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PHYSIOLOGICAL MECHANISMS FOR POTATO DORMANCY RELEASE AND SPROUTING: A REVIEW

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ABSTRACT

Potato (*Solanum tuberosum* L.) tubers undergo a period of dormancy, during which visible bud growth is inhibited. The length of the dormancy is determined by environmental, physiological and hormonal control mechanisms. Dormancy is the final stage of tuber life, which serves to preserve tubers as organs of vegetative reproduction under unfavourable growth conditions. Since the duration of potato tuber dormancy and sprouting time bear significant economic importance, this review considers the regulation of dormancy and sprouting of potato by phytohormones and reactive oxygen species. Two phytohormones, ABA and ethylene suppress tuber sprouting; however, the exact role of ethylene remains to be elucidated. Cytokinins and gibberellins are required for bud breaking and sprout growth, respectively. The auxin seems to play a role in vascular development. Thus, tuber dormancy and sprouting can be controlled in potato by manipulation of Reactive Oxygen Species (ROS), especially H_2O_2 metabolism *via* the inhibition of catalase (CAT) activity.The possible mechanisms by which CAT inhibitors or H_2O_2 overcome dormancy and promote sprouting in the potato tuber are discussed.

Key Words: Cytokinins, ethylene, gibberellins, *Solanum tuberosum*

RÉSUMÉ

La pomme de terre (*Solanum tuberosum* L.) connaît une période de dormance durant laquelle la germination des bourgeons visibles est inhibée. La durée de dormance est déterminée par des mécanismes de contrôle environnemental, physiologique and hormonal. La dormance est le stade final de la vie des tubercules servant à préserver les tubercules comme organes de reproduction végétative sous condition de germination défavorables. Etant donné que la durée de la dormance des tubercules de la pomme de terre et le temps de rejet revêtent une importance économique significative, cette revue considère la régulation de la dormance et le rejet de la pomme de terre par des hormones et d'espèces réactives d'oxygène (ROS). Deux phytohormones ; ABA et éthylène empêchent le rejet des tubercules ; par ailleurs, le rôle extractif de l'éthylène reste à élucider. Les cytokinines and les gibbérellines sont nécessaires dans l'élimination des bourgeons et la croissance des rejets, respectivement. L'auxine semble jouer un rôle dans le développement vasculaire. Ainsi, la dormance et les rejets des tubercules peuvent être contrôlés par manipulation d'espèces réactives d'oxygène (ROS), spécialement le métabolisme du H_2O_2 à travers l'inhibition de l'activité de la catalase (CAT). Les mécanismes possibles par lesquels les inhibiteurs du CAT ou H_2O_2 surmontent la dormance et facilitent le rejet de la pomme de terre sont discutés.

Mots Clés: Cytokinines, éthylène, gibbérellines, *Solanum tuberosum*

INTRODUCTION

After reaching physiological maturity, potato (*Solanum tuberosum* L.) seeds may enter a state of deep dormancy, during which potato seeds do not germinate after planting. Dormancy is the physiological state of the tuber in which tubers do not sprout even when placed in ideal germination conditions (Reust, 2002; Sonnewald and Sonnewald, 2014). The dormancy period varies from 2 to 3 months, depending on genotype and conditions of pre-and post-harvest. Therefore, it should be evaluated before releasing any variety so that farmers are able to store their produce for a desired period of time under traditional storing conditions or in refrigerated infrastructure.

For quality of a particular potato clone, its dormancy period and sprouting behaviour are major criteria that should be documented before any promising clone is released (Viratanen *et al.,* 2013). Initiation of dormancy break begins before the visible sprout development. In this contex, researchers continue to examine the physiological processes associated with dormancy, and subsequent sprout development. It is believed that the five major plant hormones are involved in the process; abscisic acid and ethylene are involved in the induction of dormancy, cytokinins are involved in dormancy break, and gibberellins and auxins are involved in sprout development.The importance of hydrogen peroxide and antioxydant system was also demonstrated by Delaplace *et al.* (2008) as factors implicated in potato dormancy release.

There is a complex sequence of events that takes place for dormancy to break, and cell division and elongation to produce a visible sprout (Teper-Bamnolker *et al.,* 2010). However, the physiological mechanisms involved in inducing dormancy release and altering apical bud dominance is poorly understood. Although the postharvest potato tuber is used as a model system for the study of metabolic processes associated with dormancy release and sprouting, very few studies have been done on meristematic cells. Therefore, in the present review, we focus on the environmental, genetic and molecular mechanisms by which hormones cause dormancy and sprouting of potato tuber in the different tissues of the tuber and in particular in the meristematic tissues.

Tuber dormancy. Dormancy is a physiological state characterised by a period during which autonomous sprout growth does not occur, even under optimal sprouting conditions (darkness, 15 to 20 °C, relative humidity about 90%). Dormancy is regarded as a period in the tuber life cycle from initiation to the time when sprouting starts. However, since this period is difficult to determine, post-harvest dormancy is used for practical purposes, and is defined as the period from dehaulming to the time when 80% of tubers show sprouts at least 2 mm long (Pande *et al.,* 2007). A dormancy value or duration gives an insight on how long the potato will store before it initiates sprout development. Knowledge of dormancy duration provides information for selecting varieties for short to long-term storage, planning for proper timing of sprout inhibition products, and marketing of the potatoes. For fresh market potatoes, detrimental quality concerns develop once sprouting begins; such as changes in carbohydrate status, increase in respiration rate, additional weight loss, and storage management issues like impeded airflow. Seed producers may need to accelerate or retard sprout development depending upon the time of year and intended seed market (Johansen *et al.,* 2008; Salimi *et al.,* 2010).

The biological advantage of a dormancy period in a plant concerns the survival of the species. The inherent dormancy of potatoes allows for most varieties to overwinter, barring any freezing conditions, and resprout in the spring, thereby reproducing and perpetuating the species. Tuber dormancy keeps the potatoes from sprouting in the fall, thereby reducing chances of the species being killed by unfavourable winter conditions (Essah and Honeycutt, 2004). Conversely, the tuber dormancy period provides great advantage in storage to allow for many months of storage, with or without sprout control product application. Quality can be maintained when using a tuber's inherent dormancy traits to our advantage (Veerman and Wustman, 2005).

Physiology of dormancy and sprouting. There are three classes or types of dormancy that can be described in potatoes.

(a) "Endodormancy" which occurs after harvest, due to the internal or physiological status of the tuber (Suttle, 1998). In this situation, even if tubers are placed in conditions favourable for sprout development, sprouting will not occur (Lang *et al.,* 1987; Aksenova *et al.,* 2013).

(b) "Ecodormancy" is when sprouting is prevented or delayed by environmental conditions. An example of this would be potatoes stored at lower temperatures, having a longer dormancy period compared to those stored at warmer temperatures.

(c) "Paradormancy" is comparable to endodormancy, although the physiological signal for dormancy originates in a different area of the plant from where the dormancy occurs. An example of this is apical dominance of a tuber, the apical meristem or dominant bud/eye, impedes development of secondary bud or sprout development. Some varieties have stronger paradormancy than others. The growing season or pre-harvest conditions can also affect dormancy length along with post-harvest conditions such as temperature and light (Knowles and Knowles, 2006; Aksenova *et al.,* 2013).

The end of endodormancy is marked by the emergence of the apical bud; while paradormancy is marked by apical dominance, and the end of the ecodormancy manifested by the emergence of axillary buds or proximal buds (Bajji *et al.,* 2007). Studies have suggested that apical dominance is determined by the ratio of concentrations of Indole Acetic Acid (IAA) and Gibberellic Acid (GA) (Sorce *et al.,* 2009). Teper-Bamnolker *et al.* (2012) has demonstrated that the concentration of IAA significantly increasesin the apical dominance. However, according to Sarath *et al.* (2007), IAA as well as cytokinins and abscisic acid, may be involved in the removal of apical dominance.

When dormancy is broken, sprouting begins. Sprouting is the major visible milestone in determining tuber physiological age. The earliest observable stage of sprouting is characterised by visible small white buds, often termed as "pipping" or "peeping" (Sonnewald, 2001; Daniels-Lake and Prangel, 2007). The physiological age of the tuber has a great effect on the pattern of sprout growth, but the basis is genetic. In turn, the physiological age of the tuber is greatly influenced by growing conditions, storage conditions, and length of storage period (Alexopoulos *et al.,* 2008).

Development of physiological age

Incubation. The incubation period is defined as the period between the beginning of tuber sprouting and tuberisation during storage in the dark at a temperature between 15 and 20 °C and, relative humidity ranging between 90 and 95%. This period ends when the diameter of the tuber doubles that of stolon, which covers 80% of the main stems. This period depends on the variety and temperature (Caldiz *et al.,* 2001).

Senescence. This is the last phase of development of the mother tuber, where a series of irreversible events increasingly occur leading to cell degeneration and sometimes programmed cell death begins. This phase consists of metabolic changes, which result in short or long term death of the mother tuber (Zentgraf, 2007).

Apical dominance. Apical dominance is a physiological phenomenon characterised by the exhibition of a dominant bud over the others, that is suppressing the sprouting of other buds (Pavlista, 2004). The suppressing bud is at the apical end of the tuber, which is the furthest bud from where the tuber was attached to the vine. Physiological young tubers exhibit apical dominance and, thus the apical sprout will need to be removed (de-sprouted) for the other buds to develop sprouts. Multiple sprouting develops gradually in time as apical dominance diminishes, and is characterised by the appearance of several buds sprouting along the tuber. The duration of apical dominance as well as the number of sprouts

per tuber is a varietal characteristic (Carli *et al.,* 2012).

Middle age. Middle aged tubers exhibit multiple sprouts, and are at the optimum stage for planting. However, as mentioned before, this pattern can be induced in young tubers by removing the apical sprout, although apical dominance may be reinstated by growing the next bud closest to the apical end (Pavlista, 2004). In such a situation, a second de-sprouting will be necessary for inducing more sprouts (Carli *et al.,* 2012; Aksenova *et al.,* 2013).

Branching. Branching appears as middle aged tubers age further. Since sprouts comprise of multiple nodes with meristematic tissue and leaf primordia at each node, branching occurs when apical dominance within the sprouts is overcome, either after the sprouts are sufficiently large because of tuber senility, or following damage to the apex. These branches are referred to as "hairy" because they tend to be weak. Even more, old tubers may also show proliferation of small stolons (Daniels-Lake and Range, 2007; Leyser, 2009). Since the sprout depends on the tuber for the materials for growth, if there are several sprouts on the tuber, an inter-sprout competition for growth factors will be imposed by the size of the tuber. With fairly large tubers, no effect of size will be noticeable, but with decreasing size, a point can clearly be reached at which growth will be impaired. This competition has been shown to be independent of the distance between the competing sprouts, suggesting that it is not a local matter but of growth factors distributed throughout the tuber (Fernie and Willmitzer, 2001).

Weight loss. Weight loss determines the longevity of tubers' storability and, hence, their keeping quality. Variations in weight loss among cultivars is attributed to either their periderm characteristics or their sprouting behaviour. Weight loss in unsprouted tubers occurs through the periderm, and for a minimum proportion through the lenticels. Hence, varieties with a thick periderm (a large number of cell layers in the periderm) and less lenticels on the tuber surface lose less weight than their counterparts (Struik and Wiersema, 1999; Ezekiel *et al.,* 2004; Pande *et al.,* 2007). On the other hand, sprouted tubers lose much more weight than unsprouted ones. After the onset of sprouting, the rate of sprout growth and number of sprouts determine weight loss in potatoes. Greater water loss with sprout growth occurs because of the high permeability of sprout wall to water vapour. A significant correlation between weight loss and both the length of the longest sprout and number of sprouts per tuber was encountered by Pande *et al.* (2007).

Role of environmental conditions. Dormancy is considered to be a varietal character, yet is influenced by environmental and management conditions. Since dormancy is not related to earliness of varieties, it is possible to breed late varieties with relatively short dormancy and early varieties with relatively long dormancy. Dormancy period depends also on soil and weather conditions during growth, tuber maturity, storage conditions, and whether the tuber is injured or not. High temperatures, low soil moisture and fertility during tuber growth accelerate physiological development and reduce the dormant period (Kloosterman *et al*., 2005; Delaplace *et al.,* 2008). However, tubers harvested immature have a longer post-harvest dormancy than those harvested at maturity. On the other hand, fluctuating storage temperatures shorten dormancy more than constant high temperatures (Eremeev *et al.,* 2008). Therefore, storage temperatures should remain as consistent as possible when retarding sprout development is desired. Moreover, tuber injuries caused by harvest or by diseases and pests, can result in earlier sprouting (Fauconnier *et al.,* 2002).

Soil conditions after haulm destruction but before harvest, probably have the largest effect on tuber dormancy. It also depends on the size of tuber and the size of mother tuber. Certainly, the period of dormancy is positively correlated with the dormancy period of the mother tuber. Furthermore, it was shown that the dormancy of tubers of small size is longer than the big size (Vreugdenhill, 2004).

The dormancy period also depends on the environmental conditions during growth and tuber storage. Indeed, it has been reported that tubers stored at temperatures below 3 or above

30 °C sprout prematurely (Law and Suttle, 2004). Although cool temperatures during storage can prolong the dormancy period, they generally result in an increase in reducing sugar content, primarily glucose, which is undesirable in the processing industry due to darkening of fried products (Wurr *et al.,* 2001; Suttle *et al*., 2012).

During dormancy, biochemical and physiological processes occur, but they do not trigger immediate morphological changes (Brown *et al.,* 2003). Yet these processes are relevant for the number of sprouts produced after breaking of the dormancy and for the growth vigour of the seed tuber. Conditions during dormancy and, thereafter, affect the progress of the physiological ageing and, therefore, influence the performance of the seed tuber. Heat and cold shocks, and similar accumulated day-degrees built up in different ways, may all have specific effects, depending on cultivar (Struik*,* 2007; Sincik *et al*., 2008). Diffuse light may prevent rapid ageing of seed tubers (Virtanen *et al.,* 2013).

Chemicals leading to dormancy release. To break dormancy tubers, several methods are deployed. Thiourea (a catalase inhibitor), for instance, breaks dormancy according to Pérez and Lira (2005). It also stimulates sprouting of potato; thereafter, it allows the tuber to produce more seeds. In fact, some authors partulate that soaking tubers at harvest in solutions of thiourea (1-2% for 2 hours or 3% for 1 hour) breaks dormancy (Rehman *et al.,* 2003; Mani *et al.,* 2013). These findings are consistent with earlier works of Kwan-Sam and Sang-Soo (2000), Ju *et al.* (2001) and Hassan-Pannah *et al.* (2007a), which showed that tuber treatment with thiourea (1 or 5%) was more effective in breaking dormancy than treatment with IAA or GA3.

Other substances that release tuber dormancy are nitrate (Bethke *et al.,* 2007), ethylene (Bleecker and Kende, 2000; Gamble *et al.,* 2002) and hydrogen peroxide (Bajji *et al.,* 2007). It seems that these substances act on dormancy by regulating the synthesis of abscissic acid and gibberellins on one hand, and between auxins and brassinosteroids, on the other hand (Wang *et al.,* 2002). More recent studies have shown that hydrogen peroxide regulates the synthesis of ethylene, jasmonic acid and salicylic acid, which removes dormancy (Kwak *et al*., 2006). Indeed, its direct application releases dormancy of several species (Perez and Lira, 2005).

Thiourea. Among the chemicals applied for breaking down the potato nodes dormancy, is thiourea. Thiourea triggers potato tubers germination and healing of tuber injuries (Bajji *et al.,* 2007). Thiourea solution in an appropriate concentration, not only facilitates germination, but also produces more than one sprout in each eye of potato. Thiourea dominates in inhibiting effects of major sprouts over the minor ones in each eye, and neutralises terminal buds capacity to stop lower buds growth in seeding tubers. It is reported that using thiourea and/or applying H_2O_2 enables removalof tuber dormancy (Bajji *et al.,* 2007). In addition, treating cut tubers or newly harvested ones with1-2% thiourea solution for 1-2 hours, and with 3% for 1 hour breaks dormancy (Hosseini *et al.,* 2011).

It was also reported that using 1% thiourea GA3 hormone, of 5 ppm concentration is more efficient in increasing sprout number and length in 5 varieties of normal tubers of potato, than control treatments. It was declared that treating tubers with amixture of GA3 (1 ppm) and thiourea with 1% concentration, increases plant growth and decreases dormancy period significantly, in comparison with other treatments (Biemelt *et al.,* 2004; Germchi *et al.,* 2010).

Gibberellins. GA3 has the potential to relieve dormancy and improve sprouting of mini-tubers in many potato cultivars. The only restrain for GA3 application is its efficient penetration into the internal tissues of tuber (Otroshy and Struik, 2006). Since the tuber skin is a main hinderance for chemical permeation, it is advisable to apply these chemicals on tuber slices and/or tubers with damaged or cracked skin (for example on newly harvested tuber) (Shekari *et al.,* 2010). GA3 application as liquid solutions accelerates eye growth *via* sprout emergence and produces more slim accessory shoots (Rehman *et al.,* 2003). Morphologically, 2-3 mm initial growth of sprout is a reliable criterion for dormancy breaking of tuber. GA3 application has been reported to efficiently alleviate tuber dormancy (Mosley *et al.,* 2007). Moreover, GA3 application effectively

reduces dormancy period and time needed for mini-tubers sprout emergence. However, there is controversy towards deciding the suitable GA3 concentration for dormancy soothing of potato mini-tubers (Hassan-Panah *et al.,* 2007; Khorshidi-Benam and Hassan-Panah, 2008).

In an experiment, 1500 ppm GA3 and 5% thiourea reduced the dormancy period of 'Agria' potato by 50% (Hassan-Panah *et al.,* 2007). A study of the effects of dormancy breaking treatments on mini-tubers of 'Macaca' (short-dormancy needs) and 'SMIJ 46-1' (long-dormancy needed) potato cultivars revealed that the highest dormancy alleviation belonged to 'Macaca' with 30 ppm GA3 application (Benedetti *et al.,* 2005). Meanwhile, 5 ppm GA3 has been noted as the appropriate amount for dormancy relief and yield improvement of 'Agria', 'Marfona' and 'Gloria' potatoes (Rehman *et al.,* 2003).

Higher concentrations of GA3 had adverse effects on plants in form of tremendous stem growth, reduced root growth, delayed tuber formation, compacted shoots and deformed tubers (Shekari *et al.*, 2010). Similar works undertaken by Chapman (2006) and Vreugdenhill and Struik (2006) indicated that GA3 is a dominant regulator in tuber formation and promotes stolon elongation, and inhibits tuber formation.They treated dormant or sprouted seed potatoes with various concentrations of gibberellic acid and indicated that emergence of plants from treated seed was faster than from untreated ones. They proved that growth of secondary buds in potato stolons, was intrigued and this phenomenon should predominate final dominancy. They found that before tuberisation, the shoots contained large quantities of gibberellin-like substances, which decreased after tuberisation. They suggested that these substances are of importance in the control of tuberisation. In the same contex, Barani *et al.* (2013) reported that GA3 leads to smaller tubers resulting in increased bud numbers and stolons by removing apical dominance. Otherwise, foliar application of GA3 (5 and 10 ppm) increased the length of stems and stolons, and decreased tuber fertility, but causedelongation of the stolons (Rentzsch *et al.,* 2011).

Ethanol. The effect of ethanol on dormancy of tubers was tested by transferring *in vitro* tubers to medium with 0.5% ethanol and low or high levels of sucrose (Bologa *et al.,* 2003). Ethanol, combined with a low level of sucrose, resulted in the growth of sprouts; while ethanol in combination with a high level of sucrose resulted in development of secondary tubers. Thus, in both cases, ethanol breaks dormancy, while the sucrose level determines the identity of the secondary structure.

For seeds, it has been suggested that conversion of ethanol *via* alcohol dehydrogenase (ADH) is required for the effect of ethanol on breaking of dormancy (Corbineau *et al*., 1991). In the same way, low amounts of ethanol, applied as vapour or dissolved in the medium, can result in similar activation of bud growth of tubers grown *in vitro*. The dormancy-breaking effect of ethanol was visible, either as the growth of a sprout, or as the formation of secondary and tertiary tubers. This observation of direct action of ethanol is a circumstantial indication that ethanol may be involved in dormancy breaking under field conditions. Ewing *et al.* (2004) found that soil compaction results in severe induction of second growth. This may now be attributed to poor aeration of soil resulting in anaerobic conditions and accumulation of ethanol, produced either by the tuber itself or by the soil micro-organisms. Within 10 hr after transfer to a medium supplemented with ethanol, cell cycle and storage-related gene expression (as quantified by LUC Luceferase activity in the whole tuber) declined relative to that in tubers on medium without ethanol. This indicates that processes within the tuber, namely cell division and synthesis of reserves, normally associated with tuber development (Verhees *et al*., 2002), are rapidly blocked by ethanol. As a control, expression of the CaMV 35S promoter in tubers under similar conditions was monitored. In these tubers, no effect of ethanol on LUC activity was observed, suggesting that the changes in cell cycle- and storage-related LUC activity are likely due to changed promoter activity of these reporter genes and do not result from other more general changes which may affect *in vivo* LUC

activity, for example, ATP, oxygenor luciferin uptake (Classens *et al.,* 2005).

The early effects of ethanol on cell cycle and storage-related gene expression in the tuber tissue are not directly related to detectable growth activity of the apical bud: the down-regulation of gene expression in tuber tissue was visible within <10 hr; while the actual growth of the apical bud was only visible at 2 - 3 days after transfer to medium with ethanol. Moreover, in older tubers, the effect of ethanol on cell cycle-related gene expression was as rapid as in young tubers (within <10 hr), but sprouting was only visible after 5 days (data not shown) (Classens *et al.,* 2005).

Treatment with 4-MP inhibited sprouting and prevented ethanol-induced down-regulation of gene expression. Since 4-MP is an inhibitor of plant ADH activity (Perata and Alpi, 1991), this suggests a role for ADH in the effect of ethanol in breaking of dormancy. A role for ADH enzyme activity in dormancy breaking by alcohols is further substantiated by the fact that only ADH substrates (primary alcohols) and not secondary alcohols affect dormancy and gene expression. The fact that 4-MP alone also inhibits sprouting suggests either that the compound itself inhibits dormancy breaking, or that ADH activity plays a role in breaking dormancy, even in the absence of exogenous ethanol (Hubbard *et al.,* 2010).

Hormonal regulation. Tuber dormancy is controlled by phyotohormones, which play important roles in the initiation or inhibition of dormant potato tubers. Cytokinins are involved in the induction of tuber dormancy and gibberellins in the regulation of tuber sprouting (Suttle, 2004). In fact, biochemical analysis indicates changes in concentrations of phytohormones at the beginning of dormancy. Thus, the entry into dormancy is associated with increased concentrations of abscissic acid (ABA) and a decrease in gibberellins (Fernie and Willmitzer, 2001; Weiner *et al.,* 2010).

Some evidence has implicated indole acetic acid (IAA), an auxin in sprouting. Indole acetic acid has been suggested to mediate the suppression of sprouting of lateral axillary buds by apical dominance (Pavlista, 2004). Quantitative trait loci (QTL) analyses have indicated that tuber dormancy is controlled by at least nine distinct loci. The potential role of ABA in dormancy has also been supported by the observation of three of these QTL influencing ABA levels (Classens and Vreugdenhil, 2000; Sorce *et al.,* 2000; 2009). Sprouting is associated with many physiological changes, including the conversion of starch to sugars, respiration, water loss, and glycoalkaloid content. Also, Seo and Koshiba (2002) and Bolandi and Zorghai (2004) indicated that the amount of abscissic acid present in a three weeks tuber is equal to 214 umol g^{-1} tuber and drops to 23 mmol g^{-1} tuber at sprouting. However, during dormancy, there is a progressive increase in gibberellins and decrease in abscissic acid concentrations.

Suttle (2000) reported that dormancy release is accompanied by activation of monooxygenases which converts hydrogen peroxide into oxygen to produce gibberellins. In the same context, it has been established that abscissic acid and ethylene are responsible for entering tuber dormant and that only abscissic acid is essential for the maintenance of dormancy; while cytokinins are responsible for breaking it (Nambara and Marrion-Poll, 2005). Similar results have been reported in other species such as Arabiodopsis (Saiko *et al.,* 2004). These results are consistent with those of DeStefano *et al.* (2006a) who isolated two genes: StNCED StNCED 1 and 2 from meristemtic cells of cortical dormant tuber tissue. These genes encode the synthesis of abscissic acid. These results are further confirmed by a recent study undertaken by Eshel and Teper-Bamnalker (2012) who showed that meristematic cells in the apical bud regulate tuber dormancy by controlling a Programmed Cell Death (PCD).

Abscisic acid. In potato tubers, ABA is involved in the regulation of tuber dormancy and wound healing (Lulai *et al.*, 2008; Suttle *et al.,* 2012). In the case of tuber dormancy, ABA content is highest immediately after harvest when meristem dormancy is deepest. ABA level falls gradually during storage as dormancy weakens. Despite considerable differences in tuber dormancy duration among cultivars, the relationship between ABA content and dormancy progression has been demonstrated in a number of potato cultivars stored under a variety of conditions

(Biemelt *et al.*, 2004). Chemically induced reduction in tuber ABA content, using the biosynthesis inhibitor fluridone, resulted in premature tuber sprouting, thus demonstrating the sustained requirement for ABA synthesis and action to maintain tuber dormancy. In contrast, exogenous ABA typically elicits only a marginal and ephemeral effects on tuber sprouting. ABA is metabolically labile, and the failure of exogenous ABA treatments to delay sprouting for a more extended period is probably due to its rapid metabolism (Destefano-Beltrán *et al.*, 2006a). Because of this, the effects of sustained elevations in ABA content on potato tuber dormancy are unknown.

Other genetic studies showed that the transition from dormant to nondormant state in tuber meristems was associated with a decrease in endogenous abscisic acid (ABA) content and in ABA-regulated transcripts and tuber specific genes such as patatin (Simko *et al.,* 1997; Campbell *et al.,* 2008; 2010). The sprout inhibitors, CIPC and DMN, did not result in an increase in ABA, but led to an increase in expression of some ABA-regulated transcripts. Both sprout inhibitors resulted in transcript profiles that were significantly different from the dormant state and, thus did not prevent sprout growth by maintaining or inducing dormancy.

A chlorpropham (CIPC) resulted in cell division arrest in the G2/M-phase (Cell Cycle phase) of the cell cycle; while 1,4-dimethylnaphthalene (DMN) resulted in cell cycle arrest in the G1/S (Cell Cycle phase)-phase based on the lack of measurable DNA synthesis. Transcriptional analysis of DMN-treated tubers indicated that there was an increase in expression of RNA encoding the cell cycle inhibitors KRP1 and KRP2, which are known to suppress cell division in the G1/S-phase. Based on these data, we conclude that the sprout inhibitors DMN and CIPC have distinct modes of action and do notprevent growth through a prolongation of the dormant state (Faivre-Rampant *et al.,*2004; Campbell and Suttle, 2012).

Exogenous C_2H_4, an effective dormancy release agent, also caused decreased ABA levels within 24 hr. (Veramendi *et al.,* 2002). It also enhanced dormancy release and further promoted ABA losses by gas I. Gas II treatment led to slight reductions in ABA levels that were further decreased by C_2H_4. Sprout length was modelled successfully by multiple regression analysis in terms of glucose and ABA levels within the apical eye tissues of tubers immediately after, and regardless of, previous gas treatments or storage temperatures (Coleman, 2002).

Recently, changes in ABA content and expression of genes encoding key enzymes of the synthesis and ABA catabolism have been reported for three different tuber tissues (meristems, surrounding peridermand underlying cortex) during natural dormancy progressionof cold-stored tubers (Hartman *et al.,* 2011). On the other hand, natural release from dormancy is not uniform, and meristems on different potato tubers from a single harvest can emerge from dormancy weeks apart according to Suttle (2000). This asynchrony, together with the extended time span required for natural dormancy progression, complicated interpretation.

These studies demonstrated that a chemically forced dormancy break mimics natural dormancy release in at least these two important developmentally related aspects in potato tubers. ABA is actively metabolised in tuber tissues throughout dormancy and, in general, tuber ABA content has been shown to decline during storage (Biemelt *et al.,* 2004). It was shown that following Bromoethane (BE) treatment, ABA content in meristems increased by 2-fold after 24 hr, had declined dramatically (>80%) by day 4, and then remained at levels >2-fold lower than those at the start. This pattern of change in ABA content is reminiscent of that observed in tuber meristems during natural dormancy progression where ABA content rose 43% during the first 27 days of cold-storage, and then fell steadily towards the end of the study (150 days); except for a small but statistically significant increase at 111 days of cold-storage. Also, the present results are in general agreement with earlier reports describing changes in ABA content in whole potato tubers undergoing natural dormancy progression (Biemelt *et al.,* 2000) or following release from dormancy by synthetic cytokinin or heat stress (van den Berg *et al.,* 1991; Hartman *et al.,* 2011).

Previous studies demonstrated that decline in endogenous ABA content during tuber

dormancy was not accompanied by increase in ABA-glucose ester and that exogenous [3H](+)-ABA was metabolised in intact tubers exclusively to Phaseic Acid (PA) and ultimately to Diphaseic Acid (DPA) (Suttle, 1995). Sorce *et al.* (1996) also found an increase in tuber DPA content during storage, while ABA glucose ester content fell. Collectively, these results suggest that during tuber dormancy, ABA catabolism occurs predominately *via* oxidation, initially catalysed by cytochrome P450 ABA 89-hydroxylase (Cutlerand Krochko, 1999).The metabolism studies with meristems of BE-treated tubers, not only confirmed that ABA 89-hydroxylation was the main route for ABA metabolism; but also demonstrated that dormancy break was preceded and accompanied by an increased rate of ABA degradation. A similar increase in ABA catabolism was observed in meristems during natural dormancy progression (Campbell *et al*., 2010). In tuber meristems, a temporal correlation between changes in ABA content and expression of certain ABA biosynthetic and catabolic genes has recently been established during natural dormancy progression (Hubbard *et al.,* 2010; Suttle *et al.,* 2012). In particular, changes in ABA content closely mirrored the expression of a member of the 9-cisepoxycarotenoid dioxygenase gene family (StNCED2).

The role, if any, of the other NCED member (StNCED1) was uncertain because its expression pattern was unrelated to changes in ABA content. Furthermore, StNCED2 transcript abundance was 32-fold higher than that of StNCED1 (De Stefano *et al.,* 2006a). Likewise, decreases in ABA content correlated with up-regulated expression of two members of the potato CYP707A gene family (StCYP707A1 and StCYP707A2) that encode putative ABA 8'-hydroxylases. Expression of a third member (StCYP707A3) did not change significantly during dormancy (Kitahata *et al.,* 2005; Kondo *et al*., 2009). In many tissues, NCED is considered to be the regulatory enzyme of ABA biosynthesis, and its expression is well correlated with endogenous ABA content (Seo and Koshiba, 2002; Nambara and Marion-Poll, 2005). Also, in most plant tissues, NCED is encoded by a gene family (Chernys and Zeevaart, 2000; Lulai *et al*., 2008; Nonogaki *et al.,* 2010). In potato tubers, two NCED genes (StNCED1 and StNCED2) have been characterised by De Stefano *et al.* (2006b). In meristems of BE-treated tubers, StNCED2 transcript abundance not only exceeded that of StNCED1 by 24-fold, but its expression closely mirrored changes in ABA content, while StNCED1 transcript showed little variation (Suttle *et al*., 2007; Suttle *et al.,* 2012).

Moreover, in other studies, the increase in ABA content upon wounding in tuber cortical tissues was accompanied by aparallel increase in StNCED1 (but not StNCED2) transcript abundance (De Stefano *et al.,* 2006b). These data support the earlier suggestion that ABA biosynthesis in meristems during dormancy progression is mediated and perhaps controlled by the StNCED2-encoded protein. Differential NCED expression has also been described in both Avocado and Arabidopsis, where multiple NCED genes have been identified that exhibit either tissue-specific or developmentally regulated expression (Chernys and Zeevaart, 2000; Tan *et al.,* 2003; Okamoto *et al.,* 2011).

The decline in endogenous meristem ABA content after BE treatment suggested an increased rate of ABA catabolism during this period (Alexopoulos *et al.,* 2009). Consistent with this notion, the metabolism of exogenous [3H] ABA remained constant for 24 hr after treatment; and increased substantially thereafter. By 7 days post-treatment, metabolism of exogenous ABA increased by >2-fold over the initial levels. Collectively, we suggest that the initial increase in ABA content, following BE treatment, was a result of increased expression and activity of StNCED2 together with basal ABA 89-hydroxylase activity. Further, the dramatic decline in ABA content between days 1 and 4, may reflect decreased expression of StNCED2, coupled with dramatically increase in StCYP707A expression and activity. It is possible that additional ABA was being formed by accelerated release from a conjugate such as ABA-glucose ester. Alternatively, ABA-89-hydroxylase activity in tubers may also be regulated post-transcriptionally. Further studies are needed to clarify this issue.

In tubers, as in other plant tissues (Chernys and Zeevaart, 2000; Tan *et al.,* 2003; Kushiro *et al.,* 2004), multiple genes encode these potentially regulatory steps. Thus, unequivocal identification

of specific genes regulating ABA homeostasis in potato tubers during dormancy will require additional experimental evidence. Current research using both antisense and RNAi strategies is directed toward elucidating the role of individual gene members in these two families in the regulation of ABA levels during tuber dormancy and post-harvest storage (Ueno *et al.,* 2005; Suttle *et al.,* 2012). So,it is clear that tuber dormancy is influenced in a complex manner by both genetics and environment with both most likely mediated by changes in hormone status. In fact, sustained synthesis and action of endogenous ABA is required for both the initiation and maintenance of tuber dormancy. Although, the fundamental molecular mechanisms controlling ABA content during dormancy in tubers are unknown, a complex picture has started to emerge.

Bromoethane. Analyses examined in tubers, chemically forced dormancy to break by Bromoethane (BE) treatment. Bromoethane is used in both potato disease certification programmes and the potato seed industry to stimulate early sprouting and emergence (Coleman, 1983; Alexopoulos *et al.,* 2009). Despite its efficacy in terminating tuber dormancy, the mechanisms of action of BE in this regard are unknown. Using BE, the protracted duration of the natural dormancy cycle has been compressed from150 days to a much more predictable and uniform 10 days period. BE treatment of dormant Russet Burbank potato tubers resulted in visible (>2 mm) sprout growth from nearly all eyes after 7–9 days, which is preceded by increased de novo DNA synthesis as suggested by the thymidine incorporation assays. BE treatment has previously been used to monitor changes in chromatin remodelling (histone H3 and H4 multi-acetylation, DNA cytosine methylation) during tuber dormancy progression (Law and Suttle, 2004).

Phytohormones and ethanol. ABA has been implicated in the control of dormancy and has been shown to prevent second growth of tubers (Ewing *et al*., 2004). Whether the effects of ethanol could be blocked by applications of ABA was tested. It has been demonstrated that ABA at 10 µM nearly completely prevented sprouting in control tubers. Moreover, this concentration of ABA partly counteracted the effect of 0.5% ethanol on tuber sprouting. Higher concentrations of ABA were even more effective. Despite this clear interaction between ethanol and ABA on the rate of sprouting, no effect of ABA was found on the ethanol-induced decrease of storage-related reporter activities (Kondo *et al.,* 2009).

GAs are able to break the dormancy of seeds and potato tubers. It was, therefore, of interest to test whether effects of ethanol on sprouting were mediated through changes in endogenous GA levels. A possible role of endogenous GA in the mode of action of ethanol was analysed by studying the effect of the GA-synthesis inhibitor CCC, in the presence of ethanol. It was reported that CCC did not abolish ethanol-induced sprouting, but delayed it by 1 day. Application of GA without ethanol resulted in rapid and complete sprouting 1 day earlier than that obtained with ethanol. Application of ethanol with CCC resulted in rapid sprouting, regardless of the presence or absence of additional GA. Moreover, CCC did not affect ethanol-induced reduction of the λPat21-LUC reporter gene activity or ethanol-induced reduction of AGPase, cycB1;1, and CDC2a reporter gene activity (Classens *et al.*, 2005; Salimi *et al.,* 2010; Wang and Deng, 2011).

Although the implications of both cytokinins and auxins on dormancy has been shown, observations made during the tuber sprouting showed the implication of both cytokinins and auxins on formation of vascular tissues. In fact, numerous new vascular strands had formed between two and six days of the beginning of sprouting; the phloem which primarily transports organic nutrients from photosynthetic tissues to sink tissues, and the xylem which mostly serves as water and mineral conduit (Dettmer *et al.,* 2009; Scarpella *et al.,* 2010; Vera-Sirera *et al.,* 2010; Zhou *et al.,* 2011). This study indicates that two phytohormones, auxin and cytokinin, play major roles in the control of vascular development. Indeed, vascular stem cell specification was found to be dependent on expression of *ARF5/ MONOPTEROS*, an auxin-resposive transcription factor. *ARF5*, in turn, directly activates expression of *AtHB8*, a homeobox gene specific to

procambial cells of newly forming vascular tissue (Mähönen *et al.,* 2006; Scarpella *et al*., 2006; Helariutta, 2007; Nieminen *et al*., 2008; Dettmer *et al.,* 2009; Elo *et al.,* 2009; Ilegems *et al.,* 2010; Muraro *et al.,* 2011).

Vascular development and hormones. In potato, vascular development could, in part, be followed on the transcriptional level by analysis of micro array data from *in vitro* sprouting experiments. Up-regulation of transcripts for *ARF5* and *AtHB8*, indicative of the start of vascular tissue formation and in accordance with array data from *in vitro* trans differentiation of *Zinnia elegans* cells (Aloni *et al.,* 2006; Bishopp *et al*., 2011), could be seen after induction of sprouting with both BAP and GA3. Up-regulation of ESTs representing *YUC1* and *YUC4* in tubers treated with either 6-Benzyl Amino Purine (BAP) or GA3 is consistent with an increased auxin production, required for proper vascular patterning. Two days after BAP and three and five days after GA3 treatment, expression of the *APL* transcript is up-regulated, reflecting the difference between bud break by cytokinin and additional sprout outgrowth triggered by gibberellin. Micro-array data from one Sprout Release Assay (SRA), in which the newly formed sprout and the subjacent parenchyma at three days after GA3 treatment had been sampled and analysed separately, showed expression of markers for vascular tissue formation in both tissues, illustrating that vascular bundles are required for nutrient supply from the tuber to the sprout, as well as for nutrient distribution within the sprout. Taken together, the micro-array data point toward vascular tissue formation and differentiation as a process accompanying sprouting. Whether this process also represents a layer of regulation for dormancy release, remains to be determined.

Hydrogen peroxide and antioxidant system. In contrast with hormonal regulation of potato dormancy, little attention has been paid to the possible involvement of reactive oxygen species (ROS) and antioxidant enzymes. The role of ROS, including superoxide anion (O2-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH-) of the antioxidant system, in the dormancy and sprouting, has been demonstrated in several species, especially rice (Kazuhiro *et al.,* 2004) and vine (Halliwell, 2006). Among the antioxidant enzymes, catalase, superoxide dismutase and ascorbate peroxidases play important roles in the antioxidant system of the plant *via* the ascorbate-glutathione cycle. Their role in the ascorbate-glutathione cycle is illustrated as follows: superoxide dismutase metabolise O_2 and produce H_2O_2,which are then metabolised by catalases or peroxidases to produce H_2O and O_2. While catalase directly converts H_2O_2 to H_2O, they have little affinity with H_2O_2, unlike ascorbate peroxidases. This reaction produces monodehydroascorbate (MDH).

To break dormancy, catalase uses 65% of the intracellular hydrogen peroxide; the rest (35%) is used by ascorbate peroxidase and glutathione peroxidase. But when catalase is repressed, intracellular hydrogen peroxide will be more available for ascorbate peroxidase or glutathione peroxidases which will take over to ensure the metabolism of hydrogen peroxide to break dormancy (Bhate and Ramasarma, 2010). So, even when catalase is not activated during sprouting, the metabolism of hydrogen peroxide continues in the mitochondria, in cortical tuber tissue since superoxide dismutase is activated. In this case, 0.9 to 1.5% of the oxygen present in the mitochondria is converted to hydrogen peroxide by superoxide dismutase. Therefore, mitochondrial membranes are an important source of intracellular hydrogen peroxide that provides out-of-tuber dormancy under normal conditions (Mani, 2012). Consequently, oxidative stress accelerates dormancy release since it inhibits catalase; therefore, peroxidase activity increases leading to dormancy release and sprouting of potato tubers (Feierabend, 2005; Mani, 2012).

It has been reported that hydrogen peroxide is involved in breaking potato dormancy since it affects cellular balance, causing a cascade of biochemical reactions that include migration of the calcium ion to the meristems, increase in cellular respiration and increase in production of adenosine triphosphate (ATP) (Delaplace *et al.,* 2008). These reactions can explain the emergence of apical and proximal buds; and the decrease of membrane integrity in the tuber at sprouting (Zabrouskov *et al.,* 2002). These findings are consistent with recent studies indicating that

moderate oxygenation of cells through hydrogen peroxide causes an increase in intracellular Ca^{2+}, in the concentration of iron, and an active entry into mitosis, causing sprouting (Jones and Smirnoff, 2005). On the other hand, some studies suggest that hydrogen peroxide oxidises the sprouting inhibitors naturally present in the plant (Mizuno *et al.,* 2005). So, to break dormancy and stimulate sprouting, sprouting inhibitors such as chlorogenic and caffeic acid must be separated by an oxidant such as hydrogen peroxide (Macheix *et al.,* 2005). However, when the concentration of hydrogen peroxide is excessive in mitochondria, dormancy is maintained and sprouting decreases. Indeed, high concentrations of hydrogen peroxide are toxic to plants; it activates lipid peroxidation and causes damage in the membrane wall, which causesa decrease in membrane integrity (Hendriks and Taylor, 2003).

Alternatively, it was suggested by Reape and McCabe (2008) that accumulation of reactive oxygen species and more specifically the hydrogen peroxide, is a major factor responsible for oxidative stress and functional decline of older cells. This causes oxidation and accumulation of several proteins by glycation, glycoxidation, deamidation, ubiquitination and conjugation with lipid peroxidation products; which may cause a decrease in sprouting capacity of tubers and may even cause their death. However, in some cases, even when the concentrations of hydrogen peroxide in potato cells are very high, dormancy is broken. So, it is possible that the potato cells can adapt to high concentrations of exogenous hydrogen peroxide by regulating its own production of intracellular hydrogen peroxide (Halliwell, 2006), making the cells unresponsive to a temporaly increase in thesupply of hydrogen peroxide. It is also possible that potato tubers can regulate excessive amounts of hydrogen peroxide by using the phenolic compounds located in the epidermis of the tuber. They disable hydrogen peroxide with redox coupling ascorbate and monodehydro-ascorbate.

Studies have been conducted to elucidate the mechanism by which hydrogen peroxide breaks potato dormancy (Rehman *et al.,* 2001). Some of these suggest that hydrogen peroxide regulates the expression of genes, whose expression products are involved in dormancy. A positive correlation between hydrogen peroxide and activation of genes (1 GA ox, ox 2 GA and AGA 3 ox), whose transcription products are involved in the biosynthesis of active gibberellins exists (Kloosterman *et al.,* 2005). In contrast, *in vitro* biochemical studies have shown that potato treatment with hydrogen peroxide resulted in a decrease in the level of endogenous abscissic acid, due to deactivation of protein phosphatases 1 and ABI ABI 2, type 2C, involved in the biosynthesis of abscissic acid.

Other studies suggest that hydrogen peroxide directly activates the production of systolic calcium, protein kinases and phosphatases, which trigger the breaking of dormancy. Besides, it was suggested that hydrogen peroxide may play a mediating role, and at a certain concentration, it directly stimulates abscissic acid and ethylene to break dormancy.

Hydrogen peroxide acts on the protein metabolism of the tuber. Indeed, sprouting is accompanied by protein carbonylation of reserves, making them more sensitive to proteases and proteolysis, and a decrease in the activity of the pentose phosphate pathway. This explains the depolymerisation of starch into reducing sugars (glucose and fructose) found in the potato tuber at the end of dormancy. The possible roles of oxygen and carbon dioxide treatments on tuber dormancy release in potato were examined recently. Using two gas compositions (I: 60% CO_2–20% O_2–20% N_2 and II: 20% CO_2–40% O_2–40% N_2), the phase of tuber dormancy and previous storage temperature were demonstrated to be important parameters for dormancy release (Coleman, 2002). Gas I caused decreased abscisic acid levels within 24 hr regardless of previous storage temperature; although this effect was reversible.

CONCLUSION

Tuber dormancy is controlled by phyotohormones, which play an important role in the initiation or inhibition of dormant tubers of potato. Sustained synthesis and action of endogenous ABA is required for both the initiation and maintenance of tuber dormancy, while ethanol and gibberillins may be involved in

dormancy breaking. These phytohormones play major roles in the control of vascular development during sprouting. Reactive oxygen species including hydrogen peroxide are involved in breaking potato dormancy, since they affect cellular balance, regulate the expression of genes whose expression products are involved in dormancy and act on the protein metabolism of the tuber.

Inhibition of sprout growth is critical for the maintenance of tuber nutritional and processing qualities during long-term storage of potatoes. To date, all chemicals registered for sprout suppression act through non-specific growth inhibition or tuber meristem injury. Suppression of tuber sprouting through extension of natural dormancy by manipulating endogenous hormones offers an attractive alternative to current suppression strategies; other strategies will have to be developed. Although, multiple ABA gene expression and tuber encode the regulatory steps of tuber dormancy, identification of specific genes regulating ABA homeostasis in potato tubers during dormancy will require additional experimental evidence. Current research using both antisense and RNAi strategies is directed toward elucidating the role of individual gene members in these two families in the regulation of ABA levels during tuber dormancy and post-harvest storage.

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