Chapter

Molecular Host-Nematode Interactions and Tuber Development

Refik Bozbuga and Selman Uluisik

Abstract

Potato, *Solanum tuberosum*, the most important non-grain food crop and essential crop globally, has been widely cultivated around the world for centuries. The significance of this plant is increasing due to high nutritional value of the tubers combined with the simplicity of its propagation. As a plant organ, tuber of potato, is mainly edible part of it and popular as nutrient for almost all nations. Tuberization in potato is a very complex biological occurrence affected by numerous ecological signals, genetics, plant nutrition and several different hormones. Many pests including nematodes limit potato tuber development that plant hormones play roles in nematode feeding cell formation. Parasitic nematodes, important pests which cause damage to plants, tubers, suck up nutrients from plants and weaken plant development and yield losses. Many genes involve in tuber development and plant response nematodes. The aim of this chapter is to demonstrate the new advances in the field of molecular host-nematode interactions and tuber development.

Keywords: Nematode, gall, tuber, potato, molecular, gene, interactions

1. Introduction

Potato (*Solanum tuberosum*) is one of the first domesticated vegetables with cultivation over 6000 years. It is the fourth most important staple food crop produced worldwide with continuously growing production capacity up to 370 million tonnes/year [1]. Potato tuber is rich in health-promoting carotenoids, anthocyanins, and antioxidants such as polyphenols, essential minerals, and amino acids [2].

The production of potatoes has been expeditiously increasing in the last forty years, especially in industrialising countries. However, the average amount of potatoes produced in developing countries is only half that of developed countries. The reasons for this are that modern agriculture is quite different between both developed and developing countries, and only limited contributions have been observed on potato yields revealed by modern breeding strategies in developing countries [3]. Because of these reasons, novel genes associated with yield, such as those related to flowering, tolerance to a/biotic stress conditions, and enhanced postharvest quality attributes should be characterised and introgressed into cultivated potato genotypes. The advances in different omic platforms (transcriptomic, metabolomic, and proteomic) not only reduces the costs but also provides expanded knowledge about diversity in crop genomes. The datasets provide an excellent resource for

selecting new genetic resources (e.g., single nucleotide polymorphisms, SNPs arrays) for introducing agronomically important improved varieties. The better linkage maps, gene annotations and much easier deciphering the genes related to different quality parameters, such as tuberization have been provided by releasing of potato genome sequence [4]. For example, 185 clones that had previously been SNP genotyped by the Solanaceae Coordinated Agricultural Project (SolCAP) and detected 981 features which represent a mixture of metabolites, and hydrolysed fragments of abundant proteins were examined [5]. Therefore, with the help of new genetic technologies, the quicker screening of large populations which improve the identification of quality candidate traits and genes will be more accessible and chargeable [6].

Potato tuberisation (tuber formation) is a complex physiological phenomenon regulated by both exogenously (environmental factors) and endogenously (metabolic pathways, hormones and genes) [7, 8]. Contrary to most plants that develop from roots, potato tuber originates from an underground specialised stem or stolons, accumulates starch which results in enlargement in favourable conditions [9]. This complex development process can be examined in four stages in its simplest form, which are stolon initiation, enlargement of apical and subapical parts of the stolon, cell divisions and enlargement for tuber is triggered, and resource storage (starch accumulation) until tuber reaches its final mass [10]. The induction of tuberisation is favoured under conditions of long dark periods, cool temperatures, and low amount of nitrogen fertilisation, regulation of a graft-transmissible signal transported from leaves to stolon tips for tuber-inducing stimuli [11]. Initiation of tuberisation signalling and the transition from stolon to tuber is a very dynamic process at the molecular level. Identification of FLOWERING LOCUS T (FT)-like protein (StSP6A), CONSTANS (CO), POTATO HOMEOBOX 1 (POTH1), StBEL5 transcription factor, and microRNA156 and-172 revealed the governing the tuber formation process in potato [12–15]. In stolon tips, before the onset of tuber initiation, StBEL5/StKNOX complex coordinates hundreds of genes, including the genes involved in phytohormone synthesis [11]. Signalling and crosstalk of phytohormones, abscisic acid (ABA), auxins, cytokinins (CKs), gibberellins (GAs), ethylene, and strigolactones (SLs), and other compounds, such as carbohydrates and organic acids are known to play important key roles in regulating the morphological events of tuber development [16].

Several biotic stress factors effect negatively on potato plants that plant parasitic nematodes which are among them cause significant damage to potato growth and tuber development.

2. Plant parasitic nematodes and host-plant interactions

Plant-parasitic nematodes are significant crop pests and cause billions of dollars around the globe [17]. Plant-parasitic nematodes (PPNs) have more than 4,100 species in the world [18]. They infect many crops encompassing from the Solanaceae family to Fabaceae and Poaceae families [19]. Plant-parasitic nematodes may divide based on feeding behaviour as ectoparasites, semi-endoparasites, and endoparasites [19, 20]. Ectoparasites do not spend their life cycle within the plant. However, endoparasitic nematodes spend all their life cycle within plant hosts. Root-knot nematodes (RKNs) are best examples of endoparasitic nematodes that complete their life cycle within a plant after entering the root. The RKN (*Meloidogyne* species) and *Globodera rostochiensis* and *Globodera pallida* (cyst nematodes) are known as noteworthy sedentary endoparasitic nematodes. The RKNs cause a unique feeding structure termed feeding site by modification of cell

wall molecular architecture. The host cell differentiation occurs in plant tissues following the infection of RKNs [21, 22]. After entering the root, cyst nematodes move intercellularly, Meloidogyne species move between the cells within the plant roots and cause galls. RKNs and cyst nematodes secrete nematode effectors to manipulate plant defence mechanisms and manipulate the cell wall for increasing the nematode parasitism [23].

During the pathogen attack, plants recognise pathogens with different pathogen recognition systems such as pathogen-associated recognition systems (PAMP) and damage-associated molecular patterns (DAMPs) [19, 24].

Many plant-parasitic nematode (PPNs) species cause damage in potatoes and decrease the tuber quality. There are many nematodes species are found in potato plants: *B. longicaudatus, H. pseudorobustus, H. galeatus, T. claytoni, Pratylenchus andinus, P. brachyurus, P. coffeae, P. crenatus, P. mediterraneus, P. minyus, P. neglectus, P. penetrans, P. scribneri, P. thornei, P. vulnus, P. zeae, N. dorsalis, D. dipsaci, Paratrichodorus spp., Trichodorus spp., Belonolaimus longicaudatus, Helicotylenchus pseudorobustus, Hoplolaimus galeatus, Tylenchorhynchus claytoni, Rotylenchulus reniform, Radopholus similis, Meloidogyne acronea, M. arenaria, M. incognita, M. fallax, M. hapla, M. javanica* and *Xiphinema spp* species [25]. Among those, some of them are major species: potato cyst nematodes (PCNs) *Globodera rostochiensis* and *G. pallida*, RKNs *Meloidogyne* spp., specifically *M. chitwoodi*, the root-lesion nematode *Pratylenchus* spp., *Ditylenchus destructor, Nacobbus aberrans* [25].

Among the plant-parasitic nematodes, RKNs are one of the most damaging nematode genera, particularly *Meloidogyne chitwoodi*, the most damaging species on tuber and decreases tuber quality (**Figure 1**). Therefore, this chapter mainly focuses on plant-root knot interactions.

Root-knot nematodes, which are found in the *Meloidogyne* genus, are economically significant PPNs in the world. They are obligate PPNs that cause damage to roots and tubers, resulting in a high amount of yield losses. This group of nematodes is mostly found in tropical and temperate zones around the globe. In addition to direct crop loss, RKNs have also quarantined organisms for many countries and need regulation [26]. There are many RKN species in the world. Meloidogyne chitwoodi is one of the most common and most damaging RKNs in potato areas among these species.

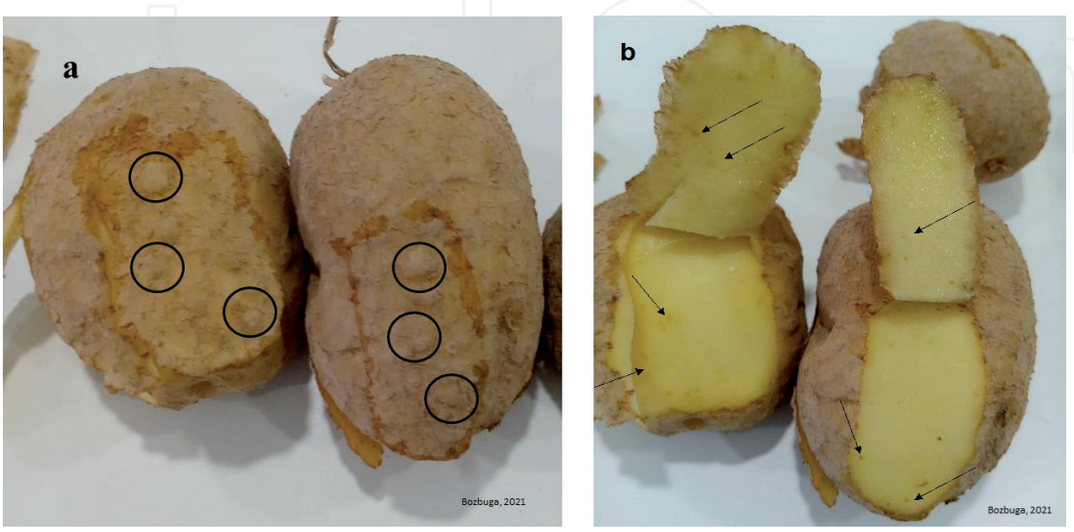

Figure 1.
Symptoms of an RKN species, Meloidogyne chitwoodi*, on potato tubers.* M. chitwoodi *Induced tuber deformations are shown (a). The nematode caused small swellings (pimple-like structures) on the tuber represent within circles (a). Damage caused from the nematode is seen when the potato tuber is peeled (b). Nematodes can be found in discoloured spots (indicated by arrow) in the potato tubers and feed there (b).*

Meloidogyne incognita, Meloidogyne arenaria, Meloidogyne luci and *Meloidogyne javanica*, are RKN species which are found in vegetable areas in Turkey [27]. Even *Meloidogyne* species has different races, for instance, *M. incognita* race 1, 2, 3, *M. javanica* race 3, and *M. arenaria* race1 and 3 [27]. Nematodes are densely found in many orchards where agriculture is carried out with cultivated plants belonging to the Solanaceae family, such as tomato, pepper, and eggplant [28]. *M. javanica, Meloidogyne acronea, M. fallax, M. chitwoodi, M. incognita, M. hapla, M. arenaria* are RKN species that cause damage to potatoes [25].

Potatoes are exposed to diseases and pests while growing. Nematodes that damage the tuber due to the propagation of potatoes by tubers constitute a serious problem in potato production. Nematode species such as potato cyst nematodes, RKNs (*Meloidogyne* spp.) are important potato pests [29]. Root-knot nematodes take the first place among plant-parasitic nematodes in terms of the level of economic damage they cause on plants [17].

In the second stage, juveniles and males of *M. chitwoodi* are thread-shaped, females are pear or lemon-shaped microscopic worms. The life cycle of *M. chitwoodi* takes place in approximately 3-4 weeks under favourable conditions. Although most reproduce parthenogenetically, sexual reproduction is also seen [30]. *M. chitwoodi* spends its first offspring on the potato roots, infects the tuber in the following generations, and develops there. A female can lay approximately 1000 eggs. The number of offspring per year varies, depending on the host plant condition and environmental conditions, especially temperature. *M. chitwoodi* needs 600-800 days to complete the first generation and 500-600 days to complete the next generations [31]. *M. chitwoodi* may infect many plants, but potato and tomato are good hosts and economically important nematode causing damage on potato [32]. It causes many pimple-like structures on tubers, and it is added to the quarantine list in Europe to prevent the distribution within this continent [32]. *Meloidogyne chitwoodi,* feeding in potato plant tubers, may occur in the form of spots caused by the colours visible on the bottom when the tuber is peeled off, causing quality problems (**Figure 1a**). Many necrotic spots are seen on the fleshy parts of the potato tuber. Therefore, the tuber's quality decreases, and it's caused by the nematode (**Figure 1b**).

The second stage is the juvenile root-knot nematodes, an infective stage that is found in free form in the soil which enters the root tip [33]. Chemotactic genes may be involved in host-finding strategies, e.g., *Meloidogyne incognita*. Sucrose, glucose, arabinose, galactose, and mannitol are chemo-attractants of *Meloidogyne incognita*, and signal transduction may involve Mi-odr-1, Mi-odr-3, Mi-tax-4 and Mi-tax-2genes [34–36]. Vanillic acid, lauric acid (signal transduction may require *Mi-odr-1, Mi-odr-3, Mi-tax-2 and Mi-tax-4* genes) [34–37], arginine, lysine [34–36] and calcium chloride [35, 38], *Mi-odr-3, Mi-tax-2, Mi-tax-4* genes are chemotactic genes involve in *Meloidogyne incognita* and predicted functions are membrane-bound guanylyl cyclase that produces secondary messenger, α protein that regulates cyclic nucleotide metabolism, subunits of cyclic nucleotide-gated cation channel involved in G-protein-mediated signalling, respectively [35, 36]. Carbon dioxide (CO2) is an important attractant released by roots for RKNs [39], and lauric acid controls the chemotaxis of root-knot nematodes [37].

In the second stage, juveniles move between the cells (without damaging cells) and reach the feeding site [40]. Sugar transporter genes: Sugars Will Eventually be Exported Transporter (SWEET), vacuolar glucose transporter (VGT), tonoplast monosaccharide transporter (TMT), and sucrose transporter (SUT/SUC) genes may be involved during early infection of *M. incognita* [41]. The host gene expression is manipulated by RKNs [42]. Nematodes secrete several effectors to enable parasitism that macrophage migration inhibitory factors (MIFs) are among them

that MIF-like effector overwhelms the *Arabidopsis* immunity and enables *M. incognita* parasitism by cooperating with plant annexins [43]. Similarly, SlWRKY3 plays a role in plant resistance to *Meloidogyne javanica* by involving lipids and hormone activation [44]. Mi gene decreased ability for the nematode infection in tomato through the infection of *M. incognita* [45]. *Meloidogyne incognita* Profilin 3 (MiPFN3) effector results in the actin cytoskeleton of *Arabidopsis* [46].

During the feeding, the nematode creates a feeding tube where it inserts the stylet to release nematode secretions of glands to manipulate plant resistance and create a feeding site [47]. Karyokinesis occurs without cytokinesis in nematode feeding sites termed giant cells in plant tissues [48]. Several nuclei are found in giant cells, and giant cells are much larger than normal cells. The thickness of giant cell walls in the vascular cylinder is much higher than the thickness of neighbouring cell walls (CWs) induced by *M. incognita*. The thickness of giant cell walls may change depending on the host plant [49]. The thickness of giant CWs of Aduki bean is thicker than *Arabidopsis* and maize, and the giant cell walls are a minimum of 2.5 times thicker than neighbouring cell walls [49].

3. Formation of galls and plant- nematode molecular interactions

Nematodes cause damage to plants by influencing the phytohormone structure and modify plant development to establish feeding sites in plants [50]. Plant hormones such as auxin and cytokinin play an important role in forming a sedentary nematode (Cyst and RKN) feeding site [50]. Auxin, a plant hormone, is involved in the formation of galls after infection of RKN, *Meloidogyne javanica* in plant roots [51]. Auxin triggers the gall initiation; however, it is not needed for the later development of the galls [51]. Cytokinin and ethylene may be involved in plant gall formation processes [48]. Ethylene involves in RKN, *Meloidogyne javanica*, induced gall formation in tomato plants [52]. Some plant hormones (jasmonate acid and salicylate (SA)) are involved in plant defence; however, the nematode secretes chorismate mutase to decrease plant defence [50]. The increased level of Pathogenesis related 1 and Pathogenesis related 5 gene expressions are seen during the SA-induced *M. incognita* infection [53, 54]. Auxin performs a function in a cell division and development in host roots [55]. Auxin transport involves developing gall and expansion in the roots of *Arabidopsis thaliana* after the infection of *M. incognita* [56]. Modification of the auxin accumulation and distribution in the roots of plants is observed after infection of *M. javanica* [51]. Plant growth hormones, particularly cytokinin and auxin, play an important role in causing plant galls in pathogen-infected hosts [57].

Small RNAs are differentially expressed in the galls induced by *Meloidogyne javanica* in *Arabidopsis* [58]. Acting as vital mechanisms in gene expression, MicroRNAs are small non-coding RNAs, play an important role in plant nematode interactions. For example, miR159 and MYB33 play an essential role in establishing giant cells of *Arabidopsis* infected by RKN [59]. The specific gene expression patterns appear in nematode induced galls caused by the RKN [60]. Root-knot nematodes and cyst nematodes (CNs) are significant plant parasitic nematode genera of PPNs [17]. They cause hypertrophied and multinucleate feeding cells in the host plant to allow nutrient flow, and they are metabolically active with many organelles, dense cytoplasm, and modifying cell walls [49, 61, 62]. The second stage juveniles of RKNs choose few parenchyma cells and stimulate dedifferentiation into giant cells through succeeding mitosis deprived of cytokinesis [22, 63]. During the nematode infection, nematodes manipulate plant functions, plant defence, phytohormone [50], and cell wall modification [22]. Auxin and ethylene are

involved in the transfer cells (TCs) in initial nematode feeding cells of *Arabidopsis* [64]. Auxin and cytokinin are involved in expansion of phloem in nematode induced feeding sites [65]. The atypical transcription factor, DP-E2F-like 1 (DEL1), suppresses salicylic acid (SA) gathering in *Meloidogyne incognita*-induced galls and increased the level of lignification in galls are found in the roots of *Arabidopsis thaliana* [66].

Pattern-triggered immunity (PTI) responses involve camalexin and glucosinolate biosynthesis that BAK1-dependent and -independent PTI are nematode recognition mechanisms in *Arabidopsis* [67]. Msp40 effector of RKN manipulates plant immunity to enable parasitism by suppressing PTI and/or ETI signals [68]. Nematode-associated molecular pattern (NAMP) plays an important role [69].

Microbes attaching to endoparasitic phytonematodes: PTI-responsive defence genes, particularly jasmonic acid-mediated PTI marker genes TFT1 and GRAS4.1, are up-regulated following microbe infections and *M. hapla* in suppressive soil, stimulating initial basal defences in plants by this way overwhelming nematode act in plant roots [70]. TIR-NB-LRR immune receptor DSC1 (DOMINANT SUPPRESSOR OF Camta 3 NUMBER 1) and TIR-NB-LRR-WRKY-MAPx protein WRKY19 adjust basal stages of immunity against *M. incognita* in *Arabidopsis* [71].

Nematodes may modify several plant hormones for successful parasitism. Furthermore, each defined hormone co-ordinately stimulates (IAA, CKs, ABA, and JA) or suppresses (GAs) the formation of tuberization. Numerous researches have reported the importance of the hormones and the genes to play key roles in the synthesis for tuberization. In this part of the chapter, recent studies will be discussed by bringing together the genes related to hormones that are involved in the formation of potato tubers.

4. Hormonal regulation of tuberisation

With respect to the involvement of hormones, gibberellic acid (GA) has been described as one of the most important regulators for tuber development [72, 73]. It is the required hormone for the elongation of stolon meristems during the initiation of tuberisation [74]. Copalyl pyrophosphate synthase (CPS), ent-kaurene synthase (KS), ent-kaurene oxidase (KO), GA-20 oxidase (GA20ox), and GA-2 oxidase (GA2ox) are described as the key enzymes involved in the synthesis of GAs. CPS is the first key enzyme of the gibberellin biosynthesis pathway, which can be stopped by mutating the CPS. However, there is no study that reveals the functioning mechanism of the *CPS* gene, its expression increases during potato elongation [75]. GA20ox and GA3ox catalyse the last two steps of active GA biosynthesis; the former is directly related to the photoperiod of short/long days [76]. Knocking down the expression of the potato *GA20ox-1* gene, resulted in reduced stem elongation and increased tuberisation and yield of tubers [77]. While over-expression of *StGA3ox2* slightly delayed tuberisation phenotype, down-regulation of it did not change the time point of tuber initiation with a smaller average tuber weight [78]. Higher expression of *StGA2ox1* was observed during the early stages of potato tuber development, increased and decreased levels of the gene expression resulted in earlier and delayed tuberisation, respectively [79]. In a recent study, potato plants transformed with the AtGA20-oxidase or *AtGA2-oxidase* genes, the former promotes biosynthesis of bioactive gibberellins (GAs) and the latter acting oppositely, respectively. While tuber formation was increased in plants transformed with *AtGA2-oxidase*, the potato productivity was reduced in plants transformed with AtGA20-oxidase, which promotes active GA synthesis [80]. Overall, GAs levels are quite high at the stolon tips of potato plants and go down intensely when the stolon

tip starts swelling and remains at a low-level during tuber formation [81]. These previous and recent studies confirm that GAs are the main tuberisation inhibitors.

Auxin is an exceptional plant hormone. It plays pronounced roles in many plant developmental processes, including tuber initiation, which is crosstalk with gibberellin and strigolactone. In other words, at the initiation of tuber development, the number of GA decreases, whereas that of auxin increases in the stolon subapical region which results in a swollen stolon [82]. The roles of auxin hormone in various biosynthesis metabolisms have been explained in detail [83]. The amount of endogenous auxin positively correlated to tuber growth rate [84]. If it is zoomed at molecular studies, changes in the expression of auxin transport (PIN gene family), auxin response factors (ARF), and Aux/IAA genes during the tuber initiation have been shown [85, 86]. Auxin transcription factor6 (ARF6) decreased its expression several-fold during the transition from longitudinal to transverse cell division at swelling stolon tips [85]. In transgenic potato plants, tuber formation was stimulated by an additional auxin biosynthesis gene (*tms1*) under the control of the tuber-specific B33 promoter [80]. *StARF1/2a* expression was relatively high in stolons, which might have contributions to the swelling of stolons [87]. Indole-3-acetic acid (IAA), one of the most abundant natural forms of auxin, was found extensively across the plants. The role of *StIAA* genes in tuber development was assessed, and 12 genes highly expressed in stolon organs and during the tuberisation stages. Therefore, *Aux/IAA* genes could be used as novel potential candidate genes to improve tuber development of potatoes. With the advent of bioinformatic analysis, it was observed that the gene regulatory network and tuberisation pathway controlled by mobile RNAs (StBEL5 and POTH1) and proteins (StPTB1/6 and StSP6A) have appeared to be conserved among storage root crops like potato, carrot and radish. In this way, StBEL5 targeting genes involved in auxin biosynthesis was unveiled and may prove to be one of the key factors involved in the initiation of potato tuberisation [88]. The *PIN* genes have a central role in polar auxin transport and subsequently mediate the growth of different plant tissues, and 10 of PIN genes were identified in potatoes [73]. *StPIN2* and *StPIN4* genes are highly homologous with *Arabidopsis thaliana* PINs, displayed a role for auxin in tuber development [86]. Although it is insufficient to examine the auxin hormone alone, and the exact role of this hormone is still controversial, a moderate organ-specific increase in auxin level may be suggested as an encouraging approach for improvement of potato productivity by biotechnological methods.

Abscisic acid (ABA) is also well characterised and has been shown to have a supportive effect on tuber development when applied exogenously and to act antagonistically towards GAs, auxins and cytokinins [89]. However, the main role for ABA was determined as dormancy induction and maintenance by different working groups [90]. Genes encoding most enzymes of the ABA synthesis pathway have been identified and cloned from different species [91]. Over-expression of the ABA synthetic gene *StNCED2* promotes tuber yield due to the increase of single potato tuber weight, not the tuber number. ABA signalling transcription factor (TF) *StABF1* and GA metabolism gene *StGA2ox1* were up-regulated while GA synthetic genes *StGA3ox2, StGA20ox1*, and GA signalling TF GAMYB were down-regulated in stolon and tubers of over-expression lines, suggesting there might be a direct interaction between ABA and GA. Ectopic expression of *Arabidopsis ABF4* or *ABF2* (ABRE-binding factor) proteins are transcription factors involved in ABA and stress signalling, which positively regulate potato tuber induction. Increasing of ABA also resulted in decreased expression of GA metabolism genes, which shows ABA-GA signalling crosstalk during tuberisation [92].

Among the phytohormones, it has long been known that cytokinins (CKs) function as universal regulators of storage-organ formation in plants. It was previously

shown that CKs have a stimulating effect on tuber formation [93, 94]. CKs are an agronomically and commercially important trait, as CK application before tuber formation can increase tuber yield [95]. However, although there are many effects of CKs on tuber development, tuber development regulated by CKs has not been fully elucidated at molecular level. The role of CKs for tuberisation is closely related to differential expression level of the genes, which can directly reflect the changes of related protein levels and metabolism regulation. Over-expression of *AtCKX1* from *A. thaliana* in soil-grown potato (*Solanum tuberosum* L.) displayed a severely altered phenotype, including reduced tuber yield and morphology. *AtCKX1*-over-expression negatively affected tuber number and tuber size per plant, proving that cytokinin deficiency had significant effects on tuber induction and tuber initiation/growth [96]. In another study, introducing of the *ipt* gene related to bacterial cytokinin biosynthesis, under control of a chalcone synthase promoter (PCHS) generated potato plants with more tubers but reduced tuber weight and nitrogen content [97].

Strigolactones (SLs), carotenoid-derived plant metabolites, have emerged as an important new plant hormone, making it more attractive than other endogenous plant hormones. They mainly regulate various aspects of plant architecture, including the inhibition of shoot branching [98]. Because SLs is a new hormone class, knowledge about SLs related genes in tuberisation and their regulation is much less compared to other hormones. Transgenic potato plants generated by down-regulating *CAROTENOID CLEAVAGE DIOXYGENASE8* (*CCD8*) gene, key in the SL biosynthetic pathway, resulted in changes in potato tuber morphology [99]. Therefore, interestingly, stolons of the StCCD8 RNAi lines tend to emerge from the soil and form aerial shoots. The transgenic lines also provided a higher number of tubers but smaller in size. As it has just been mentioned, SLs is quite a new plant hormone. Therefore, more genes on the SLs synthesis pathway should be functionally characterised in potato tuber development.

5. Postharvest

Potato tubers are generally consumed fresh, but they can also be consumed throughout the year. Therefore, it might be necessary to store them under favourable conditions for an extended period like from one growing season to another one. After the potato has completed its maturation process, they transit to the dormancy period, in which reserves of starch and protein are kept for future sprouts [100]. A major commercial issue is dormancy breakage following sprouting, resulting in quality losses and reduced tuber marketability. CIPC ([isopropyl-N-(3-chlorophenyl) carbamate) is particularly important as a sprout suppressant for potatoes during storage. However, CIPC has been proven not to be safe for humans and the environment in recent years [101]. Therefore, alternate sprout suppressant approaches, for example constant ethylene supplement, could be used to suppress post-harvest sprouting [102]. Storing potato tubers which were treated with/without ethylene binding inhibitor 1-methylcyclopropene (1-MCP at 1 μL L − 1 for 24 h), in air or air enhanced with constant ethylene (10 μL L − 1) [103], revealed extended ecodormancy in the potato samples treated with grouping of ethylene plus 1-MCP, while the inhibited sprout elongation in exogenous ethylene treated samples. Moreover, at the molecular level, continuous ethylene application activated two genes coding 1-aminocyclopropane-1-carboxylate oxidase (ACO) and parenchymatic ABA catabolism via *CYP707A*, encoding ABA 8´hydroxylase upregulation. Consequently, this novel study provided information on how exogenous ethylene and/or 1-MCP elicited their results on the tuber quality of potato.

Another technology that can be used instead of CIPC is in order to grow new potato cultivars with reduced rate of sprout development and/or a long dormancy period. For example, down- and up-regulation of StCEN accompanying to an enhanced and decreased of sprout development than controls, respectively [103, 104], showed that there is no link between exogenous ethylene and *StCEN* expression. This result supports [104] as endogenous ethylene production from transgenic *StCEN* tubers, generally, is not meaningfully dissimilar from controls. The dormancy period of tubers is regulated by both internal/external factors and plant hormones, genetic factors, post-harvest storage conditions, and particular signalling molecules, such as nitric oxide (NO) and gibberellins [105, 106]. Although there are many studies specific to the mentioned factors, this part will try to concentrate on main molecular studies related to the post-harvest condition of potato tuber.

The plant cell wall composed of mainly pectin, is a complex and dynamic network of polysaccharides. Cell wall compositions function in plant development, stress responses, shelf life and plant growth. Basically, the primary cell wall (CW) consists of cellulosic (1,4-β-D-glucan), hemicellulosic polysaccharides for example xyloglucan (XG), and pectic polysaccharides for example homogalacturonan (HG) and rhamnogalacturonans I-II, which are all explained very well in different studies [107]. The recent vision of the plant cell wall (PCW) suggests that the relationship of cellulose–pectin is more extensive and makes more important contributions to wall biomechanical properties than was previously thought [108]. The CWs of tuber tissues are constitute of cellulose and hemicellulose which hold together a large amount of pectic polysaccharides [109]. The texture of plant products is highly affected by the cell wall structure, and modifications of this part of the cell are the biggest contributors to texture. Generally, during fruit maturation, enzyme activities of hemicelluloses (HCL), celluloses (Cel), β-galactosidases (β-Gal), polygalacturonase (PG) and increase to lessen the intercellular associations and accomplish cell seperation, ensuing in modifications in fruit roughness and softening [110, 111]. Potato tuber texture is one of the most important quality characteristics of cooked potato and an obviously dominant trait that influences consumer preference, as mainly affecting the taste, aroma, and mouthfeel of the storage roots in potato [112]. Two types of potatoes that differ in terms of texture represented an extreme variant in textural properties. The expression levels of the genes encoding two important cell wall degrading enzymes, pectin acetylesterase and xyloglucan endotransglycosylase, were significantly higher in Phureja, an accession that greatly reduced cooking time compared to Tuberosum accession [113]. In another recent study, the correlation between the texture of cooked potato and β-amylase activity shows the negative correlation between the enzyme activity and firmness in cooked sweet potato [114].

Moreover, various studies have been conducted to elucidate the cell wall mechanism and texture changes in potato tuber. For example, two potato varieties showing significant differences in texture (Yushu No 10 with soft texture, Mianfen No 1 with firm texture) have been recently characterised in terms of the cell wall composition content and cell wall-related enzyme activities [60]. The 'Yushu No 10′ have more than twice soluble pectin content than 'Mianfen No 1′, but the unsolvable pectin ingredient was lower than that of 'Mianfen No 1′. It has been an important correlation of gumminess and chewiness between hemicellulose activity of 'Yushu No 10', and 'Mianfen No 1′ having an unimportant correlation with Cel, PG, HCL, and β-Gal enzymes [115].

Potato is a highly heterozygous crop. Therefore, genetic advance of this crop using conventional breeding is labour-intensive and time-consuming work. For this reason, genetic engineering offers an opportunity to progress a limited genetic gain whilst retaining the well-known advantages of traditional varieties. The

genetically modified potatoes show developments in quality traits that benefit farmers [116], consumers [117], and for the land in terms of sustainability [118]. In recent years, with the increasingly aggravated global warming conditions, the research concentrated more on generation potato crops tolerant against extreme conditions such as salinity and drought [119]. However, due to the concept of this chapter, we try to cover the transgenic studies using cell wall related enzymes. Transgenic potato made by the introduction of the gene encoding rhamnogalacturonan lyase (RGL) from *Aspergillus aculeatus* had a surface with a wrinkled appearance [120]. The expression of a β-galactosidase (β-Gal) gene from *Cicer arietinum* introduced into the potato and resulted in the removal of the galactan side chains from RG-I [121]. In a more recent study, genes encoding β-Gal or RG-I lyase were introduced to wild-type potato Karnico. The mutant lines of β-Gal contained 54% less galactose, representing shorter galactan side chains. Over-expression RG-I lyase potato lines contained more galacturonic acid and less galactose, which was due to the removal of galactan-rich RG-I branches [122]. Over-expression of endo-1,5-α-arabinanase of *A. aculeatus* caused no modified phenotype comparison the wild type but reduced galactan sidechains of RGI and increased the number of uronic acids [123].

High-throughput RNA sequencing (RNA-Seq) is a powerful tool for revelaing the variability of gene expression levels between different samples. An RNA-Seq was performed to investigate the potato tuber dormancy release process, and 5912 and 3885 DEGs (differentially expressed genes) from dormancy tuber (DT) vs. dormancy release tuber (DRT) and DRT vs. sprouting tuber (ST), respectively [124]. In another study carried out by iTRAQ labelling strategy, a total of 1752 proteins associated with tuber dormancy release in DT, DRT, and ST were identified. lncRNAs generally have structural features of mRNA, with exceptional roles in DNA methylation, histone modification, chromatin remodelling, and other biological processes. Moreover, lncRNAs regulated the expression of target genes by interacting with DNA, RNA, and proteins [125]. In a recent study, 235 potato miRNAs out of 386 lncRNAs differentially expressed during sprouting were identified as putative targets. The results provided lncRNAs were involved in the potato tuber sprouting process and identified their possible functions in dormancy and sprouting [126]. Based on these results, it can be said that tuber dormancy release is a complex process, and the genes upregulated during this period suggest the activation of multiple mechanisms enabling the tuber dormancy release.

Enzymatic browning is a serious problem for both producers and the industry as the tubers can be affected during storage and distribution. This problem is usually overcomed by applying chemical and/or physical agents or storing the potato in controlled storage conditions [127]. However, keeping harvested potato tubers at low temperatures causes physiological changes, such as photosynthetic capacity, electrolyte leakage, and respiration rates [128]. Transcriptomic and proteomic analysis were carried out in potato tubers stored at 15°C, 4°C, and 0°C to examine the mechanism of cold responses during post-harvest storage. The results showed that sugar accumulation increased at low temperatures.

Moreover, fifteen heat shock proteins (Hsps) were upregulated by low temperatures, which may act to prevent damage from cold stress [129]. Application of the CRISPR/Cas9 to induce mutations in the StPPO2 gene in the tetraploid variety 'Desiree' reduced up to 69% in tuber PPO (Polyphenol oxidase) activity and 73% in enzymatic browning in transgenic lines compared to control [130]. This result demonstrated that the CRISPR/Cas9 system has been successfully used to generate new potato varieties that reduce enzymatic browning through specific regulation of a single member of the StPPO gene family.

6. Conclusion

Plant hormones are involved in the gall formation and tuber development of potato plants. Numerous nematode species infects potato and cause an adverse effect on plant development and crop quality. Specifically, CNs (*Globodera rostochiensis* and *G. pallida*) and RKNs (*Meloidogyne chitwoodi*) cause severe damage to potato plants and RKNs cause gall formations in the roots of plants. The gall formation has not been fully understood yet. *M. chitwoodi* causes damage to tubers, too. In addition to direct damage of these nematodes, some nematode species, such as root-knot nematodes, are also quarantined organisms that cause restriction of trade. For this reason, they are extremely important organisms for potato production due to causing crop losses. Many genes are involved in nematode parasitism and plant defence mechanism. Plant-parasitic nematodes cause damage in potato tuber by manipulating plant hormones to create feeding sites in potatoes. Understanding the molecular mechanisms of plant nematode interactions (gall formation) and molecular mechanism of tuber development may share some similarities, leading to the researcher creating better potato crops against biotic stress as a future aspect. In this way, using improved pest management strategies and new insights in genetic breeding against nematode may lead to producing healthier crops and high-quality tubers using new molecular and genetic methods.

To improve future potato tuber quality, it should be worked with industry and academic groups to meet producer and consumer preferences. With molecular and improved phenotyping techniques, knowledge about the mechanisms affecting potato tuber development, texture and post-harvest storage conditions will be increased for potato tuber quality. Furthermore, this combined information will profit the improvement of new cultivars by enlarging sustainable agricultural practices and storing approaches. Therefore, the combination of novel molecular techniques (gene-editing technologies) and pre/post-harvest applications will help the improvement, protection and viability of upcoming tuber quality.

Conflict of interest

The authors declare no conflict of interest.

Author details

Refik Bozbuga[1*] and Selman Uluisik[2]

1 Biological Control Research Institute, Adana, Turkey

2 Burdur Food Agriculture and Livestock Vocational School, Burdur Mehmet Akif Ersoy University, Burdur, Turkey

*Address all correspondence to: refikbozbuga@gmail.com

References

[1] FAO, Food and Agriculture Organization of the United Nations, http://www.fao.org/home/en/(Date of access: 21.03.2021).

[2] Fogelman E, Oren-Shamir M, Hirschberg J, Mandolino G, Parisi B, Ovadia R, Tanami Z, Faigenboim A, Ginzberg I. Nutritional value of potato (*Solanum tuberosum*) in hot climates: anthocyanins, carotenoids, and steroidal glycoalkaloids. Planta. 2019; 249: 1143-1155. DOI: https://doi.org/10.1007/s00425-018-03078-y

[3] Ghislain M., Douches DS. The Genes and Genomes of the Potato. In: Campos H., Ortiz O. (eds) The Potato Crop. Springer, Cham. 2020. https://doi.org/10.1007/978-3-030-28683-5_5

[4] The Potato Genome Sequencing Consortium. Genome sequence and analysis of the tuber crop potato. Nature. 2011; 475: 89-195. DOI: https://doi.org/10.1038/nature10158

[5] Levina A V, Hoekenga O, Gordin M, Broeckling C, De Jong WS. 2020. Genetic analysis of potato tuber metabolite composition: Genome-wide association studies applied to a nontargeted metabolome. Crop Science. 2020; 61 (1): 591-603. DOI: 10.1002/csc2.20398

[6] Khlestkin VK, Erst TV, Rozanova IV, Efimov VM, Khlestkina EK. 2020. Genetic loci determining potato starch yield and granule morphology revealed by genome-wide association study (GWAS). Plant Biology. 2020; 8:e10286.

[7] Paradiso R, Arena C, Rouphael Y, d'Aquino L, Makris K, Vitaglione P, De Pascale S. Growth, photosynthetic activity and tuber quality of two potato cultivars in controlled environment as affected by light source. Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology. 2019; 153(5): 725-735. https://doi.org/10.1080/11263504.2018.1549603

[8] Cheng L, Wang D, Wang Y, Xue H, Zhang F. 2020. An integrative overview of physiological and proteomic changes of cytokinin-induced potato (*Solanum tuberosum* L.) tuber development in vitro. Plant Physiology. 2020; 168(3): 675-693. DOI: 10.1111/ppl.13014

[9] Fernie AR, Willmitzer L. Molecular and biochemical triggers of potato tuber development. Plant Physiology. 2001; 127: 1459-1465. DOI: https://doi.org/10.1104/pp.010764

[10] Viola R, Roberts AG, Haupt S, Gazzani S, Hancock RD, Marmiroli N, Machray GC, Oparka KJ. Tuberization in potato involves a switch from apoplastic to symplastic phloem unloading. Plant Cell, 2001; 13: 385-398. DOI: 10.1105/tpc.13.2.385

[11] Hannapel DJ, Sharma P, Lin T, Banerjee AK. The multiple signals that control tuber formation. Plant Physiology, 2017; 174: 845-856. DOI: https://doi.org/10.1104/pp.17.00272

[12] Martin A, Adam H, Díaz-Mendoza M, Zurczak M, González-Schain ND, Suarez-Lopez P. Graft-transmissible induction of potato tuberization by the microRNA miR172. Development. 2009; 136 (17): 2873-2881. DOI: https://doi.org/10.1242/dev.031658

[13] Navarro C, Abelenda, JA, Cruz-Oró E, Cuéllar CA, Tamaki S, Silva J, Shimamoto K, Prat S. Control of flowering and storage organ formation in potato by FLOWERING LOCUS T. Nature. 2011; 478(7367):119-22. DOI: 10.1038/nature10431.

[14] González-Schain ND, Díaz-Mendoza M, Żurczak M, Suárez-López P. Potato CONSTANS is involved

in photoperiodic tuberization in a graft-transmissible manner. The Plant Journal. 2012; 70(4): 678-690. https://doi.org/10.1111/j.1365-313X.2012.04909.x

[15] Sharma P, Lin T, Grandellis C, Yu M, Hannapel DJ. The BEL1-like family of transcription factors in potato. Journal of Experimental Botany. 2014; 65: 709-723. https://doi.org/10.1093/jxb/ert432

[16] Alamar MC, Tosetti R, Landahl S, Bermejo A, Terry LA. Assuring Potato Tuber Quality during Storage: A Future Perspective. Frontiers in Plant Science. 2017; 8: 2034. doi: 10.3389/fpls.2017.02034

[17] Jones JT, Haegeman A, Danchin EG, Gaur, HS, Helder J, Jones MG., et al. Top 10 plant-parasitic nematodes in molecular plant pathology. Mol. Plant Pathol. 2013; 14 (9): 946-961. doi: 10.1111/mpp.12057

[18] Decraemer W, Hunt D. Structure and classification, in Plant Nematology, eds Perry RN, Moens M. (Wallingford: CAB International. 2006; 3-32.

[19] Sato K, Kadota Y, Shirasu K. Plant Immune Responses to Parasitic Nematodes. Front. Plant Sci. 2019; 10:1165. doi: 10.3389/fpls.2019.01165

[20] Decraemer W, Hunt, DJ. Structure and classification, in Plant Nematology, 2 ed. Eds. Perry RN, Moens M. Wallingford, UK: CABI Publishing. 2013; 3-39. doi: 10.1079/9781780641515.0003

[21] Perry RN, Moens M, Starr JL. Root-knot Nematodes Root-Knot Nematodes. 2010. Oxfordshire, UK: CAB International.

[22] Bozbuga R, Lilley CJ, Knox JP, Urwin PE. Host-specific signatures of the cell wall changes induced by the plant parasitic nematode, *Meloidogyne incognita*. Sci Rep. 2018; 8, 17302 https://doi.org/10.1038/s41598-018-35529-7

[23] Gheysen G, Mitchum MG. How nematodes manipulate plant development pathways for infection. Curr. Opin. Plant Biol. 2011; 14 (4), 415-421. doi: 10.1016/j.pbi.2011.03.012

[24] Jones JD, Dangl JL. The plant immune system. Nature. 2006; 444 (7117), 323-329. doi: 10.1038/nature05286

[25] Lima FSO, Vanessa SM, Edvar SS, Maria A.S. Carvalho, Teixeira RA, Silva JC, Correa VR. Nematodes Affecting Potato and Sustainable Practices for Their Management, Potato - From Incas to All Over the World, Mustafa Yildiz, IntechOpen 2018; DOI: 10.5772/intechopen.73056.

[26] Moens M, Perry RN, Starr JL .*Meloidogyne* species: A diverse group of novel and important plant parasites. In: Perry RN, Moens M, Starr JL (eds) Root-Knot Nematodes. CABI Publishing, Wallingford. 2009; 1-17

[27] Gürkan B, Çetintaş R, Gürkan T. Gaziantep ve Osmaniye Sebze Alanlarında Bulunan Kök-ur Nematodu Türleri (*Meloidogyne* spp.)'nin Teşhisi ile Bazı Nematod Popülasyon Irklarının Belirlenmesi. KSÜ Tarım ve Doğa Derg. 2019; 22(Ek Sayı 1): 113-124. DOI: 10.18016/ksutarimdoga.v22i49073.551240

[28] Yağcı M, Kaşkavalcı G. Distribution and identification of root-knot nematode (*Meloidogyne* spp) species in Peach growing areas of Aegean Region, Ege Univ., Ziraat Fakültesi dergisi. 2018; 55, (3): 305-310.

[29] Avcı GK, Pırlak U, Toktay H, Özarslandan A, İmren M, Canhilal R. Tohumluk Patates Yumrularinda Kök-Ur Nematodu (*Meloidogyne chitwoodi*) Zarari Ve Mücadele Yöntemleri . Uluslararası Katılımlı Türkiye 6.

Tohumculuk Kongresi Bildiri kitabı. 2018; 78-83.

[30] Van der Beek JG, Karssen G. Interspecific hybridization of meiotic parthenogenetic *Meloidogyne chitwoodi* and *M. fallax.* Phytopathology. 1997; 87:1061-1066 . 10.1094/PHYTO. 1997.87.10.1061

[31] Pinkerton JN, Santo GS, Mojtahedi H. Population dynamics of *Meloidogyne chitwoodi* on Russet Burbank potatoes in relation to degree-day accumulation. Journal of Nematology. 1991; 23, 283-290.

[32] Hunt D, Handoo Z. Taxonomy, Identification and Principal Species, 55-88. In Root- Knot Nematodes, (Eds. R. N. Perry, M. Moens & J. L. Starr). CABI, London. 2009; 488.

[33] Bleve-Zacheo T, Melillo MT, Castagnone-Sereno P. The contribution of biotechnology to root-knot nematode control in tomato plants. Pest Technology, Global Science Books. 2007; 1: 1-16.

[34] Fleming TR, Maule AG, Fleming CC. Chemosensory Responses of Plant Parasitic Nematodes to Selected Phytochemicals Reveal Long-Term Habituation Traits. J. Nematol. 2017; 49 (4), 462-471.

[35] Tsai AY, Oota M, Sawa S. Chemotactic Host-Finding Strategies of Plant Endoparasites and Endophytes. Front Plant Sci. 2020; 11:1167. doi: 10.3389/fpls.2020.01167.

[36] Shivakumara TN, Dutta TK, Chaudhary S, von Reuss SH, Williamson VM, Rao U. Homologs of *Caenorhabditis elegans* Chemosensory Genes Have Roles in Behavior and Chemotaxis in the Root-Knot Nematode *Meloidogyne incognita*. Mol. Plant Microbe Interact. 2019; 32 (7), 876-887. 10.1094/MPMI-08-18-0226-R

[37] Dong L, Li X, Huang L, Gao Y, Zhong L, Zheng Y, et al. Lauric acid in crown daisy root exudate potently regulates root-knot nematode chemotaxis and disrupts Mi-flp-18 expression to block infection. J. Exp. Bot. 2014; 65 (1), 131-141. 10.1093/jxb/ert356

[38] Wang C, Masler EP, Rogers ST. Responses of *Heterodera glycines* and Meloidogyne incognita Infective Juveniles to Root Tissues, Root Exudates, and Root Extracts from Three Plant Species. Plant Dis. 2018; 102 (9), 1733-1740. 10.1094/PDIS-09-17-1445-RE

[39] Rasmann S, Ali JG, Helder J, van der Putten WH. Ecology and evolution of soil nematode chemotaxis. J. Chem. Ecol. 2012; 38, 615-628. 10.1007/s10886-012-0118-6

[40] Wyss U, Grundler FMW. Feeding-behavior of sedentary plant parasitic nematodes. Netherlands Journal of Plant Pathology. 1992; 98, 165-173.

[41] Zhao D, You Y, Fan H, Zhu X, Wang Y, Duan Y, Xuan Y, Chen L. The Role of Sugar Transporter Genes during Early Infection by Root-Knot Nematodes. Int J Mol Sci. 2018; 19(1):302. doi: 10.3390/ijms19010302.

[42] Bird DM. Manipulation of host gene expression by root-knot nematodes. J Parasitol. 1996; 82(6):881-8.

[43] Zhao J, Li L, Liu Q, Liu P, Li S, Yang D, Chen Y, Pagnotta S, Favery B, Abad P, Jian H. A MIF-like effector suppresses plant immunity and facilitates nematode parasitism by interacting with plant annexins. J Exp Bot. 2019; 70(20):5943-5958. doi: 10.1093/jxb/erz348.

[44] Chinnapandi B, Bucki P, Fitoussi N, Kolomiets M, Borrego E, Braun Miyara S. Tomato SlWRKY3 acts as a positive regulator for resistance against

the root-knot nematode *Meloidogyne javanica* by activating lipids and hormone-mediated defense-signaling pathways. Plant Signal Behav. 2019; 14(6):1601951. doi: 10.1080/15592324.2019.1601951.

[45] Bozbuga R, Dasgan HY, Akhoundnejad Y, Imren M, Günay O, Toktay H. Effect of *Mi* gene and nematode resistance on tomato genotypes using molecular and screening assay. Cytology and Genetics. 2020; 54:154-164. https://doi.org/10.3103/S0095452720020048

[46] Leelarasamee N, Zhang L, Gleason C. The root-knot nematode effector MiPFN3 disrupts plant actin filaments and promotes parasitism. PLoS Pathog. 2018; 14(3):e1006947. doi: 10.1371/journal.ppat.1006947.

[47] Hussey RS, Mims CW. Ultrastructure of feeding tubes formed in gient-cells induced by root-knot nematode *Meloidogyne incognita*. Protoplasma. 1991; 162: 99-107. https://doi.org/10.1007/BF02562553

[48] Karssen G, Moens M. Root-knot nematodes. In: Perry RN, Moens M. (eds) Plant Nematology. 2006; 59-90.

[49] Bozbuga R. Characterisation of cell walls at the feeding site of *Meloidogyne incognita*, PhD thesis, University of Leeds, Leeds. 2017.

[50] Gheysen G, Mitchum MG. Phytoparasitic nematode control of plant hormone pathways. Plant Physiol. 2019; 179, 1212-1226. doi: 10.1104/pp.18.01067

[51] Hutangura P, Mathesius U, Jones MGK, Rolfe BG. Auxin induction is a trigger for root gall formation caused by root-knot nematodes in white clover and is associated with the activation of the flavonoid pathway. Australian Journal of Plant Physiology. 1999; 26, 221-231. https://doi.org/10.1071/PP98157

[52] Glazer, I., Orion, D. & Apelbaum, A. 1983. Interrelationships between ethylene production, gall formation, and root-knot nematode development in tomato plants infected with *Meloidogyne javanica*. Journal of Nematology, 15, 539-544.

[53] Bozbuga R. Effect of Submerging *Solanum lycopersicum* Roots in Salicylic Acid (SA) Solution for Different Durations on Nematode Infection and Expressions of SlPR5 Gene. Horticultural Studies. 2020; 37: 144-149.

[54] Bozbuga R. Expressions of pathogenesis related 1 (PR1) gene in *Solanum lycopersicum* and Influence of salicylic acid exposures on host-*Meloidogyne incognita* interactions. Doklady Biochemistry Biophysics. 2020; 494:266-269. https://doi.org/10.1134/S1607672920050038

[55] De Smet I, Lau S, Voss U, Vanneste S, Benjamins R, Rademacher EH, Schlereth A, De Rybel B, Vassileva V, Grunewald W, Naudts M, Levesque MP, Ehrismann JS, Inze D, Luschnig C, Benfey PN, Weijers D, Van Montagu MCE, Bennett MJ, Juergens G, Beeckman T. Bimodular auxin response controls organogenesis in Arabidopsis. Proceedings of the National Academy of Sciences of the United States of America. 2010; 107, 2705-2710. https://doi.org/10.1073/pnas.0915001107

[56] Kyndt T, Goverse A, Haegeman A, Warmerdam S, Wanjau C, Jahani M, Engler G, De Almeida Engler J, Gheysen G. Redirection of auxin flow in *Arabidopsis thaliana* roots after infection by root-knot nematodes. Journal of Experimental Botany. 2016; 67, 4559-4570. DOI: 10.1093/jxb/erw230

[57] Kant U, Ramani V. Insect induced plant galls in tissue-culture. Proceedings

of the Indian Academy of Sciences-Animal Sciences. 1990; 99, 257- 265.

[58] Cabrera J, Barcala M, García A, Rio-Machín A, Medina C, Jaubert-Possamai S, Favery B, Maizel A, Ruiz-Ferrer V, Fenoll C, et al. Differentially expressed small RNAs in Arabidopsis galls formed by Meloidogyne javanica: A functional role for miR390 and its TAS3-derived tasiRNAs. New Phytol. 2016; 209: 1625-1640. DOI: 10.1111/nph.13735

[59] Jaubert-Possamai S, Noureddine Y, Favery B. MicroRNAs, New Players in the Plant-Nematode Interaction. Front Plant Sci. 2019; 10:1180. doi: 10.3389/fpls.2019.01180.

[60] Hammes UZ, Schachtman DP, Berg RH, Nielsen E, Koch W, Mcintyre LM, Taylor CG. Nematode-induced changes of transporter gene expression in Arabidopsis roots. Molecular Plant-Microbe Interactions. 2005; 18, 1247-1257. DOI: 10.1094/MPMI-18-1247

[61] Grundler FMW, Sobczak M, Golinowski W. Formation of wall openings in root cells of *Arabidopsis thaliana* following infection by the plant- parasitic nematode *Heterodera schachtii*. Eur. J. Plant Pathol. 1998; 104, 545-551. doi: 10.1023/A:1008692022279

[62] Favery B, Quentin M, Jaubert-Possamai S, Abad P. Gall-forming root-knot nematodes hijack key plant cellular functions to induce multinucleate and hypertrophied feeding cells. J. Insect Physiol. 2016; 84, 60-69. doi: 10.1016/j.jinsphys.2015.07.013

[63] Caillaud M-C, Dubreuil G, Quentin M, Perfus-Barbeoch L, Lecomte P, de Almeida Engler J, et al. Root-knot nematodes manipulate plant cell functions during a compatible interaction. J. Plant Physiol. 2008; 165, 104-113. doi: 10.1016/j.jplph.2007.05.007

[64] Cabrera J, Barcala M, Fenoll C, Escobar C. Transcriptomic signatures of transfer cells in early developing nematode feeding cells of Arabidopsis focused on auxin and ethylene signaling. Front Plant Sci. 2014; 5:107. doi: 10.3389/fpls.2014.00107.

[65] Absmanner B, Stadler R, Hammes UZ. Phloem development in nematode-induced feeding sites: the implications of auxin and cytokinin. Front Plant Sci. 2013; 4:241. doi: 10.3389/fpls.2013.00241.

[66] Nakagami S, Saeki K, Toda K, Ishida T, Sawa S. The atypical E2F transcription factor DEL1 modulates growth-defense tradeoffs of host plants during root-knot nematode infection. Sci Rep. 2020; 10(1):8836. doi: 10.1038/s41598-020-65733-3.

[67] Teixeira MA, Wei L, Kaloshian I. Root-knot nematodes induce pattern-triggered immunity in *Arabidopsis thaliana* roots. New Phytol. 2016;211(1): 276-87. doi: 10.1111/nph.13893.

[68] Niu J, Liu P, Liu Q, Chen C, Guo Q, Yin J, Yang G, Jian H. Msp40 effector of root-knot nematode manipulates plant immunity to facilitate parasitism. Sci Rep. 2016 ;6:19443. doi: 10.1038/srep19443.

[69] Kaloshian I, Teixeira M. Advances in Plant-Nematode Interactions with Emphasis on the Notorious Nematode Genus *Meloidogyne*. Phytopathology. 2019;109(12):1988-1996. doi: 10.1094/PHYTO-05-19-0163-IA.

[70] Topalović O, Bredenbruch S, Schleker ASS, Heuer H. Microbes Attaching to Endoparasitic Phytonematodes in Soil Trigger Plant Defense Upon Root Penetration by the Nematode. Front Plant Sci. 2020;11:138. doi: 10.3389/fpls.2020.00138.

[71] Warmerdam S, Sterken MG, Sukarta OCA, van Schaik CC,

Oortwijn MEP, Lozano-Torres JL, Bakker J, Smant G, Goverse A. The TIR-NB-LRR pair DSC1 and WRKY19 contributes to basal immunity of Arabidopsis to the root-knot nematode Meloidogyne incognita. BMC Plant Biol. 2020;20(1):73. doi: 10.1186/s12870-020-2285-x

[72] Ewing EE, Struik PC. Tuber formation in potato: Induction, initiation, and growth, horticultural reviews, Horticultural Reviews, John Wiley & Sons, Inc. 1992;14. https://doi.org/10.1002/9780470650523.ch3

[73] Roumeliotis E, Kloosterman B, Oortwijn M, Visser RGF, Bachem CWB. The PIN family of proteins in potato and their putative role in tuberization. Frontiers in Plant Science 2013; 4: 524. 10.3389/fpls.2013.00524

[74] Dutt S, Manjul AS, Raigond P, Singh B, Siddappa S, Bhardwaj V, Kawar PG, Patil V U, Kardile HB. Key players associated with tuberization in potato: potential candidates for genetic engineering. Critical Reviews in Biotechnology. 2017; 37 (7): 942-957. DOI: 10.1080/07388551.2016.1274876

[75] Bin Shi, J, Ji Ye G, Zhi Yang Y, Wang F, Zhou Y, Hong Sun H, Wang AJ. The Differential Gene Expression of Key Enzyme in The Gibberellin Pathway In The Potato *Solanum tuberosum*) Mutant M4p-9. Pakistan Journal of Botany. 2016; 48(3): 1107-1117. DOI: 10.13560/j.cnki.biotech.bull.1985.2016.01.021

[76] Hedden P, Phillips AL. Gibberellin metabolism: new insights revealed by the genes. Trends in Plant Science. 2000; 5: 523-530. DOI: 10.1016/s1360-1385(00)01790-8.

[77] Carrera E, Bou J, García-Martínez JL, Prat S. Changes in GA 20-oxidase gene expression strongly affect stem length, tuber induction and tuber yield of potato plants. The Plant Journal, 2000; 22(3): 247-256. DOI: 10.1046/j.1365-313x.2000.00736.x.

[78] Roumeliotis, E, Kloosterman B, Oortwijn M, Lange T, Visser RGF, Bachem CWB. Down regulation of StGA3ox genes in potato results in altered GA content and affect plant and tuber growth characteristics. Journal of Plant Physiology. 2013; 170: 1228-1234. DOI: 10.1016/j.jplph.2013.04.003.

[79] Kloosterman B, Navarro C, Bijsterbosch G. Lange T, Prat S, Visser RGF, Bachem CWB. StGA2ox1 is induced prior to stolon swelling and controls GA levels during potato tuber development. The Plant Journal, 2007; 52: 362-373. 10.1111/j.1365-313X.2007.03245.x

[80] Kolachevskaya OO, Lomin SN, Kojima M, Getman IA, Sergeeva IA, Sakakibara H, Romanov GA. Tuber-Specific Expression of Two Gibberellin Oxidase Transgenes from Arabidopsis Regulates over Wide Ranges the Potato Tuber Formation. Russian Journal of Plant Physiology. 2019; 66: 984-991. https://doi.org/10.1134/S1021443720010094

[81] Ševčíková H, Mašková P, Tarkowská D, Mašek T, Lipavská H. Carbohydrates and gibberellins relationship in potato tuberization. Journal of Plant Physiology. 2017; 214; 53-63. DOI: 10.1016/j.jplph.2017.04.003.

[82] Roumeliotis E, Visser RG, Bachem CW. A crosstalk of auxin and GA during tuber development. Plant Signaling & Behavior. 2012; 7: 1360-1363.

[83] Kondhare KR, Patil AB, Giri AP. Auxin: An emerging regulator of tuber and storage root development. Plant Science. 2021; 306: 110854. DOI: https://doi.org/10.1016/j.plantsci.2021.110854

[84] Puzina TI, Kirillova IG, Yakushkina NI. Dynamics of

indole-3-acetic acid in organs of potato at different stages of ontogenesis and its role in regulation of tuber growth (in Russian). Izvestiya Akademii Nauk SSSR. Seriya Biologicheskaya. 2000; 2: 170-177. DOI: 10.1007/s00299-019-02395-0.

[85] Faivre-Rampant O, Cardle L, Marshall D, Viola R, Taylor MA. Changes in gene expression during meristem activation processes in *Solanum tuberosum* with a focus on the regulation of an auxin response factor gene. Journal of Experimental Botany. 2004; 55: 613-622. https://doi.org/10.1093/jxb/erh075

[86] Kloosterman B, De Koeyer D, Griffiths R, Flinn B, Steuernagel B, Scholz U, Sonnewald S, Sonnewald U, Bryan GJ. Prat S, Banfalvi Z, Hammond JP, Geigenberger P, Nielsen KL, Visser RG, Bachem CW. Genes driving potato tuber initiation and growth: identification based on transcriptional changes using the POCI array. Functional & Integrative Genomics. 2008; 8: 329-340. https://doi.org/10.1007/s10142-008-0083-x

[87] Song S, Hao L, Zhao P, Xu Y, Zhong N, Zhang H, Liu N. Genome-wide Identification, Expression Profiling and Evolutionary Analysis of Auxin Response Factor Gene Family in Potato (*Solanum tuberosum* Group Phureja). Scientific Reports. 2019; 9: 1755. DOI: https://doi.org/10.1038/s41598-018-37923-7

[88] Natarajan B, Kondhare KR, Hannapel DJ, Banerjee AK. Mobile RNAs and Proteins: Prospects in storage organ development of tuber and root crops. Plant Science. 2019; 284, 73-81. DOI:10.1016/j.plantsci.2019.03.019

[89] Xu X, van Lammeren AA, Vermeer E, Vreugdenhil D. The role of gibberellin, abscisic acid, and sucrose in the regulation of potato tuber formation in vitro. Plant Physiology. 1998a; 117: 575-584. DOI: https://doi.org/10.1104/pp.117.2.575

[90] Mani F, Bettaieb T, Doudech N, Hannachi C. Physiological mechanisms for potato dormancy release and sprouting: a review. African Crop Science Journal. 2014; 22: 155-174.

[91] Nambara E, Marion-Poll A. Abscisic acid biosynthesis and catabolism. Annual Review of Plant Biology. 2005; 56: 165-185. DOI: https://doi.org/10.1146/annurev.arplant.56.032604.144046

[92] Muñiz García MN, Stritzler M, Capiati DA. Heterologous expression of Arabidopsis ABF4 gene in potato enhances tuberization through ABA-GA crosstalk regulation, Planta. 2013; 239(3): 615-631. DOI: 10.1007/s00425-013-2001-2.

[93] Sarkar D, Pandey SK, Sharma S. Cytokinins antagonize the jasmonates action on the regulation of potato (*Solanum tuberosum*) tuber formation in vitro. Plant Cell, Tissue and Organ Culture. 2006; 87: 285-295. https://doi.org/10.1007/s11240-006-9166-3

[94] Malkawi A, Jensen BL, Langille AR. Plant hormones isolated from "Katahdin" potato plant tissues and the influence of photoperiod and temperature on their levels in relation to tuber induction. Journal of Plant Growth Regulation. 2007; 26: 308-317. DOI: https://doi.org/10.1007/s00344-007-9010-y

[95] Pavlista AD. Thidiazuron increased yield of potato cultivars. PGRSA Quart. 2001; 29: 72-80.

[96] Raspor M, Motyka V, Ninkovic S, Dobrev PI, Malbeck J, Cosic T, Cingel A, Savic J, Tadic V, Dragicevic IC. Endogenous levels of cytokinins, indole-3-acetic acid and abscisic acid in

in vitro grown potato: A contribution to potato hormonomics. Scientific Reports. 2020; 10: 3437. DOI: https://doi.org/10.1038/s41598-020-60412-9

[97] Tao G, Letham DS, Yong JWH, Zhang K, John PCL, Schwartz O, Wong SC, Farquhar GD. Promotion of shoot development and tuberisation in potato by expression of a chimaeric cytokinin synthesis gene at normal and elevated CO2 levels Functional Plant Biology. 2010; 37(1): 43-54. DOI: https://doi.org/10.1071/FP07032

[98] Zwanenburg B, Blanco-Ania D. Strigolactones: new plant hormones in the spotlight. Journal of Experimental Botany. 2018; 69: 2205-2218.DOI: https://doi.org/10.1093/jxb/erx487

[99] Pasare SA, Ducreux LJM, Morris WL, Campbell R, Sharma SK, Roumelitotis E, Kohlen W, van der Krol S, Bramley PM, Roberts AG, Fraser PD, Taylor MA. The role of the potato (*Solanum tuberosum*) CCD8 gene in stolon and tuber development. The New Phytologist. 2013; 198(4): 1108-1120. DOI: 10.1111/nph.12217

[100] Aksenova NP, Sergeeva LI, Konstantinova TN, Golyanovskaya SA, Kolachevskaya OO, Romanov GA. Regulation of potato tuber dormancy and sprouting. Russian Journal of Plant Physiology. 2013; 60: 301-312. DOI: 10.1007/s00425-013-1968-z

[101] Meng Liu J, Shan Wang S, Zheng X, Jin N, Lu J, Tao Huang Y, Fan B, Zhong Wang F. Antimicrobial Activity Against Phytopathogens and Inhibitory Activity on Solanine in Potatoes of the Endophytic Bacteria Isolated from Potato Tubers. Frontiers in Microbiology. 2020; 11. DOI: https://doi.org/10.3389/fmicb.2020.570926

[102] Foukaraki SG, Cools K, Chope GA, Terry LA. Impact of ethylene and 1-MCP on sprouting and sugar accumulation in stored potatoes. Postharvest Biology and Technology. 2016; 114: 95-103. DOI: https://doi.org/10.1016/j.postharvbio.2015.11.013

[103] Tosetti R, Waters A, Chope G. A, Cools K, Alamar MC, McWilliam S, Thompson AJ, Terry LA. New insights into the effects of ethylene on ABA catabolism, sweetening and dormancy in stored potato tubers. Postharvest Biology and Technology. 2021; 173: 111420. DOI: https://doi.org/10.1016/j.postharvbio.2020.111420

[104] Morris WL, Alamar MC, Lopez-Cobollo RM, Cañete JC, Bennett M, Van der Kaay J, Stevens J, Sharma SK, McLean K, Thompson AJ, Terry AJ, Turnbull CGN, Bryan GJ, Taylor MA. A member of the TERMINAL FLOWER 1/CENTRORADIALIS gene family controls sprout growth in potato tubers. Journal of Experimental Botany. 2018; 70(3): 835-843. DOI: https://doi.org/10.1093/jxb/ery387

[105] Wang Z, Ma R, Zhao M, Wang F, Zhang N, Si H. NO and ABA Interaction Regulates Tuber Dormancy and Sprouting in Potato. Frontiers in Plant Science. 2020; 11: 311. DOI: 10.3389/fpls.2020.00311

[106] Deligios PA, Rapposelli E, Mameli MG, Baghino L, Mallica GM, Ledda L. Effects of Physical, Mechanical and Hormonal Treatments of Seed-Tubers on Bud Dormancy and Plant Productivity. Agronomy. 2020; 10(1): 33. https://doi.org/10.3390/agronomy10010033

[107] Pogorelko G, Lionetti V, Bellincampi D, Zabotina O. Cell wall integrity. Plant Signal Behaviour. 2013; 8(9): e25435. DOI: 10.4161/psb.25435

[108] Wang D, Yeats TH, Uluisik S, Rose JKC, Seymour GB. Fruit Softening:

Revisiting the Role of Pectin. Trends Plant Science. 2018; 23(4): 302-310. DOI:https://doi.org/10.1016/j.tplants.2018.01.006

[109] Vincken JP, Borkhardt B, Bush M, Doeswijk-Voragen C, Dopico B, Labrador E, Lange L, McCann M, Morvan C, Muños F, Oomen R, Peugnet I, Rudolph B, Schols H, Sørensen S, Ulvskov P, Voragen A, Visser R. Proceedings of the Second European Conference on Plant Biotechnology. ed. / Gert E de Vries; Karin Metzlaff. Elsevier. 2006; p: 245-256

[110] Poles L, Gentile A, Giuffrida A, Valentini L, Endrizzi I, Aprea E, Gasperi F, Distefano G, Artioli G, Malfa SL, Costa F, Lovatti L, Di Guardo M. Role of fruit flesh cell morphology and MdPG1 allelotype in influencing juiciness and texture properties in apple. Postharvest Biology and Technology. 2020; 164: 111161. DOI: https://doi.org/10.1016/j.postharvbio.2020.111161

[111] Gao Y, Guo Y, Su Z, Yu Y, Zhu Z, Gao P, Wang X. Transcriptome analysis of genes related to fruit texture in watermelon. Scientia Horticulturae. 2020; 262: 109075. DOI: https://doi.org/10.1016/j.scienta.2019.109075

[112] García-Segovia P, Andrés-Bello A, Martínez-Monzó J. Textural properties of potatoes (*Solanum tuberosum* L., cv. Monalisa) as affected by different cooking processes. Journal of Food Engineering. 2008; 88: 28-35. DOI: https://doi.org/10.1016/j.jfoodeng.2007.12.001

[113] Ducreux LJM, Morris WL, Prosser IM, Morris JA, Beale MH, Wright F, Shepherd T, Bryan GJ, Hedley PE, Taylor MA. Expression profiling of potato germplasm differentiated in quality traits leads to the identification of candidate flavour and texture genes. Journal of Experimental Botany. 2008; 59: 4205-4219. DOI: 10.1093/jxb/ern264.

[114] Banda L, Kyallo M, Domelevo Entfellner JB, Moyo M, Swanckaert J, Mwanga ROM, Onyongo A, Magiri E, Gemenet DC, Yao N, Pelle R, Muzhingi T. Analysis of β-amylase gene (Amyβ) variation reveals allele association with low enzyme activity and increased firmness in cooked sweetpotato (*Ipomoea batatas*) from East Africa. Journal of Agriculture and Food Research. 2021; 4: 100121. DOI: https://doi.org/10.1016/j.jafr.2021.100121

[115] Dong W, Li L, Cao R, Xu S, Cheng L, Yu M, Lv Z, Lu G. Changes in cell wall components and polysaccharide-degrading enzymes in relation to differences in texture during sweet potato storage root growth. Journal of Plant Physiology. 2020; 254: 153282. DOI: https://doi.org/10.1016/j.jplph.2020.153282

[116] Che Y, Zhang N, Zhu X, Li S, Wang S, Si H. Enhanced tolerance of the transgenic potato plants overexpressing Cu/Zn superoxide dismutase to low temperature. Scientia horticulturae. 2020; 261: 108949. https://doi.org/10.1016/j.scienta.2019.108949

[117] Upadhyaya CP, Bagri DS. Biotechnological Approaches for Nutritional Improvement in Potato (*Solanum tuberosum* L.). Genome Engineering for Crop Improvement. 2021 John Wiley & Sons Ltd. DOI: https://doi.org/10.1002/9781119672425.ch15

[118] Upadhyaya DC, Bagri DS, Upadhyaya CP, Kumar A, Thiruvengadam M, Jain SK. Genetic engineering of potato (*Solanum tuberosum* L.) for enhanced

α-tocopherols and abiotic stress tolerance. Physiologia Plantarum. 2020. https://doi.org/10.1111/ppl.13252

[119] Li S, Zhang N, Zhu X, Ma R, Yang J, Tang X, Si H. Enhanced drought tolerance with artificial microRNA-mediated StProDH1 gene silencing in potato. Crop Science. 2020; 60(3): 1462-1471. DOI: https://doi.org/10.1002/csc2.20064

[120] Oomen RJFJ, Doeswijk-Voragen CHL, Bush MS, Vincken JP, Borkhardt B, van den Broek LAM, Corsar J, Ulvskov P, Voragen AGJ, McCann MC, Visser RGF. In muro fragmentation of the rhamno galacturonan I backbone in potato (*Solanum tuberosum* L.) results in a reduction and altered location of the galactan and arabinan side-chains and abnormal periderm development. The Plant Journal. 2002; 30:403-413. DOI: 10.1046/j.1365-313x.2002.01296.x

[121] Martín I, Dopico B, Munoz FC, Esteban R, Oomen RJFJ, Driouich A, Vincken JP, Visser R, Labrador E. In vivo Expression of a *Cicer arietinum* β-galactosidase in Potato Tubers Leads to a Reduction of the Galactan Side-chains in Cell Wall Pectin. Plant Cell Physiology. 2005; 46(10): 1613-1622.

[122] Hong Huang J, Kortstee A, Dess DCT, Trindade LM, Schols HA, Gruppen H. Modification of potato cell wall pectin by the introduction of rhamnogalacturonan lyase and β-galactosidase transgenes and their side effects. Carbohydrate Polymers. 2016; 144:9-16. DOI: 10.1016/j.carbpol.2016.02.037

[123] Oxenboll Sorensen S, Pauly M, Bush M, Skjot M, McCann MC, Borkhardt B, Ulvskov P. Pectin engineering: modification of potato pectin by in vivo expression of an endo-1,4-beta-D-galactanase. PNAS. 2000; 97:7639-7644. DOI: https://doi.org/10.1073/pnas.130568297

[124] Liu B, Zhang N, Wen Y, Jin X, Yang J, Si H. Transcriptomic changes during tuber dormancy release process revealed by RNA sequencing in potato. Journal of Biotechnology. 2015; 198, 17-30. DOI: 10.1016/j.jbiotec.2015.01.019

[125] Chekanova JA. Long non-coding RNAs and their functions in plants. Current Opinion in Plant Biology. 2015; 27, 207-216. DOI: 10.1016/j.pbi.2015.08.003

[126] Hou X, Du Y, Liu X, Zhang H, Liu Y, Yan N, Zhang Z. Genome-Wide Analysis of Long Non-Coding RNAs in Potato and Their Potential Role in Tuber Sprouting Process. International Journal of Molecular Science. 2018; 9(1):101; DOI: https://doi.org/10.3390/ijms19010101

[127] Zhang Z, Wang J, Zhang X, Shi Q, Xin L, Fu H, Wang Y. Effects of radio frequency assisted blanching on polyphenol oxidase, weight loss, texture, color and microstructure of potato. Food Chemistry. 2018b; 248:173-182. DOI: 10.1016/j.foodchem.2017.12.065.

[128] Khan TA, Yusuf M, Ahmad A, Bashir Z, Saeed T, Fariduddin Q, Hayat S, Mock HP, Wu T. Proteomic and physiological assessment of stress sensitive and tolerant variety of tomato treated with brassinosteroids and hydrogen peroxide under low-temperature stress. Food Chemistry. 2019; 15: 289:500-511. DOI: 10.1016/j.foodchem.2019.03.029.

[129] Lin Q, Xie Y, Guan W, Duan Y, Wang Z, Sun C. Combined transcriptomic and proteomic analysis of cold stress induced sugar accumulation and heat shock proteins expression during postharvest potato tuber storage. Food Chemistry. 2019;

297, 124991. DOI: https://doi.org/10.1016/j.foodchem.2019.124991

[130] Nicolás González M, Massa GA, Andersson M, Turesson H, Olsson N, Sofie Fält A, Storani L, Décima Oneto CA, Hofvander P, Feingold SE. Reduced Enzymatic Browning in Potato Tubers by Specific Editing of a Polyphenol Oxidase Gene via Ribonucleoprotein Complexes Delivery of the CRISPR/Cas9 System. Frontiers in Plant Science. 2020. DOI. https://doi.org/10.3389/fpls.2019.01649