shown [20] that in the cells of dormant tuber buds, transition from G1- to S-phase of the cell cycle is arrested: after completion of G1-phase related to the cell growth after preceding division, the cells do not transit to DNA synthesis characteristic of S-phase and required for successive mitosis. For this transition from G1- to S-phase, participation of many genes and proteins is required including D-cyclins (CYCD), cyclin-dependent kinases (CDK), histones H3 and H4, and other proteins [21]. At tuber eye transition to sprouting and also at artificial stimulation of sprout growth, expression of genes controlling DNA replication [22, 23] and progression of the cell cycle, including cyclin D3 gene [24], is activated. Activation of these genes is one of conditions for dormant bud transition to sprouting. However, signal transduction pathways controlling cell division in buds in dependence on the tuber dormancy state are not so far elucidated.

One more factor controlling bud sprouting is the bud supply with necessary metabolites from other parts of the tuber. Symplastic connections are shown to play an important role in the interaction of tuber cells and tissues [25, 26]. Symplastic transport in dormant and sprouting potato tubers of cv. Desiree was studied using a fluorescent dye carboxyfluorescein diacetate, which penetrates cell membranes. Within the cell endogenous diesterases convert it into carboxyfluorescein (CF), which can not penetrate cell membranes and can be transported only through plasmodesmata, serving a marker of symplastic unloading in tuber sink tissues. The in situ analysis of dye distribution demonstrated the complete absence of CF transport from the tuber tissues into eyes of dormant tubers. This indicates a symplastic isolation of eyes during dormancy period. Oppositely, in actively growing buds, CF distribution revealed a substantial symplast transport to their meristematic regions. These results show that symplastic connections with the storage tuber tissues may play an important role in the control of eye meristematic activity because growing buds depend completely on the structural and energetic metabolites from tuber source parts [27].

Dormancy release is associated with active bud outgrowth and sprout growth. In this period, bud respiration is markedly accelerated and the protein spec-

trum changes [28]; the synthesis of nucleic acids, especially ribosomal RNA, is activated as well [29, 30].

Unlike many other storage organs (orthodox seeds, for example), dormant tubers remain fully hydrated [6]. In spite of this fact and the abundance of stored structural and energetic materials, metabolic activity drops sharply during deep dormancy as compared to the preceding period and is kept at a very low level [30]. In the periods after potato tuber harvest and during their early storage, the rate of respiration decreases sharply, whereas the contents of proteins, nucleic acids, and lipids in tuber parenchyma are not changed or only slightly reduced [31]. Internal causes for such metabolism blocking in tubers in the state of deep dormancy are just beginning to be studied. It becomes clear that carbohydrate metabolism plays an important role in the regulation of tuber dormancy and sprouting.

The onset of deep dormancy coincides with wilting of the parent plant foliage and complete tuber isolation after harvesting. It can be assumed that, under natural conditions, one of the signals inducing tuber dormancy is the termination of their supply with metabolites and, above all, with the main product of photosynthesis – sucrose. This is consistent with the fact that sucrose is an important physiological regulator of dormancy and outgrowth of vegetative buds, in particular the underground leafy spurge buds [9, 32]. Carbohydrate metabolism, primarily sucrose and starch metabolism, plays an important role in the tuber life. In the mature tuber by the time of its entering deep dormancy, starch represents up to 25% of fresh weight and up to 75% of dry weight [31]. Due to the high practical value of potato starch, carbohydrate metabolism throughout the life of tubers and enzymes involved in it are studied in detail [34–36]. It was shown that functioning of enzymes of starch metabolism and the activity of one of key enzymes of the early steps of starch biosynthesis, ADP-glucose pyrophosphorylase (AGPase) are regulated on many levels, including transcriptional, metabolic, and recently demonstrated posttranslational ones. The investigation of the posttranslational mechanism of regulation has not been completed; however, the involvement of protein–protein interactions, redox systems, processes of reversible phosphorylation, and some mediatory molecules was shown [37]. One of such molecules is trehalose-6-phosphate (T6P) involved, as was shown in recent studies, in the establishing the connection between sucrose availability and AGPase activity [38, 39] and also in conjunction between carbohydrate metabolism and processes of plant growth and morphogenesis [40]. In experiments with transgenic potato, the participation of T6P in changes in the contents of endogenous sugars, starch, and ATP and the control with this molecule of the periods of dormancy and sprouting was demonstrated. In these experiments, tuber-specific expression of the gene of T6P synthase from *Escherichia coli* elevated the content of T6P in tubers and strongly delayed their sprouting. Tubers of transgenic potato overexpressing T6P phosphatase and thus with low T6P level released from dormancy much earlier than tubers of wild-type plants [41].

Changes in the activity of starch biosynthesis enzymes associated with dormancy and sprouting were found in in vitro grown potato microtubers [42]. Dynamics of AGPase and starch phosphorylase (SP) activities, involved in starch degradation, were followed both biochemically and histochemically, by in situ staining [43]. The latter method was most informative because it permits to observe changes in enzyme activity distribution in different tuber tissues. During deep dormancy, activities of AGPase and SP were not detected. However, these enzymes started to function at the end of the dormancy period and their activity gradually increased by the time of bud outgrowth. Before dormancy release, the activities of these enzymes were essentially restricted to the buds and surrounding tissues and also to the vascular pathways leading from the tuber parenchyma to buds. The activation of AGPase and SP in tubers started well before visible sprouting, i.e., it is an early marker of dormancy release. In these experiments, activities of AGPase and SP were localized in one and the same tuber tissues. Glucose-1-phosphate, the product of starch cleavage by SP is a substrate for starch synthesis by AGPase. Functioning of both enzymes is reversible, being dependent on substrate concentrations. This led to a suggestion that the cycles of storage starch cleavage–resynthesis can occur in tubers with successive starch re-localization to the sites of further active consumption during bud sprouting [42]. In some studies [44, 45], an enhanced enzymatic activity of α- and β-amylases and activation of their genes in the buds of sprouting tubers, especially during sprout growth, was demonstrated. Overall, the results obtained indicate an active participation of carbohydrate metabolism in the regulation of tuber dormancy and sprouting.

In parallel with starch deposition, potato tubers accumulate storage proteins patatins [46]. Patatins are glycoproteins and comprise up to 40% of all soluble proteins in the mature tuber. They consist of some isoforms encoded by a family of 10–15 genes per haploid set, i.e., there are up to 60 gene copies in standard tetraploid potato cultivars. Patatins manifest acyl hydrolase and transferase activities, which may be related to their defense functions. Patatins are tuber-specific proteins; only in rare cases, their small amounts are detected in other potato organs [46]. The complete proteomic analysis during the entire period of tuber development was performed for potato cv. Desiree [47]. In this work, proteins were separated by two-dimensional electrophoresis and identified using corresponding databases (NCBI, TIGR-EST). It was shown that most patatin isoforms were accumulated during tuber development and growth. The high content of patatins was maintained during the entire

period of dormancy until tuber sprouting. Some high-molecular patatin isoforms disappeared after tuber growth termination, possibly because of further processing of these proteins.

In the last decade, an intensive study of the regulation of tuber dormancy at the gene level was performed. Total spectra of differential gene activity in growing, dormant, and sprouting potato tubers were compared. In most works, gene expression was studied using the method of cDNA-AFLP finger-printing. For a more detailed elucidation of the processes occurring in the studied period of tuber development, the structure of transcriptionally-derived fragments (TDF) was compared with sequences of known potato genes from relevant databases.

Bachem et al. [48] studied differential gene expression in the in vitro cultivated potato at different stages of tuber development, in particular during dormancy and sprouting. The whole tubers including parenchyma and buds were taken for analyses. From tubers at different developmental stages, 18 000 TDF were isolated and studied. It was found that the number of actively expressed genes dropped more than tenfold in dormant as compared with growing tubers. More detailed analyses led to a conclusion that during dormancy the processes of anabolism inherent in growing tubers are arrested and the expression of genes related to active metabolism is simultaneously supressed as well. Tuber dormancy release was not accompanied by crucial changes in gene expression. During tuber sprouting, the content of only 3% of transcripts increased. Sequences of most stimulated TDF were homologous to the genes encoding homeosis proteins and transcription factors. The absence of changes in the expression of genes related to starch catabolism during sprouting was unexpected because by the end of dormancy the tuber is converted into the source organ and sprouts became sinks of carbohydrates. These results confirm the importance of posttranscriptional regulation of carbohydrate metabolism in the final period of tuber dormancy.

Campbell et al. [22] studied gene expression in buds isolated from dormant and sprouting tubers of potato cv. Russet Burbank grown in soil. The effect of natural dormancy release was compared with the action of bromoethane; the principal similarity of processes occurring in both cases was observed. The authors found no massive changes in gene activities in the bud meristems during tuber dormancy release. This evidently indicates the absence of crucial changes in the regulation of metabolism on the gene level related to dormancy release. These data correspond to the above described results obtained on whole tubers [48]. At the same time, the expression of some genes was changed in sprouting buds. In particular, the transcription of genes encoding precursors of storage proteins, class I patatins and other patatins, was suppressed during transition from dormancy to sprouting. These data indicate a shift in metabolism in outgrowing buds from storage of proteins to their mobilization. In the meristems of tubers releasing dormancy, the expression of genes encoding some protease inhibitors and lipoxygenases was also suppressed. After the start of sprouting, the expression of genes related to overcoming the cell cycle arrest at the G1/S-phase was enhanced in buds. The transcript level of genes encoding histones H3, H4, 2B, and other proteins involved in cell division and growth increased. A substantial increase in expression was observed for TDF of two groups of oxidative enzymes, oxoglutarate-dependent dioxygenases and cytochrome P450, indicating the activation of oxidative regime in the meristems after dormancy cessation [22]. In the buds of tubers after dormancy release, genes encoding ribosomal proteins were also activated [49]. The results of other works analyzing gene expression [50, 61] and protein profiles [47] during tuber dormancy enter and release are in agreement with above data and correspond to the character of growth and metabolism occurring during dormancy and sprouting.

However, any key genes, which expression would determine the state of dormancy or dormancy release, were not found [6]. As was noted above, many factors affect dormancy duration. The critical factor for dormancy progression is time [22]. Some time-dependent morphogenetic processes in plants, for example, duration of vernalization, are related to epigenetic changes of chromatin [52]. The end of potato tuber meristem dormancy seems to be also associated with epigenetic events, in particular 5-methylcytosine demethylation in DNA with subsequent multi-acetylation of histones H3.1, H3.2, and H4 in the chromatin [53]. The role of these changes in the control of dormancy duration is not yet known.

In general, these studies offer further perspectives in the investigation of genetic regulation of tuber dormancy.

PHYTOHORMONES

Phytohormones are most important and efficient endogenous regulators of tuber dormancy and sprouting. This is evident from the dynamics of endogenous hormones related to the stages of dormancy and sprouting and a possibility to change dormancy duration and sprouting by tuber treatment with hormonal preparations [6, 12].

Abscisic Acid

ABA is one of the main hormonal regulators of dormancy initiation and maintenance. ABA was firstly detected in potato tubers within the β-inhibitory complex including also other acidic growth inhibitors, such as para- and ortho-coumaric acids and derivatives of cinnamic and salicylic acids. This complex was present in dormant tubers, but its content dropped sharply by the end of dormancy and the onset of tuber

sprouting [12]. It was shown that the content of ABA in both eyes and tuber parenchyma increased at the onset of dormancy; it was the highest during deep dormancy and sharply declined at dormancy exit [54, 55]. The content of ABA in tubers was reduced after forced dormancy breaking as well [6]. Artificial reduction in the content of ABA in tubers by the inhibitor of ABA biosynthesis fluridone induced premature dormancy release, which could be prevented by tuber treatment with ABA [55].

The analyses performed on molecular and gene levels confirmed the important role of ABA in the initiation and maintenance of tuber dormancy. Thus, among quantitative trait loci (QTL) related to tuber dormancy state, at least two QTL coincided with loci controlling the content of ABA in tubers [56]. The study of expression of genes encoding enzymes of ABA biosynthesis and degradation during the entire period of tuber dormancy was performed by qRT-PCR [57]. It was established that enzymes of ABA biosynthesis 9-*cis*-epoxycarotenoid dioxygenase (StNCED) and catabolism ABA-8'-hydrolase (StCYP707A) play a decisive role in the maintenance of required level of ABA. The level of *StNCED* gene expression was correlated with the content of ABA during dormancy in the meristem and cortex tissues. During late dormancy, *StCYP707A* genes are activated in the meristem and periderm, and this leads to a decrease in the content of ABA in these tuber zones [58]. After dormancy release, an obvious decrease in the expression of a number of known ABA-inducible genes was observed in tuber buds. It is evident that, by the end of dormancy period, a decrease in the content of ABA in tubers is accompanied by a down-regulation of genes responding to ABA signaling [22].

Ethylene

Ethylene favors tuber dormancy initiation and maintenance; however, its role in these processes is not completely elucidated. The participation of ethylene in the first stages of dormancy maintenance is shown most clearly [29, 30]. The level of endogenous ethylene was the highest in the in vitro cultured tubers entering dormancy; then, it decreased rapidly. Treatment of tubers entering dormancy with ethylene antagonists, silver nitrate and norbornadiene, induced premature sprouting, which could be prevented by treatment with ethylene. Stabilization of dormancy under influence of ethylene was observed only in the early period of dormancy [59].

Data concerning ethylene role in further maintenance of dormancy and dormancy release are contradictory. Strengthening or weakening dormancy of tuber exposed to ethylene and its producers depended on the ethylene dose, potato cultivar, and storage conditions [60]. The temporary increase in the ethylene synthesis at dormancy interruption under the influence of wounding, treatment with bromoethane, and other approaches are likely to be the response to stressful situations [17, 61]. At the same time, a comparison of TDF profiles in dormant and sprouting tubers revealed a possible ethylene participation in the prevention of bud outgrowth during the latest period of tuber dormancy [24]. Transcripts with sequences homologous to those encoding components of the ethylene signaling pathways in tomato and arabidopsis were actively expressed in dormant buds, but their expression decreased during sprouting. At sprouting, expression of genes of primary and secondary responses to the ethylene signal was also reduced. All these data indicate the involvement of ethylene signaling in the maintenance of tuber bud dormancy.

There are also reports about ethylene interaction with ABA in the regulation of tuber dormancy. Particularly, treatment of dormant tubers with the ethylene producer 2-chloroethylphosphonic acid not only increased the content of ethylene in tissues but also stimulated ABA biosynthesis and as a result extended the period of deep dormancy [29]. This may indicate that ABA can mediate the ethylene-dependent enhancement of tuber dormancy.

Brassinosteroids

Brassinosteroids (BS) are active regulators of plant growth, but their role in potato tuber dormancy and sprouting is little studied. In this area, there are only few studies. Korableva et al. [62] treated potato cv. Nevskii tubers, being in the state of deep after-harvest dormancy, with 24-epibrassinolide. Such treatment extended the period of tuber dormancy and delayed their sprouting more than for a month; it also resulted in the enhanced ethylene formation and the accumulation of free and bound ABA in tuber buds. In addition, electron microscopic observations showed that the delay of eye outgrowth under the influence of BS was accompanied by a reduction in the cell sizes in the central part of the meristem together with an increase in the number and a reduction in the volume of vacuoles in meristematic cells [62, 63]. These data indicate a possible influence of BS on the levels of ethylene and ABA in the natural control of tuber dormancy but might be the consequence of artificial suppression of tuber bud sprouting by the high BS concentration. Further detailed studies should clarify the role of BS in the regulation of potato tuber dormancy.

Auxins

Auxins, IAA primarily, are one of the main growth-stimulating phytohormones. However, their role in the control of tuber dormancy and sprouting remains not very clear. Treatment of dormant tubers with IAA did not exert definite influence. High concentrations of exogenous IAA or synthetic auxins slightly inhibited eye growth, whereas low concentrations moderately stimulated bud outgrowth [6, 12]. The analysis of IAA

content throughout the period of dormancy gave ambiguous results. The early studies showed that the content of auxins was the lowest at the early dormancy; then it increased gradually and attained the highest level during active sprout growth [6, 64]. In more recent work [65], the highest content of both free and bound (esters, amides) IAA forms was found in tuber buds during the initial period of deep dormancy and decreased markedly by its ending. Performed immuno-histochemical analysis of IAA distribution within tuber tissues and buds allowed an assumption that auxin favors dormancy completion, accelerating bud differentiation and growth at early germination stage [65].

This assumption is in agreement with the results of Faivre-Rampant et al. [66], who isolated from sprouting potato cv. Desiree tuber transcripts encoding a protein factor similar (78% identity) to the auxin-responsive ARF6 factor of arabidopsis. These transcripts were completely absent from eyes and tissues of dormant tubers, but their level increased sharply at the onset of bud outgrowth. Transcriptional analysis of buds of sprouting potato tubers cv. Solara showed [24] that the level of transcripts encoding enzymes related to auxin biosynthesis, aldehyde oxygenase and flavin monooxydase, increased during early stages of sprouting. A substantial activation of several primary auxin-response genes and genes for PIN1-like auxin transporters was also observed [24].

The above results support the idea of the involvement of auxin in the initiation of tuber bud outgrowth and further growth. Therefore, these results were quite expected, since the active participation of IAA in processes of plant growth and differentiation is well known. However, it remains unclear whether auxin plays any more specific role in the control of initiation, maintenance, and termination of tuber dormancy.

Jasmonates

Jasmonic acid (JA) and its derivatives (tuberonic acid and others) are compounds stimulating tuber formation in potato explants cultivated in vitro [67]. However, so far there is no convincing evidence for the involvement of these compounds in the regulation of potato tuber dormancy and sprouting. The data obtained by different researchers about dynamics of JA content during dormancy and sprouting disagree. It was reported [68] that the content of jasmonates changed in different potato organs throughout the period of vegetation and attained the highest level in tubers by the onset of deep dormancy. Another detailed analysis of JA and its derivative content was performed on the minitubers of potato cv. Russet Burbank and the model system of discs cut from these tubers including the periderm and apical bud [69]. In the discs cut from dormant tubers, the content of JA remained low; it increased with the onset of bud outgrowth and then decreased again. The content of tuberonic acid was high during tuber dormancy and increased additionally during dormancy progression, whereas the level of jasmonoyl-isoleucine was very variable and differed markedly in different years.

The effects of tuber treatment with JA are also ambiguous. In some experiments, such treatment of stored tubers suppressed sprout growth [68]; in other cases, JA suppressed or stimulated tuber sprouting in dependence on the used concentration [70]. It was also reported that treatment with JA induced different responses of tuber buds when different experimental models were used: it did not affect sprouting of the whole potato minitubers but inhibited by 29% bud outgrowth in tissue discs cut from these tubers [69]. In addition, there are reports that treatment with JA affected markedly some structural features of the cells in apical meristems of quiescent tuber buds (at 4°C) and during their outgrowth [70]. In these experiments, JA changed the ultrastructure of the plasmalemma and plastid apparatus of eye meristematic cells and functioned together with other hormonal compounds, salicylic acid in particular [70, 71]. Further research is needed for more precise elucidation of JA involvement in the processes of tuber dormancy and sprouting.

Cytokinins

Cytokinins (CK) are efficient regulators of tuber dormancy and sprouting. They facilitate transition from tuber dormancy to its release and the onset of bud outgrowth. Numerous analyses of CK activity and content showed that, during deep dormancy, the content of CK in tubers is low; then it increases and attains the highest values before sprouting and during sprout emergence [12, 72, 73]. The involvement of particular cytokinin forms in these processes is not so far elucidated. During dormancy release, the total content of CK increased in tubers and buds, including *cis*- and *trans*-zeatin and cytokinins of the isopentenyl type [74].

Treatment of dormant tubers with various natural and synthetic CK, benzyladenine (BA) in particular, induced dormancy break and the onset of sprouting [6, 12]. It was shown that synthetic cytokinins, derivatives of phenylurea or nitroguanidine, were more efficient in dormancy breaking of potato cv. Russet Burbank minitubers than natural zeatin [75]. This might be related to a greater resistance of synthetic cytokinins to enzymatic degradation. An important role of endogenous CK inactivation for extending tuber dormancy period was confirmed on potato plants transformed with an arabidopsis gene encoding one of the main enzymes responsible for CK inactivation, cytokinin oxidase/dehydrogenase [24]. The expression of this gene resulted in the delay of the onset of eye growth by 5–8 weeks; treatment of such tubers with BA restored the normal timing of sprouting. In line with this, enhanced CK biosynthesis under the influence of agrobacterial *ipt* gene resulted in the shortening of bud dormancy period in the discs cut from

tubers of transformed potato [24]. It was also found that tuber sensitivity to CK changed during dormancy progression [76]. Immediately after harvest, tubers did not respond by dormancy weakening to treatments with *cis*- or *trans*-zeatin, but during storage the sensitivity to the phytohormone increased in a time-dependent manner and dormancy exit was stimulated by treatment with cytokinins. Such increase in tuber sensitivity to CK was not associated with the changes in zeatin metabolism and was evidently related to the activation of cytokinin signaling components.

The entire set of data obtained indicates the involvement of different CK forms and processes of their biosynthesis and inactivation in the regulation of tuber dormancy and sprouting. CK fulfill a number of functions in plants; in particular, they stimulate cell division and enhance tissue sink capacity [77]. The role of CK in dormancy breaking is believed to be primarily related to the stimulation of cell division due to the removal of the arrest of G1/S phase transition in the cell cycle by the time of dormancy termination. It is thought that the removal of this block occurs with the involvement of D-type cyclins [9]. In addition, the releasing dormancy buds become an active sinks of storage metabolites from other tuber parts. Therefore, the role of CK in the enhancing bud sink capacity is also possible. Functioning of other still unknown pathways of CK regulation of tuber dormancy and sprouting is not excluded either.

Gibberellins

Gibberellins (GA) are believed to stimulate active sprout growth after tuber dormancy release. According to early investigations [12], GA also favor dormancy breaking and the onset of bud outgrowth. In these experiments, it was found that the activity of endogenous GA-like compounds is low during dormancy and increases before bud outgrowth; during tuber storage their dormancy can be broken by treatment with GA. Treatment of dormant tubers with GA was even used in practice and was a commercial approach for early potato planting [13]. At the same time, the later studies do not give unambiguous confirmation of endogenous GA involvement in tuber dormancy breaking; they rather indicate their role in the stimulation of successive sprout growth [6]. Thus, duration of tuber dormancy and the timing of sprouting onset were similar in potato dwarf mutants and plants with normal phenotype in spite of the absence of noticeable GA activity (GA_1 and its immediate precursor GA_{20}) in mutants [78]. The artificial decrease in the content of endogenous GA_{20} and GA_1 by the antisense expression of the gene of GA biosynthesis *GA20ox1* did not affect substantially the duration of tuber dormancy but retarded further sprout growth [79]. Similar results were obtained on transgenic potato plants with enhanced ectopic expression of *GA2ox1* gene related to GA_1 inactivation [80].

However, other reports [24, 25] still indicate a possibility of GA-induced dormancy breaking and bud outgrowth stimulation and stimulation of further sprout growth. Further studies are needed for a final clarification of GA role in the process of potato tuber bud sprouting.

Phytohormone Interaction

Modern studies of plant hormonal regulation revealed complex interactions between different phytohormones, which were observed at the level of both physiological responses and hormonal signaling [81]. The interaction between different phytohormones was noted also in the regulation of potato tuber dormancy and sprouting. Some researchers showed close interaction between GA and CK in the control of tuber sprouting. Thus, dormancy breaking of minitubers of potato plants grown from seeds occurred much more rapidly after treatment with the mixture of GA_3 and BA than after treatments with these individual compounds [82]. Tubers of transgenic potato plants with a sharply reduced activity of endogenous CK under the influence of expression of the transgene encoding cytokinin oxidase/dehydrogenase could not respond to treatment with GA. Such blocking of GA action on sprout growth was removed by tuber treatment with CK, BA in particular [24]. The interaction between ABA and ethylene was manifested in the process of tuber dormancy maintenance [29]. During bud dormancy exit, the contents of ethylene signaling components was reduced and simultaneously the expression of elements related to the activation of IAA action was increased [24].

Overall, the consideration of hormonal regulation of tuber dormancy and dormancy release demonstrated the involvement in these processes of a complex of phytohormones, each of which performs its specific function. The interaction between different hormone groups is coordinated in time. However, the mechanisms coordinating phytohormone dynamics and functions during tuber dormancy initiation, maintenance, and breaking are still far from being understood.

As a result, the materials considered in the review provide a general picture of the processes occurring in the buds and storage tissues of potato tubers during dormancy and sprouting (the table).

CONCLUSIONS

Dormancy and sprouting are important stages of tuber development providing for successive vegetative propagation of potato. Characteristics of tuber dormancy, its duration in particular, are stable hereditary traits [6]. To date, detailed spectra of differential gene activity during tuber dormancy and sprouting were obtained. Dynamics of the expression of thousands and sometimes tens of thousands of transcripts in both

Hormonal regulation of tuber dormancy and sprouting

Physiological processes		Phases of tuber dormancy and sprouting: stimulating phytohormones		
		dormancy: ABA, ethylene, BS?	sprouting: IAA, CK, GA	sprout growth: CK, GA
Buds	growth characteristics	growth arrest; blocking G1/S-phase transition	onset of growth and morphogenesis; removal of blocking G1/S-phase transition	active growth
	metabolism specific features	low level of metabolism; limited supply with substrates	activation of metabolism; enhanced supply with substrates	high level of metabolism; active supply with substrates
Tuber tissues	growth characteristics	absence of growth and morphogenesis	absence of growth and morphogenesis	absence of growth and morphogenesis
	metabolism specific features	low level of metabolism; preservation of storage carbohydrates and patatins	transition from storage to source function; enhanced activity of carbohydrate metabolism	active supply of seedlings with energetic and structural materials

tuber tissues and eyes was studied [48]. The correspondence of gene activity and the general character of growth and metabolic processes occurring during tuber dormancy initiation, maintenance, and breaking was observed. However, genes directly responsible for dormancy regulation (genes of this process identity) were not found. Crucial changes in gene expression during tuber dormancy release and bud sprouting were not found as well [22, 48]. Further research is needed to decipher the mechanism of gene regulation controlling tuber dormancy and sprouting.

As was noted in this review, tuber dormancy and sprouting include a complex of different but coupled physiological processes. The main ones are growth and its active blocking, as well as storage or active usage of carbohydrates and proteins. It is still not completely clear how these processes are connected at the molecular and biochemical levels and how they are coordinated with each other in different parts of the tuber, the storage tissues and buds.

Phytohormones are the main integrators of the plant life. It is commonly accepted that phytohormones play a key role in the regulation of tuber dormancy and sprouting. Thus, ABA together with ethylene facilitates the establishment and maintenance of deep dormancy; CK and IAA are involved in the onset of sprouting, whereas GA stimulates sprout growth [6]. A significant progress was attained in the study of various components of phytohormone signaling during dormancy and sprouting [24, 57, 66]. Tuber treatments with phytohormones are efficient ways to regulate dormancy duration. However, the physiological causes for the regular changes in the content of endogenous hormones in tuber tissues and buds during dormancy progression and sprouting remain unclear.

Coupling of phytohormone functioning and changes in metabolism, mainly carbohydrate one, occurring in tuber storage tissues and buds is also poorly studied. Along with phytohormones, sugar molecules can also be the regulators of plant metabolism and morphogenesis [83], in particular they can influence the hormonal control of tuberization [84]. The interaction between sucrose and phytohormones in their effects on tuber initiation and growth was observed at potato explant treatment with both GA_3 and ABA [85] and CK and IAA [86–87]. There are also some reports showing the interaction of sucrose and phytohormones in their influence on the process of sprouting in vitro [35]. Treatment with GA induced the accumulation of α- and β-amylase transcripts in tuber buds and sprouts [45]. Recently, it has been demonstrated that nonreducing sugar trehalose and its phosphorylated form trehalose-6-phosphate are active signaling molecules uniting plant carbohydrate metabolism with growth processes and hormonal regulation of morphogenesis [40]. There are first reports on the impact of T6P on both tuber dormancy and sprouting and on the hormonal regulation of dormancy, in particular, the content of ABA in dormant tubers [41]. Further studies of the interaction between hormonal and metabolite (carbohydrate) regulation of dormancy and sprouting will lead to the progress in clarifying the general and specific mechanisms that control these processes.

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