Research Review

Potato tuber dormancy

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December 2021

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1. Abstract

This review details the current knowledge of potato tuber dormancy, dormancy break and sprouting, with specific focus on the current position facing GB potato growers.

Concerns over the persistence and risks associated with residues following pre-harvest treatment with Maleic hydrazide (MH), and post-harvest application of Chloropropham (CIPC) has driven the search for alternative strategies for sprout inhibition. A non-renewal notice preventing re-registration of CIPC in the EU as a sprout suppressant for potato and as a herbicide for horticultural crops came into force on the 8th July 2019. This enforcement stipulated a maximum use up grace-period up to the 8th October 2020, beyond which no CIPC application will be permitted in the UK or elsewhere in the EU.

The scope of the review covers the interaction of plant hormones in orchestrating dormancy break and sprout vigour alongside downstream signalling events, changes in transcriptional and protein activity associated with changes in meristem activity within buds linked to the cell. The influence of storage conditions and tuber respiration on dormancy break and tuber quality is covered.

The review includes a brief description of conventional and non-conventional alternative products with activity to retard sprout growth and/or extend dormancy. The final section highlights current research gaps on tuber dormancy.

2. Introduction

Lang *et al.* (1987) defined dormancy as “temporary suspension of visible growth of any plant structure containing a meristem”. The authors divided dormancy into three states; endodormancy which occurs after harvest and is regulated by internal or physiological factors within the affected structure, e.g. chilling responses; ecodormancy which is regulated by external or environmental factors, e.g. water stress, storage temperature and; paradormancy which is regulated by physiological factors outside the affected structure e.g. apical dominance in which the dominant bud/eye supresses the growth of secondary bud or sprouts. The strength of paradormancy varies between varieties. The growing season or pre-harvest conditions can also affect dormancy length along with post-harvest conditions such as temperature and light. Potato tubers are generally dormant at harvest and for the period of time during endodormancy because of endogenous signals (Suttle, 2004; Burton, 1989).

Tuber dormancy can be divided into three phases; induction, maintenance, and termination (Suttle, 1998). Dormancy is controlled by the interaction and cross-talk of phytohormones (Fernie and Willmitzer, 2001; Weiner *et al.*, 2010) stimulating changes in carbohydrate metabolism (Aksenova *et al.*, 2013). Tuber dormancy release, similar to plant seed germination, requires carbohydrate for energy metabolism to meet energy and substrate requirements (Liu *et al.*, 2015b).

Among commercial varieties there is a significant variation in the period of dormancy, and an even greater range of dormancy traits exists in more diverse genetic material (Cutter, 1992; Mani *et al.*, 2014). The relative dormancy of a range of GB varieties has been investigated by AHDB (Project 11140058). This study found that although dormancy varied, depending on location and from year to year, the relative dormancies were maintained.

3. Internal dormancy mechanisms

Dormancy is initially induced at tuber initiation through symplastic isolation of the apical meristem (Viola *et al.*, 2007). The process of vascular disconnection terminates the supply of metabolites and in particular sucrose from the subtending tuber to the potato buds. It has been reported that the process of symplastic isolation coincides with the time when there is complete separation of the tuber from the stolon and mother plant after harvest and that this process starts at the vine-kill. (Aksenova *et al.*, 2013). Symplast reconnection between the apical bud and the tuber is re-established prior to visible bud growth (Viola *et al.*, 2007).

Changes in the metabolic fluxes associated with aging of tubers at or around the time of dormancy break are not fully understood. There are a number of interconnected biochemical processes that may lead directly or indirectly to changes in the readiness of tubers to break dormancy.

Artificial breaking of tuber dormancy through exposure to bromoethane (Alexopoulos *et al.*, 2009) or gibberellic acid (Alexopoulos *et al.*, 2008) leads to an increase in starch breakdown through elevated metabolic activity of starch degrading enzymes. Increase in metabolic activity and respiration occurs before the visible signs of sprouting are observed. Akoumianakis *et al.* (2016) observed a lowering in the activity of glucose-6-phosphate dehydrogenase (G6PDH) and succinate dehydrogenase (SDH) with the advancement of tuber maturity.

G6PDH is the first committed step in glucose metabolism converting glucose-6-phosphate into 6-phosphogluconolactone and is considered the rate limiting enzyme for the pentose phosphate pathway (PPP) that is essential for cell growth (Tian *et al*., 1998). In addition, the G6PDH activity generates NADPH required for detoxifying cellular reactive oxygen species (ROS). G6PDH activity declines over time in tubers (von Schaewen *et al.*, 1995) and lowers the availability of reduced NADPH (Singh *et al.*, 2012). An increase in ROS activity has been associated with signalling events linked to the onset of germination in seeds and sprouting in tubers.

Succinate dehydrogenase (SDH) contributes to mitochondrial ROS production and regulates plant development (Jardim-Messeder *et al.*, 2015) and has been reported to regulate dormancy break in yam tubers (*Dioscorea esculenta* (Lour.) Buurk). Akoumianakis *et al.* (2016) suggested that changes in SDH activity may influence potato tuber dormancy. In addition, the authors observed that a decrease in β-amylase activity was related to the onset of dormancy, increasing again with sprout initiation. Changes in carbohydrate metabolism during tuber development due to β-amylase, G6PDH and SDH may be responsible for the induction and duration of tuber dormancy (Akoumianakis *et al.*, 2016).

Dormancy break is a dynamic process; at the transition between early dormancy break and the later stages of sprout growth, large scale transcriptional reconfiguration occurs. Liu *et al.* (2015a) reported that starch deposits, storage proteins and lipid mobilization were activated before visual signs of bud emergence, and continued activity was recorded into sprout outgrowth, involving a large scale transcriptional reconfiguration. Many of the genes transcripts identified were associated with primary metabolism (glycolytic pathway, TCA cycle, gluconeogenesis, fermentation, oxidative phosphorylation and ATP synthesis) and the transport and release of substrates (carbohydrates and lipids) for bud outgrowth (Liu *et al.*, 2015a). To understand the function of the proteins associated with tuber dormancy release Liu *et al.* (2015b) grouped the differentially expressed proteins into 9 functional categories (Metabolism, cell growth and division, protein synthesis and catabolism, cell structure, signal transduction, cell defence, transcription and development) (**Figure *1***). During dormancy release an upregulation of proteins enriched for major carbohydrate (CHO) metabolism (starch degradation), glycolysis, fermentation, amino acid metabolism, protein (ribosomal) and

transport occurs. Transcripts associated with photosynthesis and RNA regulation were downregulated. The protein profile of sprouted tubers and tubers undergoing dormancy release are different, and there is a poor correspondence in mRNA and protein levels, suggesting post-translational regulation is key to the process (Liu *et al.*, 2015b).

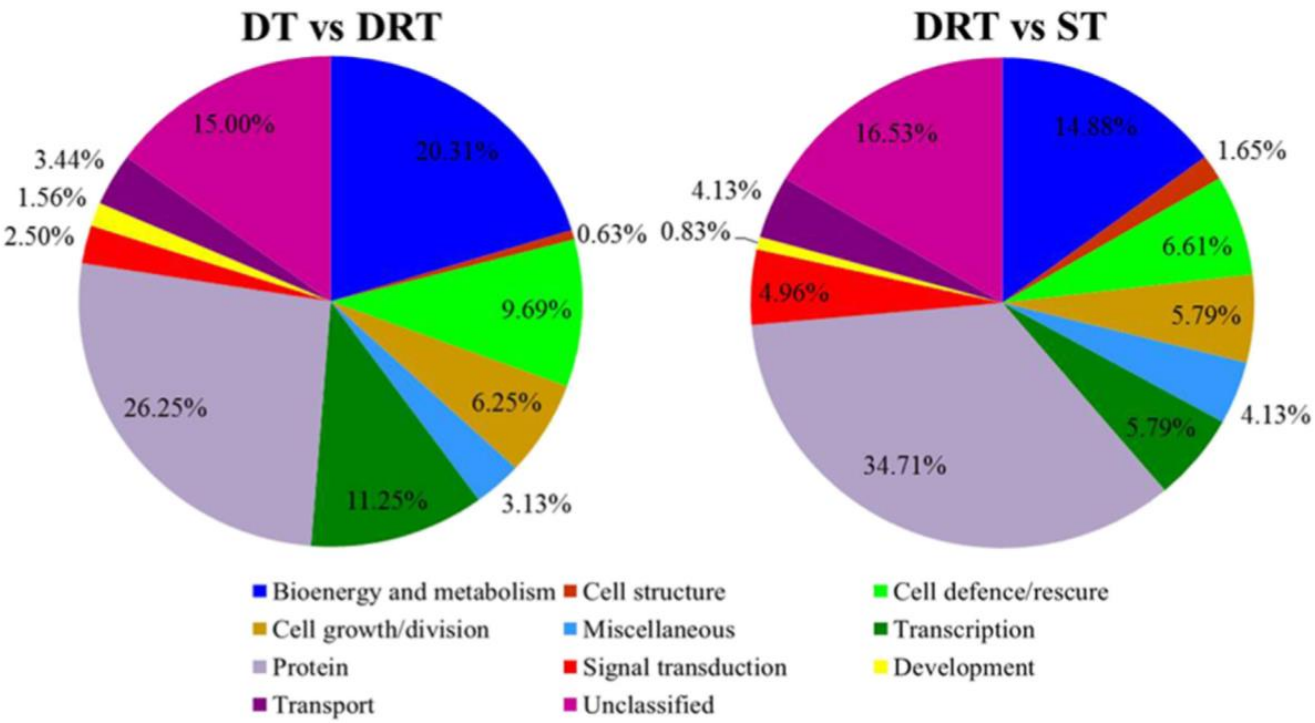

Figure 1 – Functional classification of differentially expressed proteins during dormancy release progression in potato. Two pie charts show the percentage of different categories in terms of protein abundance in DT (dormant tuber) vs DRT (dormancy release tuber) and DRT vs ST (sprouting tuber), (Liu *et al.*, 2015b).

The gene expression profiles between the transition of dormant and sprouting tuber and post-bud emergence indicates that of the process of carbohydrate metabolism including both degradation and re-synthesis) are linked with dormancy release (Liu *et al.*, 2015a; Liu *et al.*, 2015b). The initial burst of growth is fed via sucrose synthesising capacity where hexoses are converted into sucrose and large amounts of sucrose are transported to buds to meet the metabolic needs of the developing buds (Viola *et al*., 2007). It has been hypothesised that low concentrations of sucrose in the bud signals increased starch mobilisation in storage tissues in the tuber to resupply the bud with sucrose (Hajirezaei *et al.*, 2003; Sonnewald & Sonnewald, 2013).

In addition to increasing metabolic fluxes into the meristem, the progression of dormancy release in tubers is highly regulated by genes involved in ribosomal RNA biosynthesis, a requirement for rapid protein synthesis and cell division in meristematic tissues. The decrease of meristematic activity after

dormancy break is exemplified by the decrease of expression of genes for protein biosynthesis (Liu *et al.*, 2015a).

Plant Growth Hormone Interactions

The entry into dormancy is associated with an increase in abscisic acid (ABA) and a decrease in gibberellic acid (GA) (Fernie and Willmitzer, 2001; Weiner *et al.*, 2010; Aksenova *et al.*, 2013*)*. It has been established that ABA and ethylene are required for tuber dormancy initiation, however, only ABA is needed for the maintenance of tuber dormancy (Suttle, 2004). As the effect of dormancy weakens, the concentration of ABA declines and tuber sensitivity to exogenous cytokinin (CK) increases (Suttle, 2004; Nambara and Marion-Poll, 2005; Destefano-Beltran *et al.*, 2006). Increased CK sensitivity leads to the reactivation of meristematic activity (Bromley *et al.*, 2014), with an increase in endogenous CK just before or coinciding with the end of dormancy and the start of sprout growth (Suttle, 2004; Nambara and Marion-Poll, 2005; Destefano-Beltran *et al.*, 2006). With the onset of sprouting ethylene production rates increase (Daniels-Lake *et al.*, 2005b) along with an increased expression of genes related to ethylene synthesis and degradation (Liu *et al.*, 2015a).

Regulation of CK occurs through the expression of *StCKP1* (*Solanum tuberosum* cytokinin riboside phosphorylase) which suppress the synthesis of CK in potato tubers. This mechanism has been implicated in extending endodormancy. Importantly, the induction of protein synthesis of stCKP1 enzymes is regulated by cold temperatures, suggesting storage at lower temperatures supresses cytokinin synthesis (Bromley *et al.*, 2014).

Many of the differentially expressed genes linked with dormancy break are associated with cell cycle regulation (cyclins A, B, D and F) and cell division (cell division control 20, cell division proteins: cdt2, cdc6 and cdc45) and other dormancy regulators, including MAD-box-like transcription factor, ARGONAUTE-4, an auxin-repressed/dormancy-associated protein, and F-box proteins and transcription factors.

The role of cytokinin oxidase/dehydrogenase (CKX) activity in modulating dormancy progression in potato is unclear. Suttle *et al.* (2014) studied five *StCKX* genes encoding proteins with *in vitro* cytokinin oxidase/dehydrogenase (CKX) activity and found *StCKX* expression and CKX activity do not control dormancy. However, reducing CK content through overexpression of *cytokinin oxidase/dehydrogenase1* (*CKX*) genes resulted in tubers exhibiting an extended dormancy period. This supports an essential role of CK in terminating tuber dormancy (Hartmann *et al.* 2011).

A decrease in free indole-3-acetic acid (IAA) occurs in buds during dormancy progression, the rate of this decline and the final decrease in IAA concentration has been associated with triggering dormancy break, but the size of the response is cultivar specific and temperature dependent (Sorce

et al., 2009). Overall, the extent of tuber dormancy and the timing of release is regulated by a coupling between a complex cross-talk of phytohormones interactions over time, changes in the abundance of specific hormone receptors regulating downstream messaging and changes in carbohydrate metabolism (Aksenova *et al.*, 2013). In addition to hormone and carbohydrate (sucrose) metabolism, physical barriers associated with meristem activation also play a part.

Nitric oxide (NO) (Noritake *et al*., 1996) and ROS (Peivastegan *et al*., 2019) are reported to act as signalling agents. The role of NO appears to occur through modification of proteins, through the process of nitrosylation where NO conjugates itself to metal or cysteine residues on proteins leading to post-translational modifications. Nitrosylation is considered to be a mechanism that facilitates cell signalling (Hess *et al*., 2005) and can act on a number of calcium channel proteins important in cell-to-cell communication. Exogenous NO treatment is reported to break dormancy and promote germination in seeds of C4 grasses (Sarath *et a*l., 2006), while Wang *et al*. (2020) reported that the NO induced delay of potato dormancy break was due to an inhibition of ABA catabolism.

Environmental conditions affecting dormancy

Dormancy is considered to be a physiological adaptation of the tuber to prevent sprouting during intermittent periods of environmental limitations (Suttle, 2007). In most varieties, immediately after harvest, potato tubers cannot be induced to sprout even under optimal environmental conditions (Cutter, 1992). However, a great range of dormancy traits exists in the diverse genetic material of tetraploid lines, and moreover, in certain short-day length diploid Phureja species (*Solanum tuberosum var phureja*) dormancy break can occur in the field, while the tubers of *Solanum jamesii,* a wild relative of modern day potato, can remain dormant for many years when stored at 4^{o}C (Bamberg, 2010). Most often, late maturing varieties have a long dormancy that is more difficult to break than that of early maturing clones (CIP, 1989).

During tuber development the buds of the tuber successively become dormant, starting at the stolon end and ending with the apical eye (Van Ittersum, 1992). Changes in tuber dormancy after tuber set are poorly characterized, but a lessening of dormancy occurs late in the growing season as tuber bulking slows down. Detachment of tubers from the haulm strengthens tuber dormancy during the following weeks.

Tuber maturity at the point of harvest has an important bearing on dormancy. Krijthe (1962) studied the sprouting of seed potatoes and demonstrated that immature tubers have a shorter dormant period and more rapid sprout growth than the mature tubers. Characterisation of tuber maturity is often clouded in confusion due to different types of maturity being referenced, chemical (sucrose content), chronological (days from planting) and physiological. The physiological age of seed potatoes at planting has a determinant influence on subsequent tuber initiation and the life cycle of

the plant (Struik and Wiersema, 1999). Duration of dormancy period depends on soil and weather conditions during growth, tuber maturity at harvest, storage conditions, and whether the tuber is injured (Ezekiel and Singh, 2003). High temperatures, low soil moisture and low fertility during tuber growth accelerate physiological development and reduce the dormancy period. Early work in seed germination found a significant interaction of moisture stress and temperature fluctuations on dormancy break (Hegerty, 1975).

Others factors that affect the length of the dormant period are soil temperature and weather conditions during growth, timing of foliage removal, if at all, before harvesting, degree of tuber damage (bruising) and the storage regime (Burton *et al.*, 1992). For example, high temperatures, low soil moisture and low soil fertility during tuber growth accelerate physiological development and reduce the dormant period (CIP, 1985). Both pre- and post- harvest environmental factors can affect tuber dormancy duration. Of the environmental conditions affecting tuber dormancy, only temperature seems to have a major influence (Turnbull and Hanke, 1985).

Temperature has a significant impact on tuber development. High temperatures during growth and development have a negative effect on tuber formation and tuber dry matter accumulation, but lead to tuber chain formation, secondary growth and premature sprouting (Bodlaender *et al*., 1964; Levy and Veilleux, 2007). Heat stress experienced by plants during tuber maturation may interfere with dormancy onset.

The potato is a short-day plant. Night length is important for tuberization but photoperiodic response varies with different genotypes (Snyder and Ewing, 1989). The impact of photoperiod on dormancy is hard to determine and most likely a response to the time of tuber initiation or maturation (Burton, 1989). Light exposure during storage has little effect but does affect sprout morphology (Suttle, 2007).

Tuber size impacts on dormancy with smaller tubers having longer dormancy than larger ones. The maturity of seed tubers at planting impacts on dormancy of daughter tubers with immature tubers imparting longer dormancy periods on daughter tubers by several weeks.

Tuber dormancy develops during tuber formation hence factors influencing tuberization: day length, temperature, nutrient and water supply affect dormancy and sprouting (summarised in Jackson, 1999; Claassens and Vreugdenhil, 2000; Suttle, 2007).

Repeated cycles of high and low nitrogen level can also result in the formation of chain tubers (Jackson 1999), withdrawing nitrogen can decrease gibberellins and increase ABA (Kraus, 1985). Ensuring high carbohydrate partitioning into tubers through accumulation of sucrose can stimulate

earlier tuberization (Jackson, 1999) while high nitrogen content favours shoot and root formation over tuberization and hence is considered inhibitory to tuber formation.
During storage, fluctuating storage temperatures hasten dormancy break compared to constantly high temperature (Burton, 1963). Therefore, storage temperatures should remain as consistent as possible when retarding sprout development is desired. While very high concentrations of CO_2 (≥10%) have been reported to break dormancy (Coleman and McInerney, 1997), concentrations of CO_2 below 10% have no effect on dormancy break.

Impact of Environmental conditions during growth and development on tuber quality
A number of abiotic factors influence tuber maturity and both cultivar and season variability have great impact on final quality. Late planting is reported to reduce fry colour defects and tuber processing quality (Driskill *et al*., 2007). Seasonal weather patterns impact on growth rates and tuberization and lead to variance in yield, skin set properties, regulation of sugar content and tuber maturation. Driskill *et al*. (2007) reported that the processing quality (fry colour) of younger tubers, from late planting, was better than that of earlier planted tubers.

Soils must have sufficiently high organic matter and nitrogen input to meet the high nutrients that ensure good tuber quality (Nesbitt and Adl, 2014). Sustainable agricultural practices such as balanced fertilizer regimes improved not only tuber yield but also marketing quality of potato e.g. tuber size (Tan *et al*., 2016). Vine desiccation (diquat, comm. Reglone®) is another factor which strongly impacts quality; it triggers both maturation of the tuber periderm and stolon release, and in seed potato production it can control tuber size.

Potato yield and tuber composition of potato is not only dependent on the variety but on the soil, climate and agronomic practices during production (Storey and Davies, 1992). Burton and Wilson (1978) reported the effect of latitude on cultivation and sugar content of the variety Record over three growing seasons; the total content of sugar and the reducing sugar/sucrose ratio was directly correlated with location; the more Northerly sites had higher reducing sugar/sucrose ratios.

Lombardo *et al.* (2013) found that location, especially weather and soil type, had a major influence in determining yield (tuber weight) and nutritional value (mineral composition, ascorbic acid and phenolic content) for nine potato cultivars. Payyavula *et al.* (2012) showed that the change in environmental variables, such as differences in day and night temperatures, light intensity, day length, cloud cover, humidity, soil type, time of planting and coastal versus inland locations, all together were sufficient to have a significant impact on the nutritional quality of potatoes. For example, carotenoid profiles were highly influenced by genotype and also location had a correlative link on overall carotenoid content.

In addition to location there is a seasonal effect on the amylose content of tubers, which makes up approximately 30% of the starch content, with the balance made up amylopectin (Jansky and Fajardo, 2014). Moreover, Simkova *et al.* (2013), found tubers planted in high-altitude sites produced tubers with higher amylose content than the same varieties planted at sea level. However, Fajardo *et al.* (2013) concluded that the effect of location on amylose content was small. Jansky and Fajardo (2014) concluded differences between studies should be expected and were in part, due to the extent of the environmental variation among sites within a study.

Managing agronomic practices in the backdrop of variable weather conditions from planting through to harvest requires multifactorial approach to mitigate side effects which may affect quality (De Meulenaer *et al*., 2008

4. Cell cycle and changes in dormancy break

Imposition of dormancy has long been associated with an increase in long-dark photoperiods leading to a transitory rise in ABA concentrations and the arrest of the cell cycle. The length of cell cycle arrest and ensuing endo-dormancy is variety dependent, suggesting a strong genetic link. The cell cycle is divided into a series of genetically distinct phases that allow genetic material within the cell to double before the cell divides (Figure 2). The initial G1 phase prepares the cell for division. Under suitable environmental conditions the cell is committed to division and transits from G1 phase to S phase, where the genetic material within the cell is replicated, doubling the number of chromosomes. The cell moves into G2 phase where metabolic changes prepare the cell for subsequent mitosis, where a division of genetic material followed by cytokinesis that ultimately leads cells to divide. When the tuber meristem enters dormancy, the normal transition from G1 phase to S-phase is halted and cells enter cell cycle arrest termed G0 phase, where the cycle is disrupted. Cells remain in G0 phase until endo-dormancy is broken (reviewed by Sabelli, 2014).

The interaction of upstream hormonal changes and changes in cell cycle

Regulation by D-type cyclins (CYCD) and histones is required for cells to undergo transition between G1–S-phase. Cyclins are a large group of regulatory proteins that controls the progression of a cell through the cell cycle by activating cyclin-dependent kinase (CDK) enzymes or group of enzymes required for synthesis of cell cycle. A number of hormones including auxins, CK, brassinosteroids (BR) and GA are responsible for the up-regulation of CYCD and cyclin-dependent kinase (CDKA), a catalytic subunit of CYCD (reviewed by Horvath *et al.*, 2003).

Horvath *et al.* (2003) suggest that the model for G1–S and G2–M transitions followed by G1 activation and G1 progression is co-ordinated through the expression of CYCD and CDKA family of genes. The cyclin proteins are in turn regulated by the presence of an inhibitory protein (ICK1). On

removal of ICK1 from the CDKA-CYCD complex cyclins are free to initiate the transition from G1-S and G2-M; this removal of inhibitors is induced by a decline in ABA and additional phosphorylation events induced by GA.
Auxins, CK and GA have all been implicated in CYCA/B and CDKA/B expression and/or stability suggesting a pivotal signalling role between upstream environmental signals transduced by hormones and the stimulation of cell cycle leading to increased meristem activity. The phosphorylation and activation of proteins and gene expression required for cytokinesis is initiated by the interaction of CYCB with CDKB (reviewed by Horvath *et al.*, 2003).

Tubers transition from endodormancy to ecodormancy. During prolonged low temperature storage (3°C) the termination of endodormancy does not lead to a change in the cell cycle position of the meristematic cells. Campbell *et al.*, (1996) concluded that the continued arrest of cell division under such conditions must be controlled upstream from the immediate cell cycle regulation mechanisms.

A family of transcription factors (Teosinte Branched, Cycloidea, Proliferating Cell Factors 1 and 2, TCP) are responsible for the inhibition of the expression of cell cycle genes and bud outgrowth. Upstream TCP transcription factors are stimulated by rising strigolactone concentrations and inhibited by CK. The CK - TCP interaction with the cell cycle pathway seems to play an important role in plant branching and architecture. However, several important aspects concerning its regulation need more research. For example, there is evidence suggesting that increased expression of certain cell cycle genes including D-type cyclins can enhance bud outgrowth but the activity is insufficient to activate buds or stimulate shoot branching. Upregulation of CK results in increased bud activation and branching, while it has little effect on bud growth rate (reviewed by Sabelli, 2014). Similarly CEN1 genes are responsible for regulating vernalization and promotion of the floral transition in many plants, and the chilling requirement to release bud dormancy in woody plants of temperate climates. CEN1 is known to control dormancy release and meristem identity in *Populus* sp. trees and a similar role has been associated with controlling sprout vigour in potato (Morris *et al.,* 2019)

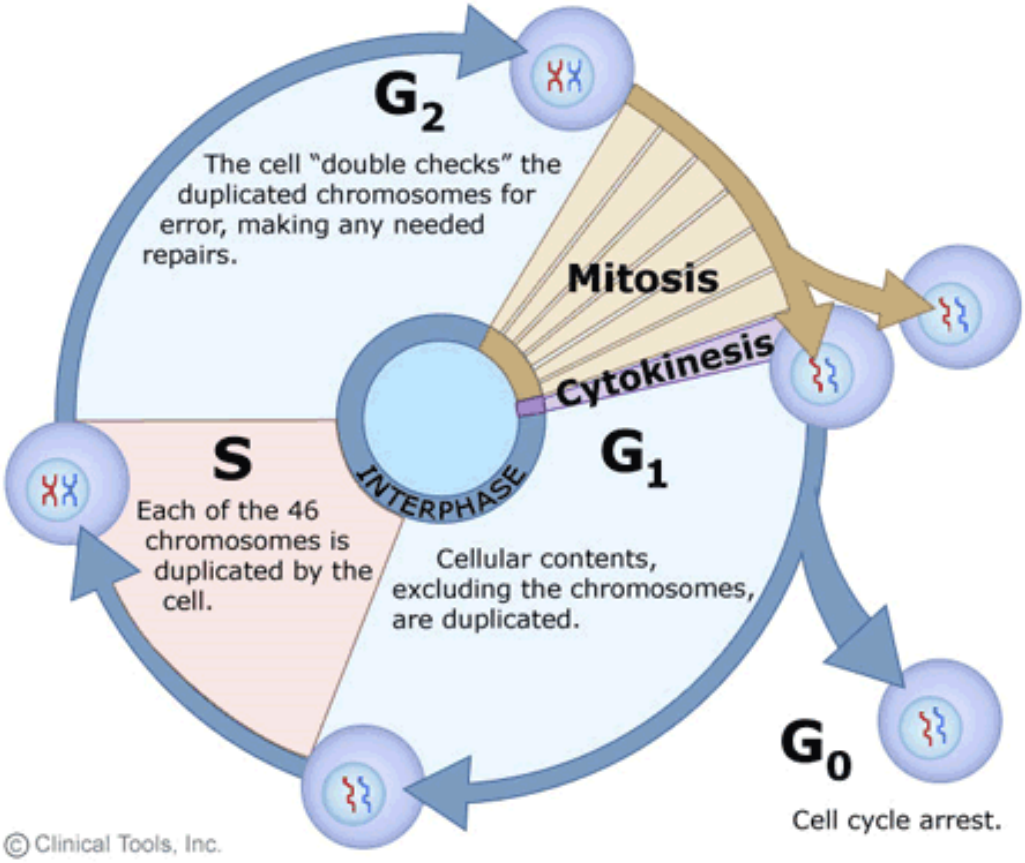

Figure 2 – The cell cycle (Source: Clinical Tools, Inc.)

5. Calcium signalling/regulation in dormancy breaking and sprout growth

Calcium (Ca^{2+}) is essential in growth and development of plants (Hepler, 2005) and has important roles in: cell division; membrane integrity and function; and as secondary messenger in various metabolic processes such as seed development, stomatal control, response to abiotic stresses and pathogen attack (reviewed by Yencho *et al.*, 2008; Palta, 2010).

Ca^{2+} acts as a messenger to a variety of environmental stimuli. In the case of regulating stomatal closure an increase in ABA causes a downstream transient increase in Ca^{2+} within the cell, caused by release of calcium from reserves within the cell vacuole, in turn promoting stomatal closure (reviewed by Sanders *et al.*, 2002; de Freitas *et al.*, 2014).

Calcium regulation is very tightly controlled because of its central role in many cell signaling events. There are two calcium pools, finite stores located in intracellular organelles (vacuole, endoplasmic reticulum) and a more substantial pool of extracellular Ca^{2+} based in the cell wall and apoplast

(Peppiatt *et al.*, 2004). Addition of calcium to soils has limited impact on tuber calcium content due to transportation through xylem (Snedden and Fromm, 2001; Zhang and Lu, 2003; Peppiatt *et al.*, 2004; Hepler, 2005). Increasing calcium content into plant organs through soil application can be problematic because calcium uptake through the root system is via xylem vessels and is translocated upwards to stems and leaves bypassing tubers. Calcium uptake into tubers is mainly via stolon root hairs so careful placement of calcium products at planting within the ridge may improve accessibility. A number of foliar calcium products are on the market that claim to have a certain degree of phloem mobility due to conjugation of calcium to other molecules that are readily translocated in the phloem having the potential to reach roots and tubers.

Symptoms of calcium deficiency disorders are characterized by cell membrane breakdown (plasmolysis) leading to a glassy 'water-soaked' appearance typically found in apples and disorders of cucurbits and tomato referred to as blossom-end wilt. In all cases loss of cellular integrity leads to eventual cell death as tissue becomes necrotic (de Freitas *et al.*, 2010). In potato tubers it is believed that Brown Centre disorder (brown tissue discolouration with necrotic lesions in the central pith) may be caused during the pre-harvest period due to stressful growth conditions, such as cool temperature soils (<10 – 15°C) and nutrient deficiency, mainly calcium and potassium (K) (Davies, 1998; Bussan, 2007; Sowokinos, 2007; Palta, 2010). Ca^{2+} increases membrane integrity and for that reason is often regarded as an anti-senescence factor (Kumar and Knowles, 1993), low Ca^{2+} concentrations in the membranes leads to leaky membranes resulting in loss of cellular salts and organic compounds, and if not reversed can lead to cell death (reviewed by Palta, 2010).

Poovaiah and Leopold (1973a; 1973b) observed that Ca^{2+} enhanced the ability of CK to retard leaf senescence and leaf abscission. In cut flowers, Ca^{2+} could be involved in senescence delay by acting as a second messenger in the signalling pathway leading to the induction of antioxidative enzymes including ascorbate peroxidase (APX), peroxidase (POD), catalase (CAT), and superoxide dismutase (SOD). The activity of these enzymes leads to a decrease in lipid peroxidation and increase in membrane stability delaying membrane deterioration and senescence (Sairam *et al.*, 2011). Nevertheless, for Dyson and Digby (1975) a major influence of calcium on the life cycle of the tuber was the rate of sprouting. A direct relationship between the calcium concentration in the tuber and the rate sprout elongation was found, with higher calcium content encouraging sprout growth, although, it was necessary to supply the growing sprout with additional calcium in order for the sprout to continue to grow (Dekock *et al*., 1975; Dyson and Digby, 1975). In recent work it was observed that calreticulin, a protein that binds Ca2+, was down-regulated during potato tuber dormancy release and up-regulated during tuber sprouting (Liu *et al.*, 2015b). Carvalho (2017) observed that by lowering calcium concentration in tuber buds, by the addition of a calcium chelator (ethylene glycol-bis(2-aminoethylether)-N,N,N',N'-tetraacetic acid, EGTA) or a plasma membrane calcium channel blocker (lanthanum (III) chloride heptahydrate, LaCl3), the buds stayed dormant for longer.

Earlier studies by Pang *et al.* (2007) found that inhibition of dormancy break in grape buds by EGTA or $LaCl_3$ could be reversed by exogenous application of calcium. In the work of Carvalho (2017) the removal of extracellular free calcium by EGTA was less of an influence on [Ca^{2+}] than $LaCl_3$. This suggests that intracellular [Ca^{2+}] is more important for regulating dormancy break and sprouting through restricting Ca^{2+} movement from the cytosol into the intercellular compartments.

Ca^{2+}-permeable ion channels in plasma membranes facilitate movement of Ca^{2+} across plasma membranes into the cytoplasm. The concentration of calcium in the cytoplasm, $[Ca^{2+}]_{cyt}$ is tightly controlled and is maintained at low concentrations (reviewed by Virdi *et al.*, 2015). Removal of $[Ca^{2+}]_{cyt}$ to the apoplast or lumen of intracellular organelles, such as the vacuole or the endoplasmic reticulum is regulated by Ca^{2+}-ATPases and H^+/Ca^{2+}-antiporters (reviewed by White and Broadley, 2003). Such movements of Ca^{2+} generate changes in Ca^{2+} cytoplasmic concentrations initiating cellular responses to a diverse range of developmental and environmental signals (reviewed by White and Broadley, 2003). Application of $LaCl_3$ to buds blocks Ca^{2+}-permeable ion channels and appears to prevent changes in cytosolic calcium responsible for the initiation of sprouting and end of dormancy in tubers (Carvalho, 2017).

In poplar (*Populus deltoides* Bartr. ex Marsh) a high degree of dormancy was maintained in buds when the $[Ca^{2+}]_{cyt}$ and $[Ca^{2+}]_{nucl}$ was kept low, causing an accumulation of Ca^{2+} in intercellular spaces and in cell walls (Jian *et al.*, 1997). This suggests a dynamic influx in Ca^{2+} across the plasma membrane and nuclear membranes in order to stimulate the cell-cycle and induce dormancy break in meristematic bud tissue. Blocking Ca^{2+}-permeable ion channels and preventing transport of Ca^{2+} to the cytosol may induce perturbations of calcium across the cell that might lead to an extension of G-phase arrest during the cell cycle and thus extend dormancy even when stored at higher storage temperatures. Alternatively, blocking calcium's activity in maintaining cell to cell cohesion and cell membrane activity may also have a more general role in contributing to extended bud dormancy through accelerating cellular senescence.

Ca^{2+} is affected by other mineral nutrients. Both magnesium and potassium can displace calcium from the pectin matrix between cell walls weakening cell to cell cohesion and accelerating tissue senescence rates. When conjugated with oxalate ions it can lead to a loss of cell wall strength, being implicated in increasing in the flexibility of cell walls (McNeil *et al.*, 1984). Oxalate is formed through the oxidation of ascorbic acid initially resulting in the transient formation of a monodehydroascorbate. Dehydroascorbic acid (DHA) spontaneously decomposes to 2,3-ketogulonate and then to threonic acid and oxalate (reviewed by Smirnoff, 1996). Cell wall oxalate can influence free Ca^{2+} concentration (Parsons *et al.*, 2011).

6. Dormancy control mechanisms

6.1. Sprouting and sprouting control

Sprout inhibition is essential to prevent losses during storage (Wustman and Struik, 2007b), because the sprout accelerates the rate of moisture loss and because sprouting tubers are not commercially acceptable or have lower value (Schouten, 1988). The increased rate of starch breakdown and accumulation of reducing sugars leads to a greater degree of processing defects. Tubers with buds/sprouts greater than 1.5-2 mm are often rejected by markets.

A brief overview of some chemical and physical methods of sprout suppression is given in the appendix.

Genetic modification to extend dormancy and reduce sprout growth

Given the genetics of cultivated potato and the difficulty in breeding for specific traits without impacting on other desired traits it is likely that production of new potato material with longer dormancy will rely on the identification and selection of target genes via marker assisted breeding or possibly through genetic modification (Sonnewald, 2001).

Sucrose utilisation during dormancy break and sprout growth makes it an active target for manipulation to extend dormancy. Sucrose utilisation requires the activity of sucrose synthase and UDP-glucose pyrophosphorylase requires inorganic pyrophosphate (PPi) (Sonnewald 2001). Experiments to inhibit PPi synthesis led to a reduction in sucrose availability resulting in delayed tuber sprouting (Hajirezaei and Sonnewald, 1999). However, similar interruption of sucrose breakdown in tuber tissue increased the amount of sucrose availability that could be fed to meristems. (Farre *et al*., 2001; Sonnewald, 2001). Interruption of sugar metabolism though down regulation of Trehalose 6 phosphate (T6P) was reported to delay dormancy (Debast *et al*., 2011). Si et al. (2016) reported that potato tuber dormancy was extended by expression of antisense genes of pyrophosphatase. As reported earlier, over-production of the gene encoding CENTRORADIALIS/TERMINAL FLOWER 1 orthologue (CEN1) reduced sprout growth vigour (Morris, 2018).

7. Quality changes in storage

7.1. Storage environment

Potato storage aims to maintain the quality of the harvested crop providing uniform high quality tuber availability throughout most of the year for table consumption and/or to the processing industry (Smith, 1987; Jadhav et al., 1991; Wustman and Struik, 2007b). Potatoes can be stored in air up to 10 months under optimal storage conditions and with repeated application of sprout suppressants

(Firman and Allen, 2007; Wustman and Struik, 2007b). The temperature at which tubers are stored is variety dependent, their susceptibility to low temperature sweetening, the length of storage required, the options for use of sprout suppressants, incidence of disease, and the destination of the stored crop (ware, processing into chips, crisps, mashed or freeze dried).

Potatoes can be stored for seed or for ware purposes with subsequent utilisation, either for fresh consumption or processed products (Wustman and Struik, 2007b). Storage of seed potatoes centres around delivering tubers sprouted or chitted at planting time, whereas in ware potato storage sprout inhibition is essential to prevent losses (Wustman and Struik, 2007b). While this study concentrates on ware potato storage it is important to take into account the physiological age of seed potatoes at planting as this can subsequently impact on harvest maturity (Groves *et al.*, 2005). The physiological age of seed tubers is important because aging modifies the biochemical, physiological and agronomic traits of both plants and tubers resulting from them (Caldiz *et al.*, 1996), which in turn influences storage quality and the propensity to undergo senescent sweetening in long-term storage (Groves *et al.*, 2005).

During storage, losses occur due either to physiological breakdown or development of bacterial or fungal disease. Moreover, during prolonged storage, potato metabolic activity changes with length of storage and storage temperature. As a consequence, respiration rates rise over time and increased water loss and a decline in fresh weight are observed. The extent to which these processes are realised is dependent on the physiological status of tubers entering store, storage temperature the uniformity of air distribution within the store. More importantly, the amount of moisture loss from the stored crop is directly related to the rate of temperature pull down, the amount of refrigeration required to maintain storage temperature and the efficiency of the cooling system. Ventilation used to reduce temperature within the store, if not maintained at high relative humidity (RH) will lead to water loss from potato tubers (Smith, 1987; Wustman and Struik, 2007a). Poorly insulated potato stores require more frequent periods of cooling which leads to more evaporation of moisture from tubers to the cooler evaporative cooling units within the refrigeration system (Wustman and Struik, 2007b).

Good store management should prevent the major types of storage losses, weight losses and losses in quality, due to respiration, sprouting, water evaporating, pests and diseases, changes in the chemical composition and physical properties of the tuber and extreme temperature damage (Smith, 1987; Jadhav *et al.*, 1991; Burton *et al*., 1992; Wustman and Struik, 2007b). These losses are most influenced by storage temperature (Krijthe, 1962). However, while it is possible to provide optimal storage conditions, Burton *et al.* (1992) suggested that “the storage potential of potatoes is already determined before the beginning of storage, by such factors as cultivar; growing techniques; type of

soil; weather conditions during growth; diseases before harvesting; maturity of potatoes at the time of harvesting; tuber damage during lifting, transport and filling of the store."

According to Wustman and Struik (2007b) it is possible to distinguish seven phases in potato storage:

1. Field drying;
2. Store loading of healthy tubers;
3. Drying at and during store loading;
4. Wound healing after store loading for about 10 days at 15°C and high RH;
5. Cooling to the desired temperature. For the different end uses the optimal temperature ranges are:
    - Seed potatoes: 3−4°C
    - Ware potatoes:
        i. Table consumption 4−5°C
        ii. French fry production 6−8°C
        iii. Crisp production 7−9°C
        iv. Flakes, granulates 7−10°C
6. Maintaining the temperature at the desired level;
7. Warming before unloading.

Potatoes can be stored in bulk or in boxes. During storage fans are used to provide controlled ventilation throughout the crop and for cooling, as well as to prevent condensation when the air is vented through apertures and re-circulated. Sometimes both refrigeration and heating may be required during storage, depending on the climate (Firman and Allen, 2007). Ideally, to limit differences in initial storage conditions, stores are loaded within 7-10 days. During the first hours of storage, ventilation assumes an important role in removing the surface moisture from the tubers (Firman and Allen, 2007). The AHDB Potato Store Managers' Guide concisely describes all aspects of potato storage with respect to maintaining potato quality throughout the store.

7.2. Tuber respiration

Respiration is the oxidative breakdown of the more complex substrates normally present in the cells, such as starch, sugars, and organic acids, into smaller molecules (CO_2 and H_2O), with the production of energy and other molecules that can be used by the cell for synthetic reactions (Burton *et al.*, 1992; Wills *et al.*, 2007). Early rise in respiration and utilisation of sucrose reserves within the bud are reported to act as a sink response stimulating starch reserves to be broken down into sugars leading to a rise in respiration (Sonnewald, 2011).

The primary purpose of respiration is the regeneration of the supply of chemical energy in the form of adenosine triphosphate (ATP) (Burton *et al.*, 1992). When in the presence of oxygen, respiration is considered aerobic (Wills *et al.*, 2007) with the overall purpose to regenerate ATP from adenosine disphosphate and inorganic phosphate with the release of CO_2 and H_2O (Burton *et al.*, 1992).

The overall respiratory pathway occurs in three interdependent reactions: glycolysis, the tri-carboxylic acid (TCA, also known as the Krebs cycle, or the citric acid cycle), and the electron transport chain (Hopkins and Hüner, 2004; van Dongen *et al.*, 2011; Hodson and Bryant, 2012). Metabolic analysis of changes in the TCA cycle have found changes in metabolite fluxes that could be used as early indication for dormancy break (Tout, 2019).

The respiration rate is a good indicator of tissue metabolic activity and the respiratory quotient (RQ), may be a useful guide for predicting the potential storage life of the tuber (Wills *et al.*, 2007). Under normal aerobic respiration, CO_2 production is equivalent to consumption of O_2 (RQ = 1) (Equation 1) (Burton, 1989). However, Burton (1974) reported RQ values of 0.8-0.9 in the early storage period when the tubers were still dormant, and RQ = 1.3 later when tubers were sprouting (Burton *et al.*, 1992). According to Isherwood and Burton (1975) senescent potato tubers have a higher production of CO_2 when compared with the O_2 consumption. Accurate measurements of RQ have in the past been difficult to determine due to sampling methods and the sensitivity of O_2 and CO_2 detectors. Older tubers characteristically have a higher respiration rate (Kumar and Knowles, 1996a; Kumar and Knowles, 1996b) and tuber respiration rate seems to be the “pacemaker” of aging in potato tubers (Blauer *et al.*, 2013). According to the work of Copp *et al.* (2000) the onset of the decline in chip colour quality correlated with the increase in the respiration rate of the stored tubers.

Equation 1

$$RQ = \frac{volume\ formed\ (CO_2\ h^{-1})}{volume\ absorbed\ (O_2\ h^{-1})}$$

Tuber respiration rate and gas permeability during storage is influenced by morphological characteristics (the skin and lenticels are very important for O_2 permeability), maturity, dormancy, physiological age, cultivar, inhibitory or stimulatory chemical compounds present, handling and healing wounds; and conditions of storage, such as temperature and the O_2 and CO_2 concentrations in the storage atmosphere (Burton *et al.*, 1992). Technology to measure respiration and calculate the RQ are available for apple storage (http://www.storagecontrol.com/products/safepod-system/), and similar technology for the potato industry is being developed. Measurement of respiration of whole tubers and relating this to changes in sprouting is currently under investigation. However, in order to use respiration as a marker for dormancy break and sprouting it is important to dissect

changes in respiration/RQ against a backdrop of changes in tuber respiration during storage associated with age-related processes, for example senescent sweetening.

When considering measuring respiration a number of points need to be considered in terms of tuber anatomy, size and shape, along with store management practices, including venting and store atmosphere components including ethylene. The ability of a tuber to respire aerobically depends on the O_2 supply to the respiring tissue, in potato tubers this is limited by the periderm, which acts as a gaseous diffusion barrier. The majority of the gaseous diffusion occurs through the lenticels (about 100 per tuber). The resistance to gas diffusion in potato tubers is not limited by the lenticels but by the intercellular spaces immediately underlying them, meaning that the O_2 and CO_2 concentrations in the tissues are equilibrated with the ambient atmosphere (Burton, 1978 in Burton *et al.*, 1992; Abdul-Baki and Solomos, 1994). The barrier layer of air surrounding the tuber and the airflow around the store will also have an influence on the rate of gas exchange.

Thus, in potato tubers, O_2 diffusion occurs through the skin lenticels followed by diffusion in the intercellular spaces where eventually respiration takes place in the cytoplasm-mitochondria. The route of respiratory CO_2 follows the reverse path (Woolley, 1962; Banks and Kays, 1988; Ho *et al.*, 2010). However, the cellular structure of potato tuber tissue is not homogeneous and varies depending on variety (Konstankiewicz *et al.*, 2002; Gancarz *et al.*, 2014). The major components of tuber tissue are parenchyma cells from the cortex and from the perimedullary zone, which contain starch granules as reserve material (Grommers and van der Krogt, 2009).

Parenchyma cells of the perimedullary area are bigger and store more starch than those from medullary zone (pith) (Reeve *et al.*, 1969; Kadam *et al.*, 1991; Konstankiewicz *et al.*, 2002; Sadowska *et al.*, 2008; Gancarz *et al.*, 2014). Devaux (1891) demonstrated that intercellular spaces in thick plant tissues are interconnected and air-filled. The microscale topology of cells and intercellular spaces determined to a large extent gas transport in the tissue, therefore, plant tissue cannot be considered as a real continuum material (Verboven *et al.*, 2008; Ho *et al.*, 2011). It was observed that the gas-filled intercellular spaces are interconnected with narrow capillary tubes (Woolley, 1962). Therefore, as the cell becomes more hydrated additional resistance to gas diffusion might be observed. In senescent tissues the intercellular spaces may become filled with cellular solution, impeding O_2 movement, resulting in anaerobic conditions within the tissue (Burton *et al.*, 1992).

It was observed that CO_2 diffusivity of the tissue was much higher than O_2 diffusivity. It was hypothesized that CO_2, besides the gas phase transport, could also be transported in the water phase from cell to cell, due to its higher solubility in the soluble phase, while O_2 is mainly transported through the gas phase (Ho *et al.*, 2007; Ho *et al.*, 2011). Ho *et al.* (2011) found that compact cell

clusters reduce the gas-liquid exchange surface and could increase the barrier to gas diffusion. In pears, it was observed that O_2 and CO_2 diffusivity was lower at the skin compared to the cortex and that along the equatorial radial direction the diffusivity of both gases was almost constant in the cortex tissue and higher in the core of the pear (Ho *et al*., 2006a; Ho *et al*., 2006b). With CO_2 diffusivity in potatoes, Abdul-Baki and Solomos (1994) showed that the peel of R. Burbank had lower CO_2 diffusivity when compared to the flesh. In a recent study on the blackheart disorder in potato Maris Piper variety, it was suggested that the discontinuity of the gas-filled intercellular spaces may be the major factor leading to the large variation in O_2 diffusivities between flesh and heart tuber tissue (Kiaitsi, 2015).

If the respiration rate is measured during all the storage phases, a respiratory pattern for the storage period can be observed (Wills *et al.*, 2007) and provides a useful indicator to determine the volume of night-time air required to ventilate the storage facility to maintain temperatures of stored potatoes and thus avoid excessive accumulation of CO_2 (Bethke and Busse, 2010).

Respiration rates decline from harvest during curing as temperatures are pulled down reaching its lowest rate around 3 months after harvest before rising again post dormancy break when tubers start to age. Respiration rates vary based on variety: Russet Burbank has a low respiration rate in store, while Maris Piper, King Edward & Melody and Lady Claire generally respire at highest rates (114R484 within https://ahdb.org.uk/knowledge-library/research-reports-on-potato-storage).

Storage temperature has an impact on respiration with rates at 4-5 ˚C recorded at 3-9 mg CO_2/kg/h rising to 7-10 mg CO_2/kg/h at 10 ˚C. In addition to temperature, ethylene within the storage atmosphere, at concentrations of ≥0.1% v/v in the air, increased the respiration rate (Burton *et al.*, 1992 and references therein). While Reid and Pratt (1972) reported that tubers cv. White Rose treated with 10 ppm (10µL/L) ethylene led to a rise in respiration rate (10-30 mg CO_2 /kg/hr) at 20 ˚C the rate of increase was dependent on the length of exposure with continuous ethylene treatment yielding the highest rate.

Besides external sources of ethylene, potato tubers produce small quantities of ethylene (0.8 to 15 nL kg^{-1} h^{-1} (0.8-15.0 ppb) and an increase of 2- to 25-fold was observed during sprouting and stress (Daniels-Lake *et al.*, 2005b). Exposure to ethylene increases tuber respiration rate and accelerates the conversion of starch to sugars causing a dose-dependent effect in the darkening of potato fry colour (Daniels-Lake *et al.*, 2005a and references therein). Additional studies by Daniels-Lake *et al.* (2005b) found the effects of elevated CO_2 concentrations, reduced O_2 concentrations and ethylene gas on the fry colour and sugar content in the variety Russet Burbank. The authors found that tubers exposed to both elevated CO_2 concentrations and ethylene were darker and with higher reducing sugar concentrations, not only than the controls, but those treated just with ethylene, suggesting a

synergistic negative effect of trace ethylene and elevated CO_2 on fry colour. Management of ethylene application such as timing application at the point of dormancy break and ramping up ethylene concentrations to a final concentration of 10 ppm in store can alleviate issues around changes in respiration rate.

8. Research gaps

Prediction of dormancy break would be of great practical benefit to growers, enabling market decisions and greatly assisting the timing of sprout control treatments. To date there are no predictive methods so there is a reliance on routine visual examination which is best practice for store managers. However, it is difficult to examine potatoes under the surface within boxes or bulk piles.

Garnett *et al.* (2018) successfully used a Visible/Near-infrared spectrometer equipped with a fibre-optic probe to stimulate and measure chlorophyll production in potato tubers as a marker for changes in tuber physiology particularly dormancy break. This methodology requires translation from laboratory bench to commercial storage.

Recent analysis (Tout, 2019) of metabolites within potato buds during dormancy break have suggested that elements of the TCA cycle can be used as very early markers of bud release from dormancy across a range of storage and growth conditions. Moreover, a quantitative analysis indicated that at certain stages the TCA cycle was functioning in a non-cyclic manner. These shifts in TCA cycling may form early indicators of changes in the activation of meristems and may provide a route to dormancy status determination through sampling and chemical analysis or possibly through specific volatile signatures.

Several proteins involved in amino acid metabolism, including aspartate aminotransferase (an enzyme controlling aspartate synthesized for N transport), methionine synthase (involved in methionine metabolism), ketol-acid reductoisomerase and N-acetyl-gamma-glutamyl-phosphate reductase have been implicated during dormancy release. However, further research is needed to elucidate how these amino acids influence tuber dormancy and sprouting (Liu *et al.*, 2015b).
Tuber dormancy and sprouting are controlled by all the major plant hormones. New genetic approaches for the identification of genes associated with quantitative trait loci (QTL) are needed for a better understanding of tuber dormancy and sprouting regulation (Bisognin *et al.*, 2018). QTL analysis will support marker assisted breeding, for example Bisognin *et al.* (2018) identified QTLs on three chromosomes (2, 3 and 7) linked with dormancy and apical dominance release that are associated with the regulation of all major plant hormones. The QTL on chromosome 2 and 3 has been linked with ABA responsive and signalling genes (chromosome 3) and on chromosome 7 with GA, IAA and ABA signalling genes.

The role of calcium as a downstream signalling molecule and its role in meristem activation requires further investigation and elucidation of its precise role in regulating cell division versus cell elongation. Manipulation of tuber calcium content may provide a method of altering dormancy durations.

A greater understanding of the interaction of environmental conditions on crop development and its relation to tuber maturity at harvest and dormancy break is required. Similarly, how store conditions impact on tuber physiological processes should be revisited using more recent potato varieties.

The non-CIPC sprout suppressants have only relatively recently been the subject of research efforts and the optimisation of application conditions, timing and dosing for repeat application for short, medium and long-dormant varieties still requires further investigation and development.

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10. Appendix 1. Sprout control

This review was published in December 2021. Refer to the Health and Safety Executive, Chemicals Regulation Division (CRD) website for up-to-date information on the products approved for use as potato sprout suppressants in GB.

Sprout inhibition can be induced by physical or chemical damage of the developing buds (Kleinkopf *et al.*, 2003), or, in some cases through chemical treatments that affect the mechanism of dormancy break. Physical interventions that significantly limit sprouting once dormancy has broken rely on cold-temperature storage (2-4^{o}C). However, this can induce low-temperature sweetening in many varieties, reducing tuber quality, especially in terms of processing quality (Sonnewald, 2001). The most widely adopted approach for processing varieties is to use chemical sprout suppressants such as those detailed below.

The rate of sprout growth changes over time, initially growth is slow, immediately after the end of dormancy, and as the tubers age, the rate of sprout growth increases to a maximum, usually with the apical sprout exerting dominance over the other buds (Krijthe, 1962). As apical dominance diminishes lateral buds emerge, and when apical dominance is overcome, individual sprouts display multiple branching. With advancement in physiological aging in old tubers formation of small micro-tubers (little tuber syndrome) is observed (Krijthe, 1962; Daniels-Lake and Prange, 2007; Suttle, 2007).

In ware potatoes, preventing sprouting during storage is important, in contrast to seed potatoes where controlled sprouting of the tubers is desired to produce stronger next-generation plants (Sonnewald, 2001). However, management of sprouting is complicated; the onset and vigour of sprouting is affected by cultivar, agronomic influences and storage conditions (Daniels-Lake and Prange, 2007). A strong varietal effect on dormancy was found in commercial varieties ranging from 2-3 months through to 8 months in varieties such as Russet Burbank when stored at 6-8ºC. AHDB commissioned research reports into the efficacy of currently available and near-market sprout suppressants on sprout control of GB fresh pack (11140057, 2018-2022) and processing varieties (11140043, 2017-2022) are available at https://ahdb.org.uk/knowledge-library/research-reports-on-potato-storage.

10.1.1. Chloropropham (CIPC)

Chloropropham (CIPC) was used for more than 40 years (Kleinkopf *et al.*, 2003). However, a non-renewal notice preventing re-registration of CIPC in the EU as a sprout suppressant for potato and as a herbicide for horticultural crops came into force on the 8th July 2019. This enforcement stipulated

a maximum use up grace period to the 8th October 2020. In some EU countries the use up period was earlier than 8th October 2020 to ensure compliance.

10.1.2. Maleic hydrazide (MH)

Maleic hydrazide (MH) acts to extend dormancy in potato by inhibiting cell division in the buds but has no subsequent effect on cell elongation during sprout growth. MH is applied in the field, as a single application during the growing season when at least 80% of the tubers have reached 25 mm diameter and at least 3 weeks before haulm killing (De Blauwer *et al.*, 2011).
A review of its use as a sprout suppressant and reports of research trials 11140043, 11140056 and 11140057 (2018-2022), which included the use of MH, can be found within https://ahdb.org.uk/knowledge-library/research-reports-on-potato-storage.

10.1.3. Alternative strategies for sprout control

Other chemicals have been evaluated as sprout inhibitors, as described in the review on sprout inhibition in storage from Kleinkopf *et al.* (2003), and research reports; within https://ahdb.org.uk/sprout-suppression, for processing varieties in the RESKIA project and Visse-Mansiaux, *et al.* (2021).

Ethylene gas provides reversible sprout control, and spearmint oil, that burns off existing sprouts are now available as commercial alternatives to CIPC (Kleinkopf *et al.*, 2003; Daniels-Lake and Prange, 2007). Other products able to control sprouting are 1,4-dimethylnapthalene (DMN), 3-decen-2-one (Smartblock), caraway oil, clove oil and orange oil.

10.1.3.1. Ethylene

Ethylene can be an effective potato tuber sprout inhibitor with two companies, Restrain Company Ltd. and Biofresh Group Ltd., providing ethylene delivery systems in the GB.

Ethylene is approved as a potato sprout suppressant and can be applied continuously throughout storage at a concentration of 10 ppm (Briddon, 2006). To maintain sprout control, ethylene application should be continuous (Rylski *et al.*, 1974). Terminating ethylene treatment early in store could result in sprout growth initiation (Foukaraki *et al.*, 2016b). Targeting ethylene treatments to the final stages of endodormancy, reported by Foukaraki *et al.* (2016b), may reduce the amount of ethylene applied and delay the onset of sprouting at the end of storage.

This suggests that ethylene terminates endodormancy but extends ecodormancy as previously shown by Rylski et al. (1974). Nevertheless, the application of ethylene at 10% eye movement may be riskier in a commercial setting. In this situation regular well managed tuber monitoring would be

essential, but will have the advantage of saving costs on ethylene application and potentially extend storage when compared with continuous ethylene application (Foukaraki *et al.*, 2016a). Foukaraki *et al.* (2016a) using cvs. Russet Burbank and Saturna noticed that if ethylene application is delayed after 10% eye movement there will be still sprout inhibition without a dramatic rise in sugar content. It may darken fry colour and is responsible for a peak in tuber respiration (Daniels-Lake *et al.*, 2005a; Daniels-Lake *et al.*, 2005b) (further information in section 6.3. Tuber respiration). However, respiration rate declines over the following few days remaining insensitive to additional ethylene exposure (Daniels-Lake *et al.*, 2006 and references therein). Methods of treatment including timing of treatment initiation and its gradual introduction and store management have been developed to minimise unwanted fry effects.

10.1.3.2. Caraway oil

Carvone contains two enantiomers S-(+)-carvone and R-(-)-carvone. The *S*-(+)-enantiomer carvone is found in dill oil at levels of 30-65% and at 50-75% in caraway oil (Hartmans *et al.*, 1995), while the R-(-)-carvone form makes up 50-80% of spearmint oil. A comparative study investigated the sprout suppressant capability of caraway, dill and spearmint essential oils and CIPC on potato tubers stored at 5, 10 and 15°C (Şanlı and Karadoğan, 2019). For effective sprout suppression repeated applications were required to maintain a low and constant concentration of carvone around the tubers (Kleinkopf *et al.*, 2003; Frazier *et al.*, 2004). In The Netherlands S-(+)-carvone (Talent) is available for sprout control of seed crops.

10.1.3.3. Spearmint oil

Spearmint oil (active ingredient R-(-)-carvone), commercially known as BIOX-M, has been used as a sprout suppressant in the UK since full registration in 2012 (BIOX-M, MAPP 16021). There are numerous studies on the efficacy of BIOX-M including AHDB-funded under different storage conditions (1140043 and 11140057).

10.1.3.4. DMN

1,4-dimethylnapthalene (DMN) is a sprout control agent with the advantage that its sprout suppressive effects are reversible and thus has the potential to be utilised in preventing sprouting in potato seed tuber stock (Beveridge *et al.*, 1981). A formulation of 1,4 DMN is 1,4 SEED® which is registered for seed tubers in the US.

For main crop potatoes DMN formulation commercially known as 1,4-SIGHT®, has been available in the US for main crop potatoes. DMN is an EU Annex 1 listed product and has received national registrations in The Netherlands, Belgium, Germany, France and Austria although its registration is still to be approved in the UK.

10.1.3.5. 3-decen-2-one

3-decen-2one, commercially known as SmartBlock®, is a volatile oily liquid usually applied to stores as a hot fog and which causes physical damage to the sprout (Paul *et al.*, 2016). SmartBlock® has been registered in the USA as sprout suppressant since February 2013, and its registration is being sought in Europe.

10.1.3.6. Clove oil

The active ingredient of clove oil, eugenol, causes physical damage to sprouts and has several registrations for use as a sprout suppressant in the USA. Clove oil has good sprout control proprieties when applied regularly at two to three week intervals (Frazier *et al.*, 2004) and can be applied when sprout control is incomplete i.e. as a corrective treatment. Biox-C is a commercial preparation (Frazier *et al.*, 2004) but not currently registered as a potato storage treatment in the UK.

10.1.3.7. Orange oil

The active agent of Orange oil is limonene, a volatile, oily liquid which was listed in EU Annex 1 in 2014. Applied as a hot-fog, it acts to burn off actively growing sprouts. Orange oil is being developed as a sprout suppressant by UPL Ltd with the trade name Argos.

10.1.3.8. Irradiation

Gamma irradiation has been reported as an effective sprout controlling method (Blessington *et al.,* 2015), however could have some negative effects on potato quality (Liu *et al.*, 1990; Lu *et al.*, 2012; Mahto and Das, 2014), The work of Soares *et al.* (2016) reported that treating Agata cultivars with a dose of 150 Gy of gamma irradiation provided a promising system to improve shelf life of potato tubers. However, consumer concerns over irradiation has limited the adoption of this technology globally (Kleinkopf et al., 2003; Daniels-Lake and Prange, 2007) and use of irradiation in foodstuffs within the EU is restricted (EU Directive 1999/2/EC).

10.1.3.9. Ultraviolet-C

Ultraviolet-C (UVC) irradiance has been tested as a method to reduce sprout growth. Cools *et al.* (2014) treated potato tubers, when 10% of the sample population had discernible eye movement, with UVC. Treatment reduced sprout growth in cvs. Cabaret, Maris Piper, Russet Burbank, Saturna and VR 808 although the dose response appeared to be cultivar dependent.