

## THE ROLE OF CYTOKININ AND GIBBERELLIN IN POTATO TUBER SPROUTING

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### ABSTRACT

Potato (*Solanum tuberosum* L.) is a highly sensitive crop to tuber dormancy. This can be initiated by various factors, including moisture stress, high or low temperature, day length, hormonal imbalance, and heredity. Breaking of tuber dormancy is therefore important for seed potato multiplication, rapid post-harvest disease testing, and early production in the field or green house. Cytokinin (CK) and gibberellin (GA) in combination will terminate dormancy and increase sprout growth earlier than using GAs alone. And also using only CK will terminate dormancy earlier than using GAs alone, but subsequent sprout growth will be hampered. In this review, the current knowledge and possible utilization of CK and GA, which can be used for termination of dormancy and sprout growth of potato tubers, have been reviewed and discussed. The role of CK and GA to mitigate the harmful effects of endogenous and environmental stresses in potato sprouting is also examined. In addition, numerous biochemical and physiological processes principal to improved potato sprouting under the consequence of these hormones are discoursed in detail.

**Keywords:** Cytokinin, Dormancy, Gibberellic acid, Growth regulators, Sprouting.

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### INTRODUCTION

Potato (*Solanum tuberosum* L.) is among the highly valuable and important food security crops in the world. In volume of world crop production, it ranks fourth following wheat, maize, and rice and first among the root and tuber crops (Douches, 2013). It is one of the widely grown root and tuber crops being a rich source of nutrients for human nutrition. A given potato crop contains 79% water, 18% starch which is good source of energy, 2% protein, and 1% vitamins, minerals mainly calcium, magnesium, and many trace elements (Ahmad *et al.*, 2011).

Potato (*S. tuberosum* L.) belongs to the family *Solanaceae* and genus *Solanum* (Thompson and Kelly, 1972). It is native to South America (Eskin and Michael, 1989). It has been introduced to Ethiopia in 1859 by a German Botanist called Schimper (Berga *et al.*, 1994b). From its introduction to Ethiopia, until recently potato was produced in small scale limited to only homesteads, as a garden crop. Although Ethiopia is endowed with suitable climatic and edaphic conditions for potato production, the land acreage under potato production is estimated to be only about 66,926 ha and the national average yield is about 13.8 t/ha, which is very low as compared to the world's average production of 19 t/ha (CSA, 2017). The major problems identified in potato production are lack of adapted varieties for the lowlands, inaccessibility and high cost of seed tubers, poor agronomic practices, pest infestation, and inadequate post-harvest handling systems (Tekalign and Hammes, 2005).

Potato tubers are stem axes developed from shortened internodes and nodes ("eyes"). They initiate from underground stolons in a sequence of developing processes consisting the termination of growth at the apex, the swelling of the stolon by subapical radial growth, and longitudinal cell divisions of the body (Xu *et al.*, 1998). The latter process is accompanied by the accumulation of starch and storage proteins and requires coordinated transcriptional and metabolic changes (Visser *et al.*, 1994; Appeldoorn *et al.*, 1999; Kloosterman *et al.*, 2005; Kloosterman *et al.*, 2008). After formation, potato tubers undergo a period of dormancy which is characterized by the absence of visible bud growth. It is generally accepted that the onset of dormancy coincides with the cessation of meristematic activity during tuber initiation (Burton, 1989). The length of the dormancy period depends

on the genetic background and is affected by pre-harvest and post-harvest conditions (Suttle and Banowitz, 2000; Sonnewald, 2001) with the start of sprouting the tuber of potato turns into a source organ supporting sprouting of potato. This is associated with structural and metabolic changes (Viola *et al.*, 2007) as well as with major changes in gene expression pattern (Ronning *et al.*, 2003; Campbell *et al.*, 2008). In addition, endogenous plant hormones play a critical role in regulation of dormancy and bud break (Hemberg, 1985; Suttle, 2004a). Gibberellins (GAs) and cytokinins (CKs) are thought to be involved in release of dormancy (Smith and Rappaport, 1961; Turnbull and Hanke, 1985a). Therefore, the aim of this paper is to review the effect of CK and GAs on termination of dormancy and sprout growth of potato tubers.

### THE PHYSIOLOGICAL BASES OF DORMANCY

In the plant life cycle, there is a time in which main activities such as growth, development, and other physiological activities temporarily stopped which is known as dormancy. This occurs in many plant species. It can be initiated by different factors including temperature variation; moisture stress, and day length (Hartmann *et al.*, 2002). Dormancy in one side is important in conserving energy as it minimizes metabolic activities of plants. According to Hemberg (1985), dormancy in plants is the phase where there is no bud formation due to endogenous and exogenous conditions. Dormancy can be categorized in three types as endodormancy (dormancy due to internal factors), paradormancy (which is determined by buds), i.e., plants maintain apical dominance and prevent axillary buds from growing through paradormancy, and ecodormancy is the inhibition of growth induced by environmental factors. For example, in summer with high temperature and moisture stress, plants will stop active elongation. As soon as environmental conditions become favorable, growth will start again (Crabbe and Barnola, 1996). According to Hilhorst and Toorop (1997), there are two types of dormancy, which are innate and induced dormancy. In seeds, innate dormancy occurs during the development phase of seed and induced dormancy occurs when there are no favorable conditions. Similar situations are also applicable in dormancy of buds. During the innate dormancy buds will not sprout even if there are favorable environmental conditions. Buds have a natural or primary dormancy period in which they will not sprout even if conditions are favorable for sprouting, but

sprouting can also be inhibited if environmental conditions are not favorable. This is termed eco- or secondary dormancy. Hartmann *et al.* (2002) also suggested that dormancy is divided into two main categories, namely primary and secondary dormancy. Endodormancy is one of the factors which is genetically determined in the plants life cycle. It is determined by cultivar as well as the growing and storage conditions (Hemberg, 1985; Burton, 1989), and termination of dormancy will only take place after a period of rest. Dormancy dictated by exogenous factors, including temperature, day length and humidity, can be terminated by altering the conditions so as to make it more favorable (Van der Schoot, 1996).

### MECHANISM OF DORMANCY

Evolutionary processes play significant role in making of plants adaptable to environmental changes. One of the strategies developed to survive extreme conditions is dormancy. Dormancy, more specific endodormancy, is part of a plant's genetic design. In endodormant phase, potato tuber protect itself against harsh conditions. According to Burton (1989), dormancy calculation should start from tuber initiation until commencement of sprouting.

A dormant bud is metabolically active even though no visible growth is observed (Burton, 1989), and DNA, RNA as well as proteins are synthesized by the resting organ (Suttle, 1996), but the process is much slower than in actively growing organs (Van der Schoot, 1996). It is indicated that plant growth regulators play significant role in dormancy of potato, but its initiation is not yet clear. The first stage of dormancy happens during a tuber is initiation in which tubers play as sink organs and buds stay dormant. In cell division, four phases can be distinguished, namely the gap 1 ( $G_1$ ); synthesis (S); gap 2 ( $G_2$ ); and mitosis (M) phases (Fig. 1). The  $G_1$  phase occurs between mitosis (M-phase) and DNA-synthesis (S-phase) and the  $G_2$  phase between DNA-synthesis and mitosis (Fairbanks and Anderson, 1999).

A  $G_0$  phase also exists where non-cycling cells are arrested. During the G-phases, it is the preparation phase for the cells to the coming phase. Between the  $G_1$ -S and  $G_2$ -M phases are checkpoints of cyclin-dependent protein kinase (Cdk). Cdk must be bound to a protein, called cyclin, for the cycle to commence through the checkpoint to the next phase of cell division (Francis and Sorrell, 2001). According to Suttle (1996), the dormant buds nuclei are mainly (77%) in the  $G_1$  phase, with only small proportion (13%) in the  $G_2$  phase.

Suttle (1996) mentioned that especially one family of regulatory proteins, the P-34 kinases of which Cdc 2 kinase is the most important, is actively involved in cell division. These proteins are regulated by cyclins. In plants, D-cyclins are required for  $G_1$  to S regulation. The D-cyclins react to external signals, and it has been found that CKs are

able to induce D-cyclins to bind to Cdk proteins and initiate the  $G_1$  to S phase (Francis and Sorrell, 2001). Thus, it is possible for CKs to stimulate non-cycling cells in the  $G_0$  phase to start division and act in the  $G_1$ -S phase. Sucrose may be involved in the  $G_1$  to S transition by inducing CycD<sub>2</sub>, and the  $G_1$  to S phase may be blocked if an energy source is not available (Francis and Sorrell, 2001).

### FACTORS AFFECTING TUBER DORMANCY

Tuber dormancy in potato is the result of many factors. The natural period of dormancy is dependent on genetic and pre and post-harvest environmental factors (Suttle, 2008). Hormones, defined as low- molecular-weight (mobile) compounds that influence growth and development in low concentrations, have often been suggested to play a crucial role in breaking potato dormancy (Vreugdenhil, 2007). Environmental factors affecting during tuber development are the ones affecting tuber. Similarly, the range of temperature during storage, if lower than 10°C delay dormancy breakage and sprout development (Burton, 1989).

The dormancy of tubers can be prematurely terminated by a different chemical treatment whose mode of actions is not well verified. Several of these agents such as GA, rindite, ethylene, thiourea, carbondisulphide, and bromoethane are used to stimulate sprout initiation and growth of potato tubers (Allen *et al.*, 1992). Dormancy which is absence of visible growth does not indicate metabolic inactivity as dormant meristems are internally metabolically active. Length of dormancy period depends on the varieties, maturity of the tuber, soil and weather conditions during growth, storage conditions and whether the tuber has damaged or not. Growth conditions during seed production (especially temperature, photoperiod, light intensity, and nitrogen fertilization) can also affect the duration of dormancy (van Ittersum and Scholte, 1992). Similar investigation also suggested that, the length of potato dormancy period is dependent on the genotype as well as on both pre and post-harvest conditions (Burton, 1989). Dormancy could be shortened by hot and dry conditions and can be extended formation of tubers under cool and wet conditions (Destefano-Beltran *et al.*, 2006).

### Genetic variation

Dormancy of potato varies among genotypes. It may also vary with in a seed lot of one cultivar from a particular origin or year. The survival advantage, the inheritance pattern of tuber dormancy is complex, and it is controlled by at least nine distinct loci (Van den Berg *et al.*, 2006). In different cultivars of potato, natural dormancy takes several months. Early cultivars are characterized by having shorted dormancy periods and late cultivars indicated by having long dormancy periods which is not strict characteristics (Burton, 1968; Harris, 1992).

### Growing conditions

The length of the dormancy period is not constant as it varies growing years, growing areas, and varietal differences (Struik *et al.*, 2006). In short-day areas, it is exhibited a short dormancy period. The duration of the dormancy period varies among and with conditions during growth (White, 1983). The growing temperature has a significant influence on the length of dormancy (Scholte, 1986). According to Struik and Wiersema (1999), potatoes grown at higher temperatures particularly at the end of the growing period have shorter dormancy. They indicated that growing conditions at the period of tuber production alter dormancy and physiological age of tubers after harvesting, even if its impact is less restricted after harvest. In addition, other conditions, mainly photoperiod, temperature, light intensity, and nitrogen fertilizer, have significant influence. On the other hand, soil conditions after haulm destruction but before harvest probably have the largest effect (Struik and Wiersema, 1999).

### Storage conditions

Environmental factors during storage affect physiological age. Relevant factors include relative humidity, temperature, photoperiod, and diffuse light (Scholte, 1986; Struik and Wiersema, 1999), especially the temperature effect is highly complex and cultivar specific. As

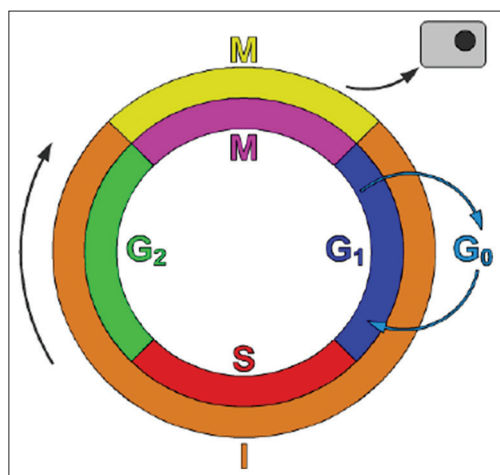


Fig. 1: Cell cycle showing different phases

metabolic processes and physiological events taking place before and after dormancy differ, the sensitivity toward environmental conditions, and especially toward temperature, during the different stages of physiological development of the seed tuber may also vary (Scholte, 1986; Struik *et al.*, 2006). Heat shocks, cold shocks, and similar accumulated day-degrees built up in different ways may all have their specific effects, depending on cultivar (van Ittersum and Scholte, 1992; Struik *et al.*, 2006). Struik and Wiersema (1999) described that diffuse light may prevent rapid aging of seed tubers. According to these authors, the positive effect is developed due to its impact on sprout development and on condition of the mother tuber.

### Temperature

Dormancy can be shortened by warm storage (Struik *et al.*, 2006) but also by a short treatment of heat (van Ittersum and Scholte, 1992) or in some cultivars also by a short treatment of cold storage (van Ittersum and Scholte, 1993b). According to Struik and Wiersema (1999), the optimum temperatures requirement to break dormancy and sprouting is different in which a higher temperature range is required to break dormancy. The author mentioned that an increase in the range of storage temperature shows an increased rate of dormancy breakage. However, storage temperature also affects sprout growth on tubers that are no longer dormant. Prolonged storage at 4°C results in more sprouts per seed tuber (Struik and Wiersema, 1999).

Burton (1989) suggested that the length of tuber dormancy is inversely proportional to storage temperatures when storage temperatures are between 3°C and 25°C. This author indicated that temperature management in stored potatoes is affected by several factors. These include whether potatoes are marketed for processing, as fresh table stock or as seed; tubers field temperature before storage; planned period of storage; damages associated with the harvest; and the presence of pest attack. Fraizer *et al.* (2004) also suggested that the length of dormancy differs by cultivar and storage temperature. Cultivar-related variations related to dormancy length is highly important to decide on optimum storage temperature and application of sprout controlling chemical. Devlin (1975) reported that dry storage at 35°C or moist storage at 20°C has been found to eliminate potato tuber dormancy and low temperatures apparently have no effect.

The effects of constant storage temperature are in general predictable although there are cultivar differences in the temperature value and range at which responses are seen within the range 3–25°C (Wiltshire and Cobb, 1996). These authors indicated that lower temperature storage tends to form a longer period of innate dormancy than storage at higher temperatures. Day and night temperatures can influence haulm growth, dormancy of tubers, and tuber yield; dormancy of tubers was significantly shorter at day/night temperatures of 32/12 than at 18/12°C (van Ittersum and Scholte, 1992).

### Light

Sprouting and dormancy are reported to be inhibited by light. The degree of growth inhibitor is related to wavelength, light with wavelength below 500 nm (blue), and above 650 nm (red and far-red) have the greatest inhibitory effect (McGee *et al.*, 1987). Small scale production by a farmer's level has characterized the system of storage in the home at a dark place to control greening. The potatoes stored in such conditions are utilized as seed material, home use, and income source by selling. However, dark storage can be a problem in the warmer lowland and coastal areas because it can increase losses by insects and excessive sprouting (Andrew, 2001).

### CO<sub>2</sub> and O<sub>2</sub> concentrations

An increase in CO<sub>2</sub> concentration in the storage atmosphere is reported to shorten the dormancy period of potato tubers (Burton, 1968). Treatment with 20% CO<sub>2</sub> for 7 days was found to be as efficient as rindite treatment for breaking tuber dormancy (Reust and Gugerli, 1984). Research report indicated increased dormancy release in a 7-day

treatment with 20% CO<sub>2</sub> by Coleman and McInerney (1997). Role of higher range of CO<sub>2</sub> in breaking dormancy has resulted in a possibility of using it as alternative to chemical treatments. Similar studies indicated that CO<sub>2</sub> and O<sub>2</sub> concentrations alone apparently have little effect on innate dormancy but dose influence sprout growth (Burton, 1989). According to Esashi (1992), dormancy is released in dormant potato tuber where high concentrations of CO<sub>2</sub> and O<sub>2</sub> have been observed repeatedly although the specific physiological mechanisms are not well known. Similarly, Wiltshire and Cobb (1996) found that in potatoes, tuber dormancy could be broken effectively with 40–60% CO<sub>2</sub> and 20% O<sub>2</sub> applied to tubers continuously for 3–7 days at 25°C. Thus, CO<sub>2</sub> and O<sub>2</sub> play a vital role in dormancy release and sprouting (Rylski *et al.*, 1974).

According to Coleman and King (1984), the CO<sub>2</sub> and O<sub>2</sub> action on dormancy release and sprout growth of potato tubers is also due to an effect on abscisic acid (ABA) and sugar levels. These authors suggested that the CO<sub>2</sub> and O<sub>2</sub> treatments were effective in reducing ABA levels in dormant tubers, decreasing tuber dormancy duration and increasing sprout growth rate. They also found negative correlation between sprout growth rate and ABA levels in potato tubers tissue. Exogenous application of ABA is also capable of inhibiting potato sprout when applied repeatedly at high concentrations (El-Antably *et al.*, 1967). Differential effects of CO<sub>2</sub> and O<sub>2</sub> mixtures also influenced on sugar levels, which lead to significantly greater levels of sucrose, glucose and fructose. Moreover, the increased availability of soluble sugars could be important for subsequent sprout growth after cell wall loosening due to acidification by high CO<sub>2</sub> levels (El-Antably *et al.*, 1967).

### Physiological age of the seed tuber

van Ittersum and Scholte (1992) indicated that in the temperate regions, there are almost no problems with the physiological age of seed tubers because of the natural dormancy period during the winter when the harvested seed potatoes are stored in good cold storage facilities. Problems associated with physiological age of seed tubers are the main problem in tropical and sub-tropical areas. This problem is caused by the short period between two potato crop cultivations and by the high storage temperatures when no cold stores are available. van Ittersum and Scholte (1992) found a relation between the size of the seed tuber and its physiological age. As a physiologically younger tuber small seed tubers stay dormant for a long period of time than the large one. However, this effect depends on cultivar. Tuber size, cultivar, and growth regulator all had a highly significant effect on the sprouting behavior of potato (Otrosky and Struik, 2008).

### Injury

Tubers attacked by micro-organisms, insect and mechanically damaged (also by cuttings), or wounding have a shorter dormancy period than healthy and undamaged tubers. Cutting and injured seed tubers can break tuber dormancy and shorten the period of dormancy (Struik and Wiersema, 1999). There is a bruise and cut during postharvest and storage. Regardless of how the stored potatoes are to be marketed, wound healing is essential to minimize the entry areas for ever-present disease-causing organisms and pre-sprout initiation. Rappaport (1967) reported that wounding also stimulates sprouting by initiating synthesis of GAs in the tubers.

## TUBER SPROUTING

### Hormonal control of sprouting

Control of dormancy is attributed mainly to three groups of plant growth regulators, namely ABA, Gas, and CKs (Arteca, 1996).

### ABA

ABA is a naturally occurring growth inhibitor present in all organs of higher plants. Its function is concentration dependent (Hartmann *et al.*, 2002). The site of synthesis of ABA (a terpenoid) is in chloroplasts and other plastids. ABA acts on various processes in plants, such as stomatal opening and closure, abscission, cold stress, and dormancy (Arteca, 1996). Transport of ABA takes place throughout the plant (Gardner

*et al.*, 1985) and inactivation can take place in a similar way as that of it is indicated that transport of ABA is similar to GAs and CKs (Arteca, 1996). One of the main roles of ABA is dormancy regulation of plants. In extreme cold winters, the potato tubers have a mechanism of survival which is by being in dormant phase. ABA plays a pivotal role in the protection against cold stress (Arteca, 1996) and it has been proven that shorter days trigger the production of ABA (Gardner *et al.*, 1985). Different authors indicated that higher level of ABA is found in freshly harvested tubers and this level declines in storage (Biemelt *et al.*, 2000; Claassens and Vreugdenhil, 2000; Fernie and Willmitzer, 2001). Leclerc *et al.* (1995) stated higher ABA in small microtubers than field grown tubers is the reason for showing longer dormant period.

According to researches, only the initial level of ABA is important in triggering dormancy (Hilhorst and Toorop, 1997; Biemelt *et al.*, 2000), but Coleman (1987) is among the one who is off the opinion by indicating ABA is also important in maintaining dormancy. According to Hill (1980) and Gardner *et al.* (1985), it is not necessarily the level of ABA, but the ratio of ABA to GAs is the regulatory factor in maintaining dormancy. If the ratio indicates higher GAs, sprouting will be enhanced and dormancy will be terminated (Hill, 1980). It is not well known which level of ABA is required to initiate dormancy, and which level is enough for sprouting to commence (Claassens and Vreugdenhil, 2000).

According to Hemberg (1985), the impact of ABA is inhibition of DNA and RNA synthesis and GAs impacted the speed up of synthesis of DNA and RNA. ABA is also produced to protect tubers against impact of cold temperature. The mechanism is by inhibition of synthesis of DNA and RNA which arrests the cell in the  $G_1$  phase of cell cycle until the stage in which GA: ABA ratio favors GAs. If the level of GAs is higher in the ratio cell division and sprouting will be enhanced. Most authors agree that exogenously applied ABA will inhibit sprouting (Suttle, 1996; Suttle, 2004a) but it is concentration dependent.

### GAs

GAs are growth promoters. There are several reports that revealed exogenously applied GAs could break dormancy, the first of these was by Brian *et al.* (1955). To date, over a hundred GAs have been isolated (Vivanco and Flores, 2000), but not all are active in plants. GAs in the 13-hydroxylation group, especially  $GA_1$  and  $GA_4$ , are the most active (Suttle, 1996; Vivanco and Flores, 2000; Suttle, 2004a; Suttle, 2004b). Increased activity is probably due to the lactone ring present in the structure of these GAs (Gardner *et al.*, 1985). GAs are mainly produced in the leaves but may also be synthesized in the roots and fruit (Gardner *et al.*, 1985; Vivanco and Flores, 2000). Transport takes place mainly in the phloem of the plants and can be both up and downward (Kefeli, 1978). GAs are generally considered to be responsible for cell elongation, rather than cell division (Kefeli, 1978; Vivanco and Flores, 2000; Francis and Sorrell, 2001), but may also play a role in stimulating cell division in meristematic areas (Kefeli, 1978; Clegg and Rapport, 1970).

In potato tuber, dormancy could be broken by the application of GAs which is reported by Hemberg (1985); Coleman (1987); Burton (1989); and Fernie and Willmitzer (2001). GAs may terminate dormancy by activating the synthesis of DNA and RNA (Clegg and Rapport, 1970; Burton, 1989; Arteca, 1996) and by decreasing the duration of the cells in the  $G_1$  and S phases (Robberts, 1988). According to Francis and Sorrell (2001), GAs may affect the Cdc 2 kinase level at the  $G_2$ -M checkpoint of the cell cycle and GAs may increase the rate at which cells are produced. The large number of different GAs found makes it confusing to identify their various roles in potato tuber dormancy/sprouting. In many cases, it appears that they can be transformed into other types. Thus, Barendse (1975) suggested that  $GA_1$ ,  $GA_4$ , and  $GA_7$  are precursors of  $GA_3$ .  $GA_1$  is the most biologically active GA (Jones *et al.*, 1988).  $GA_{20}$  has been identified as the precursor of  $GA_1$  (Jones *et al.*, 1988). Xu *et al.* (1998) found that  $GA_1$ ,  $GA_4$ ,  $GA_9$ , and  $GA_{20}$  are present in potato plants and that  $GA_4$  and  $GA_9$  levels do not change during tuber development, but only the level of  $GA_1$ . These results concur with the suggestion of Jones *et al.* (1988)

that  $GA_1$  is biologically the most active GA in tubers. Similar range was reported by Vreugdenhil and Sergeeva (1999) in the genotype *Solanum demissum*. Suttle (1996) mentioned that exogenously applied  $GA_{12}$  was metabolized in the shoot apices of potatoes to produce  $GA_1$ ,  $GA_8$ ,  $GA_{20}$ ,  $GA_{29}$ ,  $GA_{44}$ ,  $GA_{51}$ , and  $GA_{53}$ .

Carrera *et al.* (2000) indicated that, in potato tubers, ectopic expression of  $GA_{20}$  oxidase increased GA and premature sprouting, antisense inhibition of  $GA_{20}$  oxidase synthesis enhanced dwarfism, but there were no effects on tuber dormancy duration. This supports the view that GAs can break dormancy but are not necessary for dormancy to end. To confirm the role of GAs, Suttle (2004b) conducted a study to determine the effects of post-harvest storage duration on the endogenous content and bioactivities of selected GAs in relation to the dormancy status in Russet Burbank potatoes. In between days of 98 and 134 in storage condition, dormancy starts to end. The dormancy of the tubers broke in further dates of storage and at after 212 days, the tubers became non-dormant and showed vigorous sprouting. After harvesting, the endogenous  $GA_{19}$ ,  $GA_{20}$ , and  $GA_1$  contents became relatively high. The content exhibited a decrease in between 33 and 93 days of storage. Internal levels of  $GA_{19}$ ,  $GA_{20}$ , and  $GA_1$  rose slightly between 93 and 135 days of storage reaching levels comparable to those found in highly dormant tubers immediately after harvest. In vigorous sprouts levels of  $GA_{19}$ ,  $GA_{20}$ , and  $GA_1$  continued to increase. It is indicated that freshly tubers are insensitive to exogenous application of GAs. In a continued post-harvest storage time, exogenous GAs ( $GA_1$  and  $GA_{20}$ ) enhanced premature dormancy release.

Exogenous GA application enhanced sprout growth in non-dormant tubers in order of activity as  $GA_1 = GA_{20} > GA_{19}$ . Extended tuber exposure GA biosynthesis inhibitors did not show extended tuber dormancy. Suttle (2004b) study does not support a role for endogenous GA in potato tuber dormancy release but does suggest an involvement in the regulation of sprout growth. Besides the synthesis of DNA and RNA, GAs are also believed to have an effect on reducing sugar content (Hill, 1980; Mares, 1985). According to Hill (1980), the process of starch breakdown is GA dependent. GAs are also involved in seeds for synthesis of amylase which acts in the breakdown of starch into sugars.

Claassens and Vreugdenhil (2000) also mentioned that GAs in potatoes had a stimulating effect on reducing sugar content, but it could not be proven whether GAs had an effect on starch breakdown. According to Coleman (1987), GAs enhanced the synthesis of reducing sugars but after dormancy was broken in storage tissues. Tuber wounding also has a stimulatory effect on the synthesis of GAs (Shih and Rappaport, 1970). According to Ewing *et al.* (1987), wounding had an impact on termination of dormancy, but the mechanism is not clearly understood.

### CKs

The CKs most prevalent in plants are those with N6-side chain such as zeatin, isopentenyladenine and N6-benzyladenine (Vivanco and Flores, 2000; Mok and Mok, 2001). The main effect of CKs is on cell division (Arteca, 1996; Francis and Sorrell, 2001; Hartmann *et al.*, 2002; Vreugdenhil, 2004), but CKs also have an effect on cell enlargement (Hartmann *et al.*, 2002). CKs act on the  $G_1$ -S and the  $G_2$ -M phases of the cell cycle (Robberts, 1988; Francis and Sorrell, 2001; Mok and Mok, 2001; Suttle, 2004a). In the  $G_1$ -S transition, CKs function by inducing the CycD3 genes (Francis and Sorrell, 2001; Mok and Mok, 2001). Plants over-expressing CycD3 could maintain cell division without exogenously applied CKs. CKs have also been found to be active in the  $G_2$ -M transition of the cell cycle where induction of a histone-H-kinase, Cdc2, takes place (Francis and Sorrell, 2001; Mok and Mok, 2001).

Hemberg (1985) mentioned that CKs applied exogenously can break dormancy of potato tubers, and the levels of endogenous CKs increase before the termination of dormancy. Different forms of CK are reported to be found in potato tubers. Sattelmacher and Marschner (1978) as well as Van Staden and Dimalla (1977) found that zeatin riboside is the main component of CKs in potatoes, but Suttle and Banowitz (2000)

reported that cis-zeatin and not cis-zeatin riboside exhibited increase in tubers during period of dormancy and reported as a factor in termination of dormancy. The authors also mentioned that isopentenyl adenine and trans-zeatin levels increase in tubers during storage. Suttle (1998b) found eight different forms of CKs present in potato tubers with isopentenyl adenine-9-glucoside the most abundant. The levels of the zeatin-type CKs were comparable with that of the isopentenyl-type (IP) CKs. Isopentenyl adenine-9-glucoside is biologically inactive and serves as a precursor for zeatin-type CKs which are biologically active. The IP-type CKs should first be synthesized into zeatin-type CKs before termination of dormancy (Suttle, 1998b). Endogenous levels of CKs must increase before dormancy can be broken (Koda, 1982; Suttle, 2004a). Increase in CK content coincides with a reduction of acid inhibitors like ABA (Claessens and Vreugdenhil, 2000).

Tissue sensitivity to CKs is important in the regulation of dormancy (Turnbull and Hanke, 1985a), and exogenously applied CKs were only effective at certain times in the dormancy period, mostly at the beginning and end of dormancy (Coleman, 1987). According to Suttle (2001), CKs are not able to stimulate sprouting immediately after harvest but dormant tubers reacted effectively at dose-dependent rate. According to Koda (1982), resting wounded tubers formed a significant increase in the level of CKs, mainly zeatin glucoside, which could have an impact on sprouting. Based on the available literature, it is postulated that CKs are essential in the regulation of dormancy, probably acting in synergy with other hormones, especially GAs in terminating dormancy.

Tuber dormancy can be broken by the addition of both natural and synthetic CKs (Hemberg, 1970). Potato tubers of the cultivar, Majestic, which has a long dormancy period were treated with water or with the CKs, kinetin, or zeatin. The tubers treated with CKs broke dormancy after 2–3 days. Potato lines transformed with a CK biosynthesis gene show early sprouting (Ooms and Lenton, 1985). Transformed lines showed 100–200-fold higher concentrations of the biologically-active CKs, zeatin, and zeatin riboside compared with untransformed potato lines.

Immunological techniques have confirmed that an increase in CKs is detected in tubers exiting dormancy (Turnbull and Hanke, 1985a; Suttle, 2004a). Unfortunately, the antibodies used in these studies recognized both active and inactive CK metabolites. Suttle (2004c; 2005) showed that synthetic CKs terminate dormancy. In another study, Turnbull and Hanke (1985) noticed innate dormancy in the cultivar majestic remained for 9–12 weeks in storage at 10°C but was reduced to 3–4 weeks when the tubers were stored at 2°C and were treated with CKs. CKs application on tubers which do exhibit innate dormant buds showed sprout growth within 2 days. CK treatment did not accelerate the rates of cell division and cell expansion in buds where innate dormancy had already broken naturally suggesting that CKs play a role in dormancy break but do not enhance sprout growth.

**Tuber sprouting as influenced by a combination of CK and GA**

A combination of CK and GAs terminated dormancy earlier than only GAs (Rossouw, 1992). Tubers treated with only CK sprouted earlier but subsequent sprout growth was greatly reduced compared to combination treatments. According to Turnbull and Hanke (1985), GA treatments did not have an effect on the termination of dormancy but had a functional role in the growth of potato tuber buds. The role of GAs is higher in sprout initiation but has restricted impact on termination of dormancy (Suttle, 2004b).

Sprouting is fast in CK treated tubers than in tubers treated by GA. CKs have been found to be active in the regulation of D-type cyclins. D-type cyclins are responsible for the transition of the G<sub>1</sub> phase of the cell cycle and by the application of CK; D-type cyclins will initiate the cell to complete its cycle. Growth can then occur and dormancy will be terminated. According to Suttle and Banowitz (2000), CKs are responsible for the termination of dormancy but have no effect on further sprout growth.

*Average number of sprouts per tuber*

High number of sprouts was promoted in all the dormant buds due to favorable conditions such as gibberellic acid, CKs, and reserve carbohydrates (Abebe and Tekalign, 2010). van Ittersum and Scholte (1993b) reported that sprout number of tubers from plants sprayed with a high GA<sub>3</sub> concentration was significantly higher than that of tubers from control plants. Similarly, Alexopoulos *et al.* (2008) found that irrespective of the concentration, GA<sub>3</sub> treatments (1, 5, 10, and 50 ppm) significantly increased the number of sprouting buds per tuber compared to the control. Gibberellic acid treatments increase the number of sprouts (Alexopoulos *et al.*, 2006a; Otrushy and Struik, 2008), the length of the sprouts (Bruinsema and Swart, 1970), and proportion of sprouts by about 10% (Holmes *et al.*, 1970).

**Table 1: Effect of cytokinin and gibberellin treatment on sprout number and dry mass of cv.Caren measured at 20 and 32 days after treatment**

Treatment (n=30)	Mean sprout number/tuber		Mean sprout dry mass/tuber (g)
	20 Days	32 Days	
Intact tuber	0	0	0
Control	0.21 <sup>a</sup>	0.72 <sup>a</sup>	0.003 <sup>a</sup>
SRRC	0.71 <sup>b</sup>	2.27 <sup>bc</sup>	0.015 <sup>abc</sup>
0.5BA	2.96 <sup>feh</sup>	2.49 <sup>bc</sup>	0.017 <sup>bcd</sup>
0.5BA:1GA	2.69 <sup>efgh</sup>	3.72 <sup>d</sup>	0.027 <sup>de</sup>
0.5BA:0.5GA	1.89 <sup>cdef</sup>	2.44 <sup>bc</sup>	0.022 <sup>cde</sup>
0.5GA	2.26 <sup>cdefg</sup>	2.91 <sup>cd</sup>	0.027 <sup>de</sup>
1BA:0.5GA	3.28 <sup>gh</sup>	3.73 <sup>d</sup>	0.024 <sup>cde</sup>
1BA	1.54 <sup>cd</sup>	1.85 <sup>b</sup>	0.008 <sup>ab</sup>
1BA:1GA	2.47 <sup>defgh</sup>	1.90 <sup>b</sup>	0.029 <sup>ef</sup>
1BA:2GA	1.41 <sup>c</sup>	1.84 <sup>b</sup>	0.011 <sup>ab</sup>
1GA	1.80 <sup>cde</sup>	2.92 <sup>cd</sup>	0.027 <sup>cde</sup>
2BA:1GA	3.66 <sup>h</sup>	3.09 <sup>cd</sup>	0.040 <sup>f</sup>
SEM	0.12	0.10	0.004

SEM: Standard error of the mean, Means within the same column sharing the same letters are not significantly different (p<0.05). (Source: Rossouw, 2008)

**Table 2: Effects of gibberellic acid on average number and length of sprouts**

Treatments	Average number of sprouts/tuber	Average length of sprouts (mm)
Control (Ethanol and DDW)	2.00 <sup>d</sup>	48 <sup>d</sup>
Haulm application of 250 ppm GA <sub>3</sub>	4.00 <sup>abc</sup>	80 <sup>b</sup>
Haulm application of 500 ppm GA <sub>3</sub>	4.00 <sup>abc</sup>	90 <sup>a</sup>
Haulm application of 750 ppm GA <sub>3</sub>	4.33 <sup>ab</sup>	92 <sup>a</sup>
Haulm application of 1000 ppm GA <sub>3</sub>	5.33 <sup>a</sup>	93 <sup>a</sup>
Dipping tubers in 10 ppm of GA <sub>3</sub>	2.67 <sup>cd</sup>	55 <sup>d</sup>
Dipping tubers in 20 ppm of GA <sub>3</sub>	3.00 <sup>bcd</sup>	70 <sup>c</sup>
Dipping tubers in 30 ppm of GA <sub>3</sub>	3.33 <sup>bcd</sup>	80 <sup>b</sup>
Dipping tubers in 40 ppm of GA <sub>3</sub>	3.67 <sup>bc</sup>	86 <sup>ab</sup>
Dipping tubers in 50 ppm of GA <sub>3</sub>	4.00 <sup>abc</sup>	88 <sup>a</sup>
Mean	3.63	78
Cv (%)	20.58	5.31
Level of significance	**	**

Means within a column followed by the same letters are not significantly different at the prescribed level of significance. \*\*=significant at 1% probability level (Source: Abebe and Tekalign, 2010)

**Table 3: Effect of cytokinin and gibberellin treatments on sprout number and length and dry mass of sprouts of up-to-date tubers 14 days after treatment**

Treatment (n=20)	Mean sprout number/tuber	Mean length per sprout (mm)	Total sprout length per tuber	Mean sprout dry mass /tuber (g)
Intact tuber	0	0	0	0
Control	2.29 <sup>a</sup>	6.47 <sup>a</sup>	14.82	0.008 <sup>a</sup>
SRCR	4.25 <sup>b</sup>	12.94 <sup>b</sup>	54.99	0.024 <sup>bc</sup>
0.5BA	7.92 <sup>d</sup>	14.64 <sup>b</sup>	115.95	0.032 <sup>cd</sup>
0.5BA:0.5GA	8.73 <sup>de</sup>	20.36 <sup>c</sup>	177.74	0.036 <sup>de</sup>
0.5BA:1GA	10.35 <sup>ef</sup>	20.99 <sup>cd</sup>	217.25	0.042 <sup>def</sup>
0.5GA	9.64 <sup>def</sup>	24.38 <sup>de</sup>	235.02	0.051 <sup>fg</sup>
1BA:0.5GA	9.33 <sup>def</sup>	24.30 <sup>de</sup>	226.72	0.043 <sup>efg</sup>
1BA	5.51 <sup>c</sup>	8.38 <sup>a</sup>	46.17	0.015 <sup>ab</sup>
1BA:1GA	10.36 <sup>ef</sup>	23.10 <sup>cde</sup>	239.32	0.048 <sup>fg</sup>
1BA:2GA	11.02 <sup>f</sup>	24.04 <sup>cde</sup>	264.92	0.053 <sup>g</sup>
1GA	9.71 <sup>def</sup>	26.23 <sup>e</sup>	254.69	0.053 <sup>g</sup>
2BA:1GA	9.53 <sup>def</sup>	24.96 <sup>e</sup>	237.87	0.047 <sup>efg</sup>
SEM	0.07	1.4		0.004

SEM: Standard error of the mean, Means within the same column sharing the same letters are not significantly different (p<0.05), n=20. (Source: Rossouw, 2008)

In addition, Rossouw (2008) reported that both the high GA treatments (0.5 GA and 1GA) and combination treatments resulted in more sprouts per tuber than the control or CK treated tubers. Tubers treated with only CK produced less number of sprouts per tuber than the GA and CK plus GA treatments. The control (0.21) and SRCR (0.71) treatments sprouted irregularly compared to the other treatments that typically had more than two sprouts per tuber after 20 days. Sprout numbers generally increased after 32 days, with the most prominent increase in the SRCR treatment (2.27). High concentrations of GAs (0.5GA; 1GA) resulted in more sprouts than similar concentrations of CK (0.5BA; 1BA) (Table 1).

*Average sprout length per tuber*

Alexopoulos *et al.* (2007b) reported significantly higher mean sprout length per tuber by treatment of GA<sub>3</sub> or GA<sub>3</sub>+BA than the control. Similarly, Abebe and Tekalign (2010) reported that both haulm application and dipping treatments with GA<sub>3</sub> showed increasing trend of sprout length with increasing the rate of GA<sub>3</sub> (Table 2). Lim *et al.* (2004) also noted that GA<sub>3</sub>-treated potato tubers showed fast sprout growth and those tubers treated with higher dose of GA<sub>3</sub> sprouted earlier than others. Suttle (2004a) reported that exogenously applied GA<sub>1</sub>, GA<sub>9</sub>, and GA<sub>20</sub> enhanced growth of tuber sprouts and that GA<sub>1</sub> was the most active than the other forms. GA<sub>3</sub> treatments resulted in high sprout growth rates possibly due to an increase in assimilate flow toward the growing sprouts, which enhanced early establishment of crop stand and improved photosynthetic activity. Both the high GA treatments (0.5 GA and 1GA) and combination treatments resulted in longer sprouts than the control or CK-treated tubers (Rossouw, 2008). Tubers treated with only CK produced shorter sprouts than the GA and CK plus GA treatments. Tubers treated with a high concentration of CK (1BA) did not differ from the control in sprout length. The author also indicated that a lower concentration of CK (0.5BA treatment) resulted in more sprout growth (14.64 mm) than a higher concentration (1BA; 8.38 mm) (Table 3).

*Fresh and dry mass of sprouts*

Alexopoulos *et al.* (2007b) found that the fresh weight of sprouts per tuber following treatment with GA<sub>3</sub> or GA<sub>3</sub>+BA was significantly higher than that of the controls. Gibberellic acid treatment by itself increased the rate of transfer of dry matter from tubers to sprouts (Morris, 1967). Similarly, Abebe and Tekalign (2010) reported an increment of fresh and dry mass of sprouts with an application of GA<sub>3</sub> (Table 4). Therefore, it seems that increased concentration of GA<sub>3</sub> treatment increased the growth of sprouts per tuber and also the rate of transfer of dry matter from tuber to sprout and finally improved sprout dry matter.

**Table 4: Effects of gibberellic acid on fresh and dry mass of sprouts**

Treatments	Fresh mass of sprout per tuber (mg)	Dry mass of sprout per tuber (mg)
Control (Ethanol and DDW)	510 <sup>e</sup>	112 <sup>c</sup>
Haulm application of 250 ppm GA <sub>3</sub>	750 <sup>bcd</sup>	174 <sup>b</sup>
Haulm application of 500 ppm GA <sub>3</sub>	780 <sup>bc</sup>	182 <sup>ab</sup>
Haulm application of 750 ppm GA <sub>3</sub>	820 <sup>b</sup>	191 <sup>ab</sup>
Haulm application of 1000 ppm GA <sub>3</sub>	1040 <sup>a</sup>	224 <sup>a</sup>
Dipping tubers in 10 ppm of GA <sub>3</sub>	600 <sup>de</sup>	145 <sup>bc</sup>
Dipping tubers in 20 ppm of GA <sub>3</sub>	630 <sup>cde</sup>	149 <sup>bc</sup>
Dipping tubers in 30 ppm of GA <sub>3</sub>	640 <sup>cde</sup>	150 <sup>bc</sup>
Dipping tubers in 40 ppm of GA <sub>3</sub>	730 <sup>bcd</sup>	170 <sup>b</sup>
Dipping tubers in 50 ppm of GA <sub>3</sub>	730 <sup>bcd</sup>	171 <sup>a</sup>
Mean	720	170
Cv (%)	12.09	14.77
Level of significance	**	**

Means within column followed by the same letters are not significantly different at the prescribed level of significance. \*\*=significant at 1% probability level (Source: Abebe and Tekalign, 2010)

Combinations of CK and GA (1BA:1GA, 1BA:2GA, 2BA:1GA) showed a higher dry mass than the control and CK treatment 1BA. The control, SRCR, and 1BA treatments resulted in the lowest sprout mass per tuber, while GAs and combination treatments resulted in a significantly higher dry mass with the 2BA:1GA treatment producing the highest dry mass (Table 1) (Rossouw, 2008).

**CONCLUSION**

Although dormancy is largely under genetic control and differs between cultivars, numerous environmental, and endogenous factors can modulate dormancy length. Environmental factors influencing plant growth, such as light period, temperature, and water and nutrient supply, are also reflected in dormancy length as tuber formation directly depends on the plant's performance. Beside environmental conditions, dormancy length also depends on endogenous changes in phytohormone levels.

During dormancy, cells are mainly arrested in the G<sub>1</sub> phase of the cell cycle. Unblocking of this, phase can only commence if D-type cyclins are present. CKs have been found to play an important role in the synthesis of D-type cyclins. Thus, it seems that CKs are mainly responsible for the termination of dormancy and it has been shown that CK treatments terminated dormancy earlier than using GAs. Although CK terminated dormancy earlier than GA treatments, subsequent sprout growth was slower.

GAs did not necessarily terminate dormancy but stimulated sprout growth after dormancy was reduced. GAs may be responsible for cell division by regulation of the G<sub>2</sub>-M phase of the cell cycle by altering the levels of Cdc 2 kinase. GAs are also able to express B-type cyclins that are important in the regulation of the G<sub>2</sub>-M phase. By supplying GAs to cells blocked in the G<sub>2</sub>-M phase, cell division and growth can commence. GAs also function in the synthesis of reducing sugars, by conversion of starch to glucose and fructose. During termination of dormancy, a transition takes place whereupon a tuber becomes a source organ. During this transition, starch is synthesized into sugars to be used by growing sprouts.

Application of CK and GA in combination will terminate dormancy and increase sprout growth earlier than using GAs alone and also applying only CK will terminate dormancy earlier than using GAs alone, but subsequent sprout growth will be hampered. There is an interaction between CKs and GAs and CKs require the addition of other hormones to function properly. CKs are able to act upon a bud by causing a change in growth and making it possible for GAs to act upon this bud by increasing the growth rate. It seems that applying a combination of CK and GAs may well be an answer to terminate dormancy earlier and increase growth.

#### DATA AVAILABILITY

Primary data were not used to support this study.

#### DISCLOSURE

The authors confirm that the content of the manuscript has not been published or submitted for publication elsewhere.

#### AUTHORS' CONTRIBUTIONS

BDA is the first author of the review article, whereas the co-author has contributed equally for the literature collection, manuscript documentation, and its revision. All authors read and approved the final manuscript.

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#### CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

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#### REFERENCES

Abebe, C., & Tekalign, T. (2010). *Effect of gibberellic acid on tuber dormancy breaking, subsequent growth, yield and quality of potato (Solanum tuberosum L.)*. [M.Sc. Thesis].

Ahmad, N., Khan, M. A., & Binyamin, N. A. (2011). Identification of resistance source in potato germplasm against PVX and PVY. *Pakistan Journal of Botany*, 43(6), 2745-2749.

Alexopoulos, A. A., Aivalakis, G., Akoumianakisa, K. A., & Passam, H. C. (2008). Effect of gibberellic acid on the duration of dormancy of potato tubers produced by plants derived from true potato seed. *Postharvest*

*Biology and Technology*, 49, 424-430.

Alexopoulos, A. A., Akoumianakis, K. A., & Passam, H. C. (2006a). Effect of plant growth regulators on the tuberization and physiological age of potato (*Solanum tuberosum* L.) tubers grown from true potato seed. *Canadian Journal of Plant Science*, 86, 1217-1225.

Alexopoulos, A. A., Akoumianakis, A., Olympias, C. M., & Passam, H. C. (2007b). The effect of time and mode of application of gibberellic acid and inhibitors of gibberellins biosynthesis on the dormancy of potato tubers grown from true potato seed. *Journal of the Science of Food and Agriculture*, 87, 1973-1979.

Allen, E. J., O'Brien, P. J., & Firman, D. (1992). Seed tuber production and management. In: P. M. Harris (Ed.), *The potato crop* (pp. 247-291). London: Chapman and Hall.

Andrew, H. K. (2001). *Retail handling of fresh potatoes*. The State of Victoria.

Appeldoorn, N. J. G., Vreugdenhil, D., & Van der Plas, L. H. W. (1999). Developmental changes in enzymes involved in the conversion of hexose phosphate and its subsequent metabolites during early tuberization of potato. *Plant Cell and Environment*, 22, 1085-1096.

Arteca, R. N. (1996). *Plant growth substances: Principles and applications*. New York: Chapman and Hall.

Banas, A., Bielinska-Czarnecka, M., & Klocek, J. (1984). Activity of endogenous cytokinins in potato tubers during dormancy and sprouting. *Bulletin of the Polish Academy of Sciences Technical Sciences*, 32, 37-41.

Barendse, G. W. M. (1975). Biosynthesis, metabolism, transport and distribution of gibberellins. In: H. N. Krishnamoorthy (Ed.), *Gibberellins and plant growth* (pp. 65-85). New York: John Wiley and Sons Inc.

Berga, L., Gebremedhin, W., Terrisa, J., Bereke-Tsehail, T., & Yaynu, H. (1994b). Potato improvement research. In: E. Herath and L. Dessalegn (Eds.), *Proceedings of the second national horticultural workshop of Ethiopia, Addis Ababa, 1992*. Addis Ababa, Ethiopia: Institute of Agricultural Research and Food and Agriculture Organization.

Biemelt, S., Hajirezaei, M., Hentschel, E., & Sonnewald, U. (2000). Comparative analysis of abscisic acid content and starch degradation during storage of tubers harvested from different potato varieties. *Potato Research*, 43, 371-382.

Brian, P. W., Hemming, H. G., & Radley, M. (1955). A physiological comparison of gibberellic acid with some auxins. *Physiologia Plantarum*, 8, 899-912.

Bruinsema, J., & Swart, J. (1970). Estimation of the course of dormancy of potato tubers growth and storage, with the aid of gibberellic acid. *Potato Research*, 13, 29-40.

Burton, W. G. (1968). The effect of oxygen concentration upon sprout growth on the potato tuber. *European Potato Journal*, 11, 249-265.

Burton, W. G. (1989). *The potato* (3<sup>rd</sup> ed). London: Longman Group U.K. Ltd.

Campbell, M., Segear, E., Beers, L., Knauber, D., & Suttle, J. (2008). Dormancy in potato tuber meristems: chemically induced cessation in dormancy matches the natural process based on transcript profiles. *Functional and Integrative Genomics*, 8, 317-328.

Carrera, E., Bou, J., Garcia-Martinex, J., & Prat, S. (2000). Changes in GA20-oxidase gene expression strongly affect stem length, tuber-induction and tuber yield of potato plants. *The Plant Journal*, 22, 247-256.

Claassens, M. M. J., & Vreugdenhil, D. (1984). Is dormancy breaking of potato tubers the reverse of tuber initiation? *Potato Research*, 43, 347-369.

Claassens, M. M. J., & Vreugdenhil, D. (2000). Is dormancy breaking of potato tubers the reverse of tuber initiation? *Potato Research*, 43, 347-369.

Clegg, M. D., & Rapport, L. (1970). Regulation of bud rest in tubers of potato, *Solanum tuberosum* L. VI. Biochemical changes induced in excised potato buds by gibberellic acid. *Physiologia Plantarum*, 45, 8-13.

Coleman, W. K. (1987). Dormancy release in potato tubers: A review. *American Journal of Potato Research*, 64, 57-68.

Coleman, W. K., & King, R. R. (1984). Changes in endogenous abscisic acid, soluble sugars and proline levels during tuber dormancy in (*Solanum tuberosum* L.). *American Journal of Potato Research*, 61, 437-449.

Coleman, W. K., & McInerney, J. (1997). Enhanced dormancy release and emergence from potato tubers after exposure to a controlled atmosphere. *American Journal of Potato Research*, 74, 173-182.

Crabbe, J., & Barnola, P. (1996). A new conceptual approach to bud dormancy in woody plants. In: G. A. Lang (Ed.), *Plant dormancy: Physiology, biochemistry and molecular biology* (pp. 83-107). Oxon: CAB International.

CSA (Central Statistics Agency). (2017). *Agricultural sample survey*

- 2016/17 Vol. 1, Report on area and production of major crops (Private peasant holdings "meher" season), Statistical Bulletin No. 584. Addis Ababa, Ethiopia: The Federal Democratic Republic of Ethiopia.
- Destefano-Beltran, L., Knauber, D., Huckle, L., & Suttle, J. C. (2006). Chemically forced dormancy termination mimics natural dormancy progression in potato tuber meristems by reducing ABA content and modifying expression of genes involved in regulating ABA synthesis and metabolism. *Journal of Experimental Botany*, 57, 2879-2886.
- Devlin, R. M. (1975). *Plant physiology* (3<sup>rd</sup> ed). New York: Van Nostrand.
- Douches, D. S. (2013). *Breeding and genetics for the improvement of potato (Solanum tuberosum L.) for yield, quality and pest resistance*. Available from: [http://potatobg.msu.edu/program overview.html](http://potatobg.msu.edu/program%20overview.html)
- El-Antably, H. M. M., Wareing, P. F., & Hillman, J. (1967). Some physiological responses to d,l-absicisin (Dormin). *Planta*, 73, 74-90.
- Esashi, Y. (1992). Ethylene and seed germination. In: A. K. Mattoo, J. C. Suttle, (Eds.), *The plant hormone ethylene* (pp. 133-157). Boca Raton: CRC Press.
- Eskin, N., & Michael, A. (1989). *Quality and preservation of vegetables* (pp. 2-11). Boca Raton, Florida: CRS Press, Inc.
- Ewing, L. L., McMurry, S. E., & Ewing, E. E. (1987). Cutting as a method of breaking dormancy in microtubers produced *in vitro*. *American Journal of Potato Research*, 164, 329-332.
- Fairbanks, D. J., & Anderson, W. R. (1999). *Genetics: The continuity of life*. New York: Brooks/Cole Publishing Company.
- Fernie, A. R., & Willmitzer, L. (2001). Molecular and biochemical triggers of potato tuber development. *Journal of Plant Physiology*, 127, 1459-1465.
- Fraizer, M. J., Olsen, N., & Kleinkopf, G. (2004). *Organic and alternative methods for potato sprout control in storage*. United States: University of Idaho Extension. Available from: [https://info.ag.uidaho.edu/pdf/cis 1120](https://info.ag.uidaho.edu/pdf/cis%201120)
- Francis, D., & Sorrell, D. A. (2001). The interface between the cell cycle and plant growth regulators: A mini review. *Plant Growth Regulation*, 33, 1-12.
- Gardner, F. P., Pearce, R. B., & Mitchell, R. L. (1985). *Physiology of crop plants* (Vol. 29) (pp. 20-21). Ames, Iowa: Iowa State University Press.
- Harris, P. M. (1992). *The Potato crop* (p. 909). London: Chapman and Hall.
- Hartmann, H. T., Kester, D. E., Davies, F. T., & Geneve, R. L. (2002). *Plant propagation: Principles and practices* (7<sup>th</sup> ed). New Jersey: Prentice Hall.
- Hemberg, T. (1970). The action of some cytokinins on the rest-period and the content of acid growth - inhibiting substances in potato. *Physiologia Plantarum*, 23, 850-858.
- Hemberg, T. (1985). Potato rest. In: P. H. Li (Ed.), *Potato physiology* (pp. 353-379). London: Academic Press Inc.
- Hilhorst, H. W. M., & Toorop, P. E. (1997). Review on dormancy, germinability, and germination in crop and weed seeds. *Advances in Agronomy*, 61, 111-155.
- Hill, T. A. (1980). *Endogenous plant growth substances* (2<sup>nd</sup> ed). Southampton: The Camelot Press Ltd.
- Holmes, J. C., Lang, R. W., & Singh, A. K. (1970). The effect of five growth regulators on apical dominance in potato seed tubers and on subsequent tuber production. *Potato Research*, 13, 342-352.
- Jones, M. G., Horgan, R., & Hall, M. A. (1988). Endogenous gibberellins in the potato, *Solanum tuberosum*. *Phytochemistry*, 27, 7-10.
- Kefeli, V. I. (1978). *Natural plant growth inhibitors and phytohormones*. Boston: Dr. W. Junk B.V. Publishers.
- Kloosterman, B., De Koeper, D., & Bachem, C. W. (2008). Genes driving potato tuber initiation and growth: identification based on transcriptional changes using the POCI array. *Functional and Integrative Genomics*, 8, 329-334.
- Kloosterman, B., Vorst, O., Hall, R. D., Visser, R. G. F., & Bachem, C. W. (2005). Tuber on a chip: Differential gene expression during potato tuber development. *Plant Biotechnology Journal*, 3, 505-519.
- Koda, Y. (1982). Effects of storage temperature and wounding on cytokinin levels in potato tubers. *Plant and Cell Physiology*, 23, 851-857.
- Leclerc, Y., Donnelly, D. J., Coleman, W. K., & King, R. R. (1995). Microtuber dormancy in three potato cultivars. *American Journal of Potato Research*, 72, 215-223.
- Lim, H. T., Yoon, C. S., Choi, S. P., & Dhital, S. P. (2004). Application of Gibberellic acid and paclobutrazol for efficient production of potato (*Solanum tuberosum* L.) minitubers and their dormancy breaking under soil less culture system. *Journal of the Korean Society for Horticultural Science*, 45, 189-193.
- Mares, D. J. (1985). Carbohydrate metabolism in developing potato tubers. In: P. H. Li (Ed.), *Potato physiology* (pp. 280-318). London: Academic Press Inc.
- McGee, E., Jarvis, M. C., & Duncan, H. J. (1987). Wave length dependent of suppressant of potato sprout growth by light. *Plant Cell and Environment*, 10, 655-660.
- Mok, D. W. S., & Mok, M. C. (2001). Cytokinin metabolism and action. *Annual Review of Plant Physiology and Plant Molecular Biology*, 52, 89-118.
- Morris, D. A. (1967). The influence of light, gibberellic acid and CCC on sprout growth and mobilization of tuber reserves in the potato (*Solanum tuberosum* L.). *Planta*, 77, 224-232.
- Ooms, G., & Lenton, J. R. (1985). T-DNA genes to study plant development: Precocious tuberization and enhanced cytokinins in *A. tumefaciens* transformed potato. *Plant Molecular Biology*, 5, 205-212.
- Otroshy, M., & Struik, P. C. (2008). Effect of size of normal seed tubers and growth regulator application on dormancy, sprout behavior, growth vigor and quality of normal seed tubers of different potato cultivars. *Research Journal of Seed Science*, 1, 41-50.
- Rappaport, L. H. (1967). Wound induced Gibberellins. *Nature*, 214, 1149-1150.
- Reust, W., & Gugerli, P. (1984). Oxygen and carbondioxide treatment to break potato tuber dormancy for reliable detection of Potato Virus Y (PVY) by enzyme linked immunosorbent assay (ELISA). *Potato Research*, 27, 435-439.
- Robberts, L. W. (1988). Hormonal aspects of vascular differentiation. In: L. W. Roberts, P. B. Gahan and R. Aloni (Eds.), *Vascular differentiation and plant growth regulators* (pp. 22-38). Berlin, Heidelberg: Springer-Verlag.
- Ronning, C. M., Stegalkina, S. S., & Buell, C. R. (2003). Comparative analyses of potato expressed sequence tag libraries. *Plant Physiology*, 131, 419-429.
- Rossouw, J. A. (1992). *Effect of cytokinin and gibberellins on tuber dormancy* [M.Sc.Thesis]., Pretoria, South Africa: Pretoria University.
- Rossouw, J. A. (2008). *Effect of cytokinin and gibberelin on potato tuber dormancy* [PhD Thesis]. Pretoria, South Africa: University of Pretoria.
- Rylski, I., Rappaport, L., & Pratt, H. K. (1974). Dual effects of ethylene on potato dormancy and sprout growth. *Plant Physiology*, 53, 658-662.
- Sattelmacher, B., & Marschner, H. (1978). Cytokinin activity in stolons and tubers of *Solanum tuberosum* during the period of tuberization. *Physiologia Plantarum*, 44, 69-72.
- Scholte, K. (1986). *Relation between storage temperature sum and vigor of seed potatoes*. In: *abstract of conference papers 10<sup>th</sup> Tsrriennial conference EAPR* (pp. 28-29). Aalborg, Denmark: European Association for Potato.
- Shih, C. Y., & Rappaport, L. (1970). Regulation of bud rest in tubers of potato, *Solanum tuberosum* L. VII. Effect of abscisic acid and gibberellic acids on nucleic acid synthesis in excised buds. *Plant Physiology*, 45, 33-36.
- Smith, O. E., & Rappaport, L. (1961). Endogenous gibberellins in resting and sprouting potato tubers. *The Advances in Chemistry Series*, 28, 42-48.
- Sonnwald, U. (2001). Control of potato tuber sprouting. *Trends in Plant Science*, 6, 333-335.
- Struik, P. C., & Wiersema, S. G. (1999). *Seed potato technology* (p. 383). Wageningen, Netherlands: Wageningen Pers.
- Struik, P. C., Van der Putten, P. E. L., Caldiz, D. O., & Scholte, K. (2006). Response of stored potato seed tubers from contrasting cultivars to the accumulated day-degrees. *Crop Science*, 46, 10-17.
- Suttle, J. C. (1996). Dormancy in tuberous organs: Problems and perspectives. In: G. A. Lang (Ed.), *Plant dormancy: Physiology, biochemistry and molecular biology* (pp. 133-143). Oxon: CAB International.
- Suttle, J. C. (1998b). Post-harvest changes in endogenous cytokinins and cytokinin efficacy in potato tubers in relation to bud endodormancy. *Physiologia Plantarum*, 103, 59-69.
- Suttle, J. C. (2001). Dormancy-related changes in cytokinin efficacy and metabolism in potato tubers during postharvest storage. *Plant Growth Regulation*, 35, 199-206.
- Suttle, J. C. (2004a). Physiological regulation of potato tuber dormancy. *American Journal of Potato Research*, 81, 253-262.
- Suttle, J. C. (2004b). Involvement of endogenous gibberellins in potato tuber dormancy and early sprout growth: A critical assessment. *Journal of Plant Physiology*, 161, 157-164.
- Suttle, J. C. (2004c). Breaking tuber dormancy with synthetic cytokinins. *American Journal of Potato Research*, 82, 92.
- Suttle, J. C. (2005). *Hormone analogs as novel sprout - control agents*. CD ROM 2004 Potato Research Proceedings.
- Suttle, J. C. (2008). Effects of synthetic phenylurea and nitroguanidine cytokinins on dormancy break in Russet Burbank minitubers. *American Journal of Potato Research*, 85, 121-128.
- Suttle, J. C., & Banowitz, G. M. (2000). Changes in cis-zeatin and cis-zeatin riboside levels and biological activity during potato tuber dormancy. *Physiologia Plantarum*, 109, 68-74.
- Tekalign, T., & Hammes, P. S. (2005). *Response of potato to paclobutrazol*



- and manipulation of reproductive growth under tropical conditions (pp. 2-3) [PhD Thesis].
- Thompson, H. C., & Kelly, W. C. (1972). *Vegetable crops* (pp. 372-385). New Delhi: Tata McGraw Hill Publication Co. Ltd.
- Turnbull, C. G. N., & Hanke, D. E. (1985). The control of bud dormancy in potato tubers. Evidence for the primary role of cytokinins and a seasonal pattern of changing sensitivity to cytokinin. *Planta*, *165*, 359-365.
- Turnbull, C. G. N., & Hanke, D. E. (1985a). The control of bud dormancy in potato tubers: Measurement of the seasonal pattern of changing concentrations of zeatin-cytokinins. *Planta*, *165*, 366-376.
- Van den Berg, J. H., Ewing, E. E., Plaisted, R. L., McMurray, S., & Bonierbale, M. W. (1996). QTL analysis of potato tuber dormancy. *Theoretical and Applied Genetics*, *93*, 317-324.
- Van der Schoot, C. (1996). Dormancy and symplasmic networking at the shoot apical meristem. In: G. A. Lang (Ed.), *Plant dormancy: physiology, biochemistry and molecular biology* (pp. 59-79). Oxon: CAB International.
- van Ittersum, M. K., & Scholte, K. (1992). Shortening dormancy of seed potatoes by storage temperature regimes. *Potato Research*, *35*, 389-401.
- van Ittersum, M. K., & Scholte, K. (1993b). Shortening dormancy of seed potatoes by a haulm application of gibberellic acid and storage regimes. *American Journal of Potato Research*, *70*, 7-19.
- Van Staden, J., & Dimalla, G. G. (1977). The distribution of cytokinins in tuberizing potatoes. *Annals of Botany*, *41*, 741-746.
- Viola, R., Pelloux, J., Ploeg, A. D., Gillespie, T. V., Marquis, N., Roberts, A.G., & Hancock, R. D. (2007). Symplastic connection is required for but out growth following dormancy in potato (*Solanum tuberosum* L.) tubers. *Plant, Cell and Environment*, *30*, 973-983.
- Visser, R. G. F., Vreugdenhil, D., Hendriks, T., & Jacobsen, E. (1994). Gene expression and carbohydrate content during stolon to tuber transition in potatoes (*Solanum tuberosum* L.). *Physiologia Plantarum*, *90*, 285-292.
- Vivanco, J. M., & Flores, H. E. (2000). Control of root formation by plant growth regulators. In: A. S. Basra (Ed.), *Plant growth regulators in agriculture and horticulture: Their role and commercial uses* (pp. 1-16). New York: Food Products Press, Inc.
- Vreugdenhil, D. (2004). Comparing potato tuberization and sprouting: Opposite phenomena? *American Journal of Potato Research*, *81*, 275-280.
- Vreugdenhil, D. (2007). The canon of potato science. *Potato Research*, *50*, 371-373.
- Vreugdenhil, D., & Sergeeva, L. I. (1999). Gibberellins and tuberization in potato. *Potato Research*, *42*, 471-481.
- White, J. (1983). *Germination physiology of true potato seed: A manuscript* (p. 25). Lima, Peru: CIP.
- Wiltshire, J. J. J., & Cobb, A. H. (1996). A review of the physiology of potato tuber dormancy. *Annals of Applied Biology*, *129*, 553-569.
- Xu, X., Vreugdenhil, D., & Van Lammeren, A. A. M. (1998). Cell division and cell enlargement during potato tuber formation. *Journal of Experimental Botany*, *49*, 573-582.