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Review article

Regulation of potato tuber dormancy: A review

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Abstract

Dormancy is one aspect of tuber physiological age that begins with potato tuber initiation. During dormancy, biochemical and physiological processes do occur but they do not trigger immediate morphological changes, 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. This review article reports that dormancy is a complex process that depends on genetic background, stage of tuber development, environmental and management conditions during tuber growth and storage. Temperature, water supply, soil fertility and the photoperiod during plant growth are important environmental factors that regulate the sprouting behaviour. Storage temperature and gas composition regulate dormancy breaking. Endogenous as well as exogenous phytohormones are also important. When seed tubers are needed before natural sprouting occurs, it may be necessary to break the dormancy using chemical agents.

Keywords: Environment, Dormancy regulation, Genetic control, Potato tuber.
Abbreviations: CO_2_Carbon dioxide, QTL_Quantitative trait loci, O_2_Oxygen.

Introduction

In plants, dormancy is the temporary suspension of visible growth of any plant structure containing a meristem (Lang et al., 1987). Plant dormancy has been further divided into three (but often overlapping) types: endodormancy, paradormancy and ecodormancy. In endodormancy, a meristem is arrested by physiological factors arising from within the affected structure; in paradormancy, a meristem is arrested by external physiological factors while in ecodormancy, a meristem is arrested by external environmental factors (Suttle, 2007). During their life cycle, potato tubers can exhibit all three types of dormancy. In potatoes, dormancy is the physiological state of the tuber in which autonomous sprout growth will not occur within two weeks, even when the tuber is kept in conditions ideal for sprout growth (Ittersum, 1992; Struik and Wiersema, 1999). During this period, postharvest environmental conditions have only limited impact on the sprouting behaviour. Therefore, the period is classified as endodormancy. The duration of endodormancy depends largely on the cultivar and to some extent on the conditions during tuber growth (Davidson, 1958; Wurr and Allen, 1976; Burton, 1978). Temperature, water supply and the photoperiod during growth and storage are important environmental factors that regulate the sprouting behaviour (Uwe, 2001). During dormancy, biochemical and physiological processes do occur but they do not trigger immediate morphological changes 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. Dormancy is one aspect of tuber physiological age that begins with tuber initiation. However, this period is difficult to determine hence post-harvest dormancy is used for practical purposes and defined as the period from dehaulming to the time when 80% of tubers show sprouts at least 2 mm long (Van Ittersum and Scholte, 1992). Therefore, the post-harvest duration of dormancy is longer for smaller (younger) tubers than for larger (older) tubers (Suttle, 2007). Dormancy is a complex process that depends on genetic background, stage of tuber development, environmental and management conditions during tuber growth and storage (Aksenova et al., 2013). Tuber storage at an elevated temperature (up to 30^0C) and relative humidity (up to 90% of water capacity) and also changed atmosphere composition (hypoxia, anoxia, increased content of CO_2) favour dormancy breaking and premature bud outgrowth. As would be expected from a developmental trait conferring a survival advantage, the inheritance pattern of tuber dormancy is complex; quantitative trait loci (QTL) analyses have indicated that tuber dormancy is quantitatively inherited (Kotch et al., 1992) and controlled by at least nine distinct loci (Ewing, 1995; van den Berg et al., 1996). The potential role of abscisic acid (ABA) in dormancy regulation has also been supported by the observation that three of these QTLs influence ABA levels (Classens and Vreugdenhil, 2000). Given the genetic complexity of dormancy control, it is likely that the physiological processes regulating dormancy progression are equally complex. During the development of the tubers on the plant, the buds in the eyes of the tuber successively become dormant, starting at the stolon end. The apical eye is the last to become dormant (Van Ittersum, 1992).

Changes in tuber dormancy after tuber set are poorly characterized, but a lessening of dormancy late in the growing season as tuber bulking slows down has been

observed. Detachment of tubers from the vines, either as a result of natural senescence or mechanical or chemical vine removal, leads to a strengthening of tuber dormancy during the following weeks. The intensity of dormancy in stored tubers declines with time and eventually they develop the capacity to sprout. Duration of dormancy period also depends on soil and weather conditions during growth, tuber maturity at harvest, storage conditions, and whether the tuber is injured or not (Ezekiel and Singh, 2003). High temperatures, low soil moisture and low fertility during tuber growth accelerate physiological development and reduce the dormancy period. During storage, fluctuating storage temperatures shorten dormancy more than constantly high temperatures. Therefore, storage temperatures should remain as consistent as possible when retarding sprout development is desired. 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. Low storage temperature is not appropriate for potatoes destined for the processing market. On the other hand, visible sprouts on potatoes are unacceptable to consumers. Finally, tuber injuries caused by harvest or by diseases and pests can result in earlier sprouting. Understanding factors responsible for tuber dormancy is therefore important for both seed and table potatoes. This review gives a general overview of potato tuber dormancy regulation.

Regulation of potato tuber dormancy

Numerous factors contribute to potato tuber dormancy including genetic background (variety), degree of tuber maturity at harvest, environmental conditions during tuber growth, storage conditions, exposure to endogenous and applied dormancy-breaking compounds and tuber injury. Of these factors, genetic control may be the most significant (Aksenova et al., 2013).

Genetic control

A very wide range in the length of the dormant period has been observed in cultivated potato and its wild relative species. Long tuber dormancy is generally found in wild potato populations whereas the reverse is often true in potato lines developed by modern breeding (Suttle, 2007). An exception to this rule is *Solanum phureja* group which, as a whole, is characterized by very short tuber and seed dormancy (Huamân and Spooner, 2002). Conversely, tubers of *Solanum jamesii*, a wild relative species of cultivated potato that is native to Arizona and New Mexico, may remain dormant for eight years at 4^0C while still retaining the ability to sprout normally when warmed (Bamberg, 2010). In previous studies, a strong correlation was found between botanical seeds and tuber dormancy (Simmonds, 1964). He also demonstrated that the inheritance of both botanical seeds and tuber dormancy in potatoes was polygenic with at least three genes involved. Seeds have a longer dormancy period than tubers and it can last for four to nine months. Analyses of quantitative trait loci (QTL) have found between six (Freyre et al., 1994) and nine genes (van den Berg et al., 1996) that affect tuber dormancy either alone or through epinastic interactions. Two of these dormancy-related QTLs coincided with the loci associated with tuber abscisic acid (ABA) content (Simko et al., 1997). Since dormancy is not related to earliness of varieties, it is possible to breed late maturing varieties with relatively short dormancy and early varieties with relatively long dormancy (Beukema and van der Zaag, 1979). Usually, but not always, late maturing clones have a long dormancy that is more difficult to break than that of early maturing clones (CIP, 1989).

Environmental factors

Environmental conditions during growth influence tuber dormancy for many varieties and may account for some of the differences in seed lots observed between growing locations. 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, 1985a).

Temperature during plant growth

Unusually cold or hot weather during tuber development in the field often results in long or short dormancy respectively (Burton, 1989).Warm years are often associated with shorter dormancy and cool years with longer dormancy, but this is not universally true. Warm temperatures near the time of vine kill can have a large effect on physiological age in general and on the duration of dormancy in particular. Dormancy is lost most rapidly when temperatures shortly before or after harvest are warm, with the greatest reduction in dormancy at temperatures greater than 50^0C. Depending on the potato cultivar, extremely hot (>35^0C) field temperatures can result in immediate termination of tuber dormancy, a physiological disorder known as heat spouting (Suttle, 2007). Tuber dormancy is restored as field temperatures moderate back to more seasonal norms. The overall effect of this loss and restoration of dormancy is malformed and knobby tubers with reduced starch content, high levels of reducing sugars and poor processing quality (Suttle, 2007). Day and night temperature fluctuations also influence tuber dormancy; greater diurnal temperature variation has been shown to hasten loss of tuber dormancy.

Temperature during storage

Storage temperature has a marked effect on the length of the dormancy period. High storage temperature accelerates the physiological ageing processes within the tuber thus reducing the dormancy period. There is evidence that chilling (1-3 ^{0}C) shortens dormancy in some varieties possessing lengthy dormancy periods (Wurr and Allen, 1976; Harkett, 1981), but Davidson (1958) and Burton (1978) reported that only high storage temperatures (approx. 30^0C) could prematurely terminate dormancy. Between 3 and 25^0C, the length of tuber dormancy is inversely proportional to storage temperatures (Burton, 1989). Tubers stored at temperatures of 3^0C or lower will not sprout regardless of physiological dormancy status and are in a state of ecodormancy. Prolonged exposure to temperatures $\leq$ 2 or $\geq$ 30^0C abruptly terminates tuber dormancy and sprouting commences upon return to moderate temperatures (Wurr and Allen, 1976). Fluctuating the storage conditions between high and low temperatures has been shown to break dormancy in seed tubers (Burton, 1963). Wurr and Allen (1976) found that storage for 14 days at 2.8^0C increased the rate of sprout growth when tubers were

returned to 15.6^{0}C and broke dormancy in tubers stored at 10^{0}C. It was also found that tubers stored at 2^{0}C for 14 days and then at 15^{0}C contained more gibberellins and less growth inhibitor activity than those kept at 15^{0}C continuously (Thomas and Wurr, 1976). This was suggested as the reason for the increased rate of sprouting noted after a period of low temperature storage.

Storage gas phase

Storage gas phase composition has little effect on tuber dormancy provided extremes are avoided (Suttle, 2007). Both hypoxic and anoxic conditions that result in temporary anaerobiosis in the tuber can break tuber dormancy (Burton, 1989). It is well documented that temporary (about one week) and partial anaerobiosis will break dormancy regardless of tuber age (Burton, 1968; Thornton, 1933; 1938; 1939) although the physiological basis of this effect is unknown (Coleman, 1987). The ability of a water film to break tuber dormancy (Goodwin, 1966.) may reside in the rapid onset (i.e., within 2 to 6 hours depending on temperature) of anaerobic conditions (Burton, 1978). Work by Thornton (1939) indicated that high concentrations of CO_2 (10-60%) were more effective in the presence of 20-80% O_2 than complete anaerobiosis caused by nitrogen. Low oxygen concentration (<10%) for 10 days in the presence of 10 to 60% CO_2 or a high CO_2 (60%)/O_2 (40%) treatment caused dormancy breakdown irrespective of the cultivar (Coleman and McIcerney, 1997).Treatment of dormant tuber with non-physiologic concentrations of CO_2 (20%) and oxygen (40%) has been reported to effectively terminate tuber dormancy (Coleman, 1998). In contrast, CO_2 concentrations $\leq$ 10% have no effect on dormancy duration *per se* but do stimulate subsequent sprout growth perhaps by antagonizing ethylene action (Burton, 1989). Thornton (1933) initially observed that tuber dormancy could be broken effectively with 40-60% CO_2 and 20% O_2 applied to tubers continuously for 3-7 days at 25^{o}C. He subsequently demonstrated an enhancement of this effect by high (20-80%) concentrations of O_2(Thornton, 1939). Previous results indicated that the most effective mixtures for enhanced dormancy release and sprout emergence were 20% CO_2/40% O_2 or 60% CO_2/ 18-20% O_2 and their effects were further enhanced by 50ppm ethylene. In the presence of 50ppm ethylene; the 20% CO_2/40% O_2 mixture was comparable to bromoethane in effectiveness (Coleman and McIcerney, 1997). Some results showed that carbon dioxide has dual effect: sprout growth was suppressed by a concentration of 15 % and stimulated by lower concentrations (Burton, 1958). The optimum concentration and the precise limits of the opposed effects probably vary with the sample of tubers and their previous history.

Photoperiod

Under field conditions, the effects of photoperiod are difficult to determine and any effects observed may relate more to the timing of tuber initiation or rate of maturation than to dormancy per se (Burton, 1989). Dormancy duration in microtubers was significantly reduced when microtubers were exposed to 8 hours photoperiods instead of being held in complete darkness during tuber initiation (Tovar et al., 1985). The presence or absence of light during post-harvest storage has little effect on dormancy duration but dramatically affects the morphology of emerging sprouts (Suttle, 2007).

Physiological tuber age

Dormancy of tubers within a seedlot varies and for some varieties, much of this variation can be attributed to variation in tuber size with smaller tubers having longer dormancy than larger ones. Immature tubers usually have a longer post-harvest dormancy than tubers harvested at maturity. This difference in the dormancy period between immature and mature tubers can be several weeks. Seed tubers have an inherent sprouting potential which increases with age to a maximum (Krijthe, 1958) and after a long period of storage, it declines (Krijthe, 1962). The physiological ageing process continues from the time of tuber initiation (Toosey, 1964). The rate of ageing can be controlled; it is slow at temperatures below 5^{0}C and faster at higher temperatures upto 25^{0}C (Toosey, 1964). Research found that immature tubers appeared to have a greater sprouting capacity at a given point in time than mature tubers stored under the same conditions (Hutchingson, 1978b). Previous researchers also found similar results (Krijthe, 1962; Hutchingson, 1978a).

Phytohormones

In addition to environmental extremes, tuber dormancy can be prematurely terminated by a variety of chemical treatments whose mechanisms of action are currently unknown. It has been hypothesized that dormancy is regulated by the relative concentrations of growth promoters and inhibitors (Hemberg, 1985). As with many aspects of plant development, plant hormones have been assigned a primary role in the regulation of potato tuber endodormancy (Rappaport and Wolf, 1968; Hemberg, 1985). Four of the five principal classes of plant hormones (abscisic acid [ABA], cytokinins, GAs, and ethylene) have been implicated in dormancy regulation (Hemberg, 1985; Suttle, 1996). Endogenous hormones play a significant role in potato tuber bud (eye) dormancy regulation (Suttle and Banowetz, 2000; Coleman et al., 2001). Gibberellins (GA) and cytokinins are generally thought to regulate the termination of endodormancy, whereas both abscisic acid (ABA) and ethylene are required for dormancy induction but only ABA is needed to maintain bud dormancy (Suttle, 2004b). The ABA is considered to be the principal dormancy-inducing agent (Suttle, 1998). From past studies, it was concluded that gibberellins and ABA are probably not the primary regulators of dormancy (Rappaport and Wolf, 1968; Shih and Rappaport, 1970).The nodes are the sites of synthesis of gibberellins and cytokinins. Tuber dormancy is generally broken with exogenous gibberellins (GAs)(Rappaport et al., 1958). In fact, GAs (typically GA_3) are often used in seed certification programs where rapid replanting of seed tubers is required for pathogen testing. Data suggest that endogenous GAs are not intimately involved with tuber dormancy control, but that they do play a critical role in subsequent sprout elongation (Suttle, 2004a). Hemberg (1970) demonstrated that both natural and synthetic cytokinins can break tuber dormancy. An increase in cytokinin content is the principal factor leading to the loss of tuber dormancy (Turnbull and Hanke, 1985a; Suttle, 2004b) but probably do not control the subsequent sprout growth (Turnbull and Hanke, 1985a). It was found that dormancy of whole potato tuber was effectively broken with benzyladenine (BA) at a concentration of 20 ppm used for 24 hours (Suttle, 2004b). In his previous studies Suttle (1998) concluded that application of cytokinins resulted in the termination of dormancy and enhanced sprouting of potato

Table 1. Hormonal regulation of tuber dormancy and sprouting.

Physiological processes		Phases of tuber dormancy and sprouting: stimulating phytohormones		
		Dormancy: ABA, ethylene, BS?	Sprouting: IAA, CK, GA	Sprout growth: CK, GA
Buds	Growth characteristics	Growth arrest; blocking G1/S-phase transition	Onset of growth and morphogenesis; removal of blocking G1/S-phase transition	Active growth
	Metabolism specific features	Low level of metabolism; limited supply with substrates	Activation of metabolism; enhanced supply with substrates	High level of metabolism; active supply with substrates
Tuber tissues	Growth characteristics	Absence of growth and morphogenesis	Absence of growth and morphogenesis	Absence of growth and morphogenesis
	Metabolism specific features	Low level of metabolism; preservation of storage carbohydrates and patatins	Transition from storage to source function; enhanced activity of carbohydrate metabolism	Active supply of seedlings with energetic and structural materials

Source: Aksenova et al., 2013

tuber. However, there appears to be a variable sensitivity to exogenous cytokinins by the tubers depending on the specific stage in the tuber's dormancy period (Turnbull and Hanke, dormancy. The effects of exogenous cytokinins as well as changes in endogenous zeatin-like cytokinins support the view that changes in both hormone levels and tissue responsiveness to cytokinins play important roles in the dormancy control process (Turnbull and Hanke, 1985a; Turnbull and Hanke, 1985b). At harvest, the content of ABA in tubers is usually high and declines during post-harvest storage, which coincides with the breakdown of dormancy. Thus, it was speculated that ABA levels must decrease below a certain threshold level before induction of sprout growth. Previous work has indicated a significant negative correlation between sprout growth rate and initial ABA levels in tuber tissue of ten potato cultivars (Coleman and King, 1984). Exogenous ABA is also capable of inhibiting potato sprout growth when applied repeatedly at high concentrations (El-Antably et al., 1967).Ethylene is essential for the establishment of full endodormancy of microtubers (Suttle, 1998). Ethylene production from field-grown tubers is highest immediately after harvest and declines to low levels thereafter (Cvikrova et al., 1994).The involvement of endogenous ethylene in tuber endodormancy regulation, in particular, is uncertain; exogenous ethylene (or ethylene-releasing agents) has been reported to elicit seemingly contradictory responses (Suttle, 1998). Depending on the concentration and duration of exposure, exogenous ethylene can either hasten or delay tuber sprouting. Relatively short term (less than 3 day) exposure to ethylene results in the premature termination of tuber endodormancy (Alam et al., 1994), whereas long-term or continuous exposure to similar concentrations of ethylene inhibits subsequent sprout growth (Rylski et al., 1974). Both preharvest and postharvest applications of the ethylene-releasing agent ethephon resulted in significant extensions of tuber dormancy (Cvikrova et al., 1994). Similarly, application of an ethylene-releasing agent, alone or in combination with GA_3 to dormant tubers has been reported to stimulate sprouting (Shashirekha and Narasimham, 1988). Some studies have demonstrated that continuous ethylene treatment is an effective sprout suppressor in commercial settings although it also resulted in undesirable accumulation of reducing sugars (Prange et al., 1998). Bioassay data indicated that endogenous levels of IAA (an auxin) were low in dormant tuber tissues and increased 1985a). Exogenous cytokinin was effective in dormancy breaking only during brief periods immediately following the beginning of dormancy and immediately prior to the end of during early sprout growth (Hemberg, 1949). At relatively high doses, exogenous auxins such as IAA and the more stable 1-naphthalene acetic acid were found to be potent inhibitors of sprout growth (Denny, 1945). Extremely low concentrations of auxins stimulated the growth of non-dormant sprouts, but had no discernable effects on dormant eyes (Hemberg, 1949). Since then, there has been no report demonstrating that exogenous IAA (or any other auxin) prematurely terminates tuber dormancy (Suttle, 2004b). The data reported so far do not support a role for endogenous IAA in tuber dormancy control *per se;* they do suggest a role for IAA (and other endogenous auxins) in subsequent sprout growth (Suttle, 2004b).The complex involvement of phytohormones in tuber dormancy regulation is summarized in Table1.

Sprouting behaviour

At the end of the dormant period, buds in the eyes begin to grow and form sprouts. Mostly, the apical eye begins to sprout first marking the beginning of apical dominance stage. Planting seed tubers with apical dominance often results in plants with single stems and hence reduced yields (CIP, 1985). After the apical dominance stage, additional sprouts develop and the multiple sprouting stage begins. This is the optimum stage to plant seed tubers as they give rise to plants with several stems. Diffused light helps to prolong the multiple sprouting stage and to keep sprouts short and strong. Apical dominance is influenced by storage temperature management and desprouting. Storing tubers at low temperature (4^0C) until the apical dominance stage is over and then increasing the storage temperature (above 15^0C) to promote sprout growth will result in multiple sprouting. To limit the number of sprouts, maintain high storage temperature (15-20^0C); this will promote apical dominance. Removing the apical sprout of the tuber may induce the formation of multiple sprouts; this results in a uniformly sprouted tuber that produces several stems per plant(CIP, 1985). After multiple sprouting stage, the seed tubers enter the senility stage. Old tubers should not be desprouted even when sprouts become long; they may have lost their resprouting capacity or may only form thin 'hair sprouts'.

Breaking dormancy of potato tubers

Dormancy release in potato tubers by external agents has practical applications as dormancy breaking of seed tubers for export or local use, incorporation into seed multiplication programs and rapid post-harvest disease testing procedures (Coleman, 1983). The method used to break dormancy will probably depend on facilities and chemicals available as well as the genetic characteristics of the breeding materials and varieties to be treated (CIP, 1989). The common temperature treatments are the heat, and the cold shock plus heat. In the heat treatment, tubers are kept in a dark room at 18-25^{0}C until sprouting occurs. In the cold shock plus heat treatment, harvested tubers are placed in 4^{0}C for 2 or more weeks and then held at 18-25^{0}C until sprouting occurs (CIP, 1989). Most of the chemicals used in dormancy breaking often fall within the following categories: respiratory inhibitors, sulfhydryls, anaesthetics or end products of glycolysis. Some hormones (i.e., gibberellic acid, bromoethane) are used to stimulate sprout growth of seed potatoes (Coleman, 1987; Allen et al., 1992). Rindite (a three component mixture containing ethylene chlorohydrin, ethylene dichloride and carbon tetrachloride) and GA_3 have received considerable attention as routine dormancy breaking agents(Thornton, 1933, 1939). However, rindite is extremely volatile, very dangerous and corrosive and should be handled with extreme care (CIP, 1989).

Conclusions

Understanding dormancy regulation of potato tubers helps in handling genetic materials for different end-uses (ware or seed) and in planning for the next planting season.

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