Physiological Regulation of Potato Tuber Dormancy

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ABSTRACT

At harvest, potato (*Solanum tuberosum* L.) tubers are dormant and will not sprout. As the period of postharvest storage is extended, tuber dormancy is broken and sprout growth commences. The loss of tuber dormancy and onset of sprout growth is accompanied by numerous biochemical changes, many of which are detrimental to the nutritional and processing qualities of potatoes. Endogenous hormones have been proposed to play a significant role in tuber dormancy regulation. The involvement of all major classes of endogenous hormones in tuber dormancy is reviewed. Based on available evidence, it is concluded that both ABA and ethylene are required for dormancy induction, but only ABA is needed to maintain bud dormancy. An increase in cytokinin sensitivity and content appear to be the principal factors leading to the loss of dormancy. Changes in endogenous IAA and GA content appear to be more closely related to the regulation of subsequent sprout growth.

RESUMEN

Los tubérculos de papa (*Solanum tuberosum* L.), al momento de la cosecha se encuentran en estado latente y no tienen capacidad de germinación. A medida que transcurre el periodo de almacenamiento, se rompe la latencia y comienza el crecimiento del brote. La supresión de la latencia del tubérculo y el inicio del crecimiento del brote son acompañados por numerosos cambios bioquímicos, muchos de los cuales son perjudiciales para la calidad nutricional y el procesamiento de la papa. Se señala que las hormonas endógenas juegan un rol significativo en la regulación de la latencia. Se hace una revisión sobre la forma en que intervienen las principales clases de hormonas endógenas en la latencia del tubérculo. En base a la evidencia disponible se concluye que tanto el ABA como el etileno son requeridos para la inducción de la latencia, pero sólo el ABA es necesario para mantener la latencia de la yema. Un incremento en la sensibilidad a la citoquinina y su contenido, parecen ser los factores principales que conducen a la pérdida de la latencia. Los cambios en el contenido de IAA y AG parece que están más estrechamente relacionados a la regulación del crecimiento ulterior del brote.

INTRODUCTION

In 2001, worldwide production of potatoes exceeded 311.8 million MT (FAO est.). In the same year, U.S. production exceeded 438 million cwt (USDA-NASS 2002.). Roughly 70% of the fall potato crop is placed into medium-long-term storage to meet the demands of consumers and processors. Unlike other major food crops, the potato is stored in a fully hydrated highly perishable form. Annual postharvest losses in the U.S. typically amount to about 10%-15% of the harvested crop, but can be as high as 30%.

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ABBREVIATIONS: ABA, abscisic acid; BS, brassinosteroid; GA, gibberellin; IAA, indole-3-acetic acid; NAA, 1-naphthalene acetic acid

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Maintenance of postharvest market quality is of prime importance to producers and processors. Tuber deterioration during storage can result from both disease-related and physiological processes. Of the physiological processes affecting postharvest tuber quality, unregulated sprouting is one of the most important. Sprouting is accompanied by many physiological changes including increases in reducing sugar content, respiration, water loss, and glycoalkaloid content (Burton 1989). All of these changes are detrimental to processing quality. For these reasons, the majority of potatoes placed into medium-long-term storage are treated with synthetic sprout inhibitors. For seed growers, the situation is reversed. In this case, it would be desirable to rapidly break tuber dormancy to permit the sale and planting of fall-harvested potatoes in markets of the southern hemisphere. Regardless of the intended end-use, improvements in sprout control technologies are hampered by ignorance of the physiological bases of tuber dormancy.

In this review, the role of endogenous hormones as cognate regulators of tuber dormancy will be critically evaluated.

GENERAL DORMANCY CHARACTERISTICS

Botanically, the tuber is a highly compressed stem, and the eyes correspond to apical and lateral axillary buds. Tubers are vegetative over-wintering organs and like many other similar organs (seeds, corms, buds), exhibit varying degrees of dormancy (Okubo 2000). Examples of dormancy can be found at all levels of biological complexity. Dormant organs are typically more resistant to biotic and abiotic stresses. As such, dormancy is considered a survival mechanism. Potato tuber dormancy is thought to begin on or about the time of tuber initiation (Burton 1989). As would be expected from a developmental trait conferring a survival advantage, the inheritance pattern of tuber dormancy is complex, and QTL analyses have indicated that tuber dormancy is controlled by at least nine distinct loci (Van den Berg et al. 1996; see Ewing, this issue). Given the genetic complexity of dormancy control, it is likely that the physiological processes regulating dormancy progression are equally complex. Tuber dormancy can be affected by both preharvest and postharvest conditions. Between 3 and 25 C, the length of tuber dormancy is inversely proportional to storage temperatures (Burton 1989). In addition to environmental extremes, tuber dormancy can be prematurely terminated by a variety of chemical treatments whose mechanisms-of-action are currently unknown. Several of these agents (i.e., gibberellic acid, bromoethane) are used to stimulate sprout growth of seed potatoes (Coleman 1987; Allen et al. 1992).

CELLULAR BASES OF DORMANCY

Although dormancy is defined as the absence of visible growth, dormant meristems are metabolically active. In general, rates of many cellular processes such as respiration, transcription, and translation are suppressed during dormancy (Macdonald and Osborne 1988). The onset of sprout growth that follows dormancy termination is accompanied by substantial increases in cell metabolism. Recent studies have demonstrated that major changes in gene expression occur during dormancy progression (Bachem et al. 2000; Ronning et al. 2003). Although their relationship to dormancy is unclear, a number of transcripts and proteins unique to either dormant or growing meristems have been identified. As would be expected during a transition from quiescence to active growth, many of the transcripts and proteins associated with non-dormant meristems are related to basic cellular processes such as house-keeping functions.

Because dormancy is defined by the (near) absence of growth, changes in the expression and/or activities of proteins involved in cell growth are of particular importance. Nondividing, dormant tuber meristems are arrested in the G-1 phase of the cell cycle prior to DNA synthesis (MacDonald and Osborne 1988; Campbell et al. 1996). The amounts and activities of proteins and enzymes involved in cell cycle control and cell division are therefore of obvious interest. In model systems, progression through the cell cycle is regulated by the coordinate synthesis and action of a number of cyclin-dependent kinases and their downstream targets (Francis and Sorrell 2001). In these systems, release from a G-1 block is often associated with an increase in specific cyclin levels and an increase in the catalytic activities of certain cyclin-dependent kinases (den Boer and Murray 2000). Although evidence is lacking in potato tuber meristems, in *Helianthus tuberosus* L. (Jerusalem artichoke) tubers, loss of dormancy is accompanied by increases in cyclin D-type gene expression (Freeman et al. 2003). The role of post-translational modification of cell cycle proteins during dormancy is unknown and warrants investigation.

HORMONAL REGULATION OF TUBER DORMANCY: GENESIS OF THE THEORY

Early empirical studies demonstrated that free and esterified auxins inhibited sprout growth in non-dormant potatoes (Guthrie 1940). Bioassay techniques to determine endogenous contents of auxin-like compounds and growth-inhibiting substances had just been established and were being widely applied in plant developmental studies. Early studies by Hemberg (1942) indicated that the endogenous content of auxin was low during dormancy and increased as sprout growth commenced. In conducting these studies, plant materials were typically extracted with an organic solvent, fractionated into acidic and neutral materials, and subjected to paper chromatography with very simple solvent mixtures. Bioassays (using an *Avena* coleoptile test) would typically reveal zones of growth-promoting and -inhibiting substances (see Went and Thimann 1937). Hemberg (1949) was the first to recognize the importance of the growth inhibiting zones, and he demonstrated a reasonable correlation between dormancy and inhibitor content (Hemberg 1952). Later studies by others indicated that the endogenous contents of gibberellin-like and cytokinin-like activities also increased as dormancy ended and sprout growth commenced (Smith and Rappaport 1961; Engelbrecht and Bielińska-Czarnecka 1972).

Although technically imperfect, the logic and rationale of these pioneering studies is remarkable and worthy of consideration. What these investigators lacked in analytical capabilities was more than compensated for by sound reasoning. Nevertheless by today's standards, the results of these early studies were equivocal at best. Even under ideal conditions, bioassay data are notoriously difficult to interpret, the nature of the growth-promoting or -inhibiting substances are unknown, and complex plant extracts fractionated by paper chromatography are mixtures of many individual compounds often with opposing bioactivities. In the intervening years many advancements in chromatography and analytical techniques have permitted a more thorough evaluation of the roles of endogenous plant hormones in potato tuber dormancy. In the brief review that follows, current concepts on the hormonal regulation of tuber dormancy are summarized.

AUXINS AND TUBER DORMANCY

As the first class of endogenous plant hormones chemically characterized, the role of auxins in nearly all aspects of plant developmental regulation attracted early attention (see Went and Thimann 1937). Bioassay data indicated that endogenous levels of IAA were low in dormant tuber tissues and increased 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 auxin stimulated the growth of non-dormant sprouts, but had no discernable effects on dormant eyes (Hemberg 1949).

Subsequent studies using HPLC coupled with fluorometric detection essentially confirmed the earlier bioassay data that indicated no increase in free IAA content occurred until after the end of dormancy (Sukhova et al. 1993). In contrast, more recent studies using GC-MS with internal standards found that the content of free IAA in eyes increased prior to the onset of visible sprout growth (Sorce et al. 2000), prompting these authors to propose a role for IAA in dormancy control. To date, there has been no report demonstrating that exogenous IAA (or any other auxin) prematurely terminates tuber dormancy.

The data reported thus 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. This is in keeping with the proposal that auxins are essential cognate regulators of cell cycle progression in all plant tissues (Francis and Sorrell 2001). As such, threshold levels of IAA would be required for sprout growth, but would not be the initiators of this growth.

ABSCISIC ACID AND TUBER DORMANCY

Following fractionation by paper chromatography, bioassays of plant extracts typically revealed zones of growth promotion and growth inhibition. Hemberg (1949) was the first to recognize the potential importance of these inhibitors in dormancy regulation. In a series of studies, Hemberg and others demonstrated that (1) endogenous contents of acidic (but not neutral) growth inhibitors are highest in dormant tuber periderm extracts and decline during storage as dormancy weak-

ens; (2) treatments that prematurely terminate tuber dormancy also result in a rapid decline in endogenous inhibitor content; and (3) application of crude inhibitor preparations isolated from potato peelings transiently inhibited sprout growth (Blumenthal-Goldschmidt and Rappaport 1965; Franklin and Hemberg 1980; Hemberg 1985). The obviously heterogeneous nature of the inhibitory fractions isolated from plants complicated simple interpretation of these observations.

Subsequently, abscisic acid (ABA) was identified as a bioactive component of the crude inhibitor complex (Milborrow 1967). Exogenous ABA elicits a transient, dose-dependent inhibition of potato sprout growth (El-Antably et al. 1967). Endogenous levels of ABA were highest in extracts prepared from dormant tubers or periderm samples and declined during postharvest storage (Coleman and King 1984; Suttle 1995). However, no obvious threshold basal ABA content for dormancy maintenance could be established. A further complication to the interpretation of these data was introduced by Sorce et al. (1996) who reported that the ABA content in extracts prepared from tuber eyes actually increased as dormancy weakened and sprouting commenced.

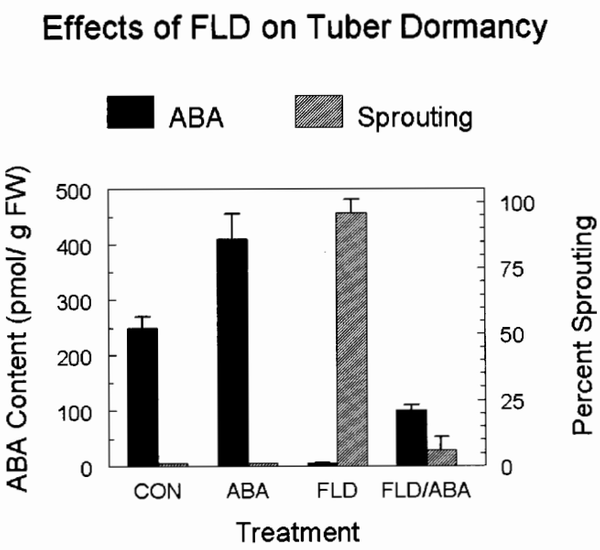

FIGURE 1.
Effects of fluridone on endogenous ABA content and dormancy status in microtubers in the absence and presence of 5μM (±)-ABA after 9 weeks of *in vitro* culture. Data adapted from Suttle and Hultstrand 1994.

The involvement of endogenous ABA in tuber dormancy was established using an in vitro microtuber system and the ABA biosynthesis inhibitor fluridone (Suttle and Hultstrand 1994). Treatment of developing microtubers with fluridone inhibited ABA accumulation by over 90% and resulted in premature sprouting of the developing microtubers (Figure 1). Application of ABA to fluridone-treated microtubers restored ABA levels to control values and completely suppressed precocious sprouting. Application of fluridone to fully dormant microtubers also resulted in a decline in ABA content and a concomitant increase in premature sprouting. Together, these results demonstrated that the sustained synthesis of ABA is required for both tuber dormancy induction and maintenance. The failure to identify a critical threshold ABA concentration below which sprouting initiates, suggests that the onset of sprouting during natural dormancy progression requires the synthesis and action of one or more growth-promoting substances (see below).

ETHYLENE AND TUBER DORMANCY

The effects of ethylene on potato tuber sprouting have been extensively studied, often with conflicting findings. An initial report (Rosa 1925) indicated that a 4-wk ethylene treatment hastened the sprouting of dormant tubers after the gas was removed. Subsequent studies failed to confirm this report (Denny 1926), whereas others indicated that ethylene responsiveness was cultivar-dependent (Alam et al. 1994). The situation was partially resolved by Rylski et al. (1974) who demonstrated that short-term ethylene treatment can prematurely terminate tuber dormancy while continuous treatment results in sprout growth inhibition. Similarly, treatment with ethylene-releasing agents has been reported to either hasten or delay sprouting (Cvikrova et al. 1994). Recent 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).

The role(s) of endogenous ethylene in tuber dormancy/sprout growth has received little attention. As in other storage organs, potato tubers produce only limited quantities of ethylene (Creech et al. 1973; Rylski et al. 1974; Suttle 2003). Ethylene production from field-grown tubers is highest immediately after harvest and declines to low levels thereafter (Cvikrova et

al. 1994). Since tubers are dormant at harvest, it is unclear whether this transient production elevation is related to tuber dormancy or the stress of harvest. Despite the low rates of production, endogenous ethylene plays a critical role in tuber dormancy. Following subculture under tuberizing conditions, ethylene production by single-node explants was transiently elevated with the highest rates of production observed immediately after transfer (Suttle 1998a). Continuous treatment with inhibitors of ethylene action resulted in premature sprouting of the developing microtubers. Exogenous ethylene reversed this response and restored microtuber dormancy. Inhibitor effectiveness was short-lived and treatments initiated 7 or more days after subculture had no effect on microtuber dormancy. These results suggest that endogenous ethylene is essential for the full expression of microtuber dormancy and that its involvement is restricted to the very earliest phase of dormancy induction. Ethylene and ABA are known to interact both synergistically and antagonistically in a number of developmental processes (de Bruxelles and Roberts 2001). The nature and extent of interactions between these two dormancy promoting substances in tubers remains to be characterized.

The rate of ethylene production increases as tubers exit dormancy and begin to sprout (Poapst et al. 1968; Okazawa 1974; Suttle 2003). The physiological significance of this increase is unclear at present. As ethylene has been found to hasten dormancy exit under certain conditions (see above), this increase may suggest a role for endogenous ethylene in dormancy termination or could be related to other events associated with early sprout growth. Future studies should clarify this issue.

GIBBERELLINS AND TUBER DORMANCY

As first reported by Brian et al. (1955) and subsequently confirmed by others (Rappaport et al. 1958; see Hemberg 1985), tuber dormancy could be broken with exogenous gibberellins (GAs). In fact, GAs (typically GA_3) are often used in seed certification programs where rapid replanting of seed tubers is required for pathogen testing. Bioassays demonstrated the presence of GA-like activities in tuber extracts and indicated that endogenous levels of certain GAs increased as sprout growth commenced (Smith and Rappaport 1961; Boo 1962; Bialek and Bielińska-Czarnecka 1975). At present, well over 100 GAs have been identified in seed plants (Heddon and Kamiya 1997). This molecular diversity, together with the usual concerns over bioassay data, renders interpretation of these data difficult.

In all species of *Solanaceae* examined to date, the predominant GAs present are members of the "early 13-hydroxyla-

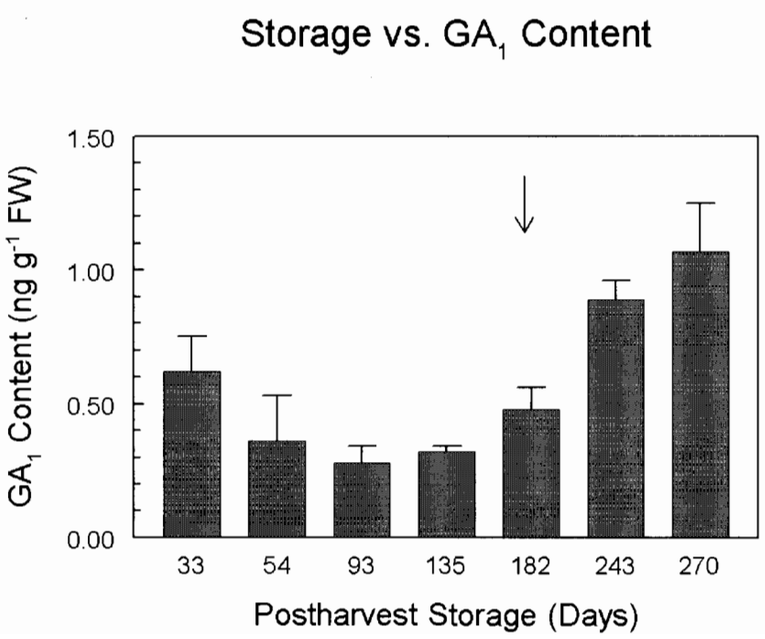

FIGURE 2.
Effects of postharvest storage on the endogenous content of GA_1 in potato tuber periderm/apical bud samples. Downward arrow indicates the end of dormancy. Data adapted from Suttle 2004.

tion" series, with GA_1 being the principal bioactive GA (Jones et al. 1988; Van den Berg et al. 1995; Carrera et al. 2000). Ectopic expression of the gene coding for the GA biosynthetic enzyme GA_{20}-oxidase resulted in elevated tuber GA content and premature sprouting (Carrera et al. 2000). In the same study, however, expression of antisense copies of this gene reduced GA levels and resulted in dwarfism, but had no demonstrable effect on tuber dormancy duration. In many respects, this situation mirrors that of the flowering response of many long-day rosette plants where exogenous GA application or the ectopic expression of GA biosynthetic genes often results in premature bolting leading to flowering, yet endogenous GAs are not the endogenous flower-inducing stimulus (Zeevaart 1976).

In a recent study (Suttle 2004), detailed determination of the endogenous contents of GA_{19}, GA_{20}, and GA_1 using GC-MS-SIM with internal standards demonstrated that the endogenous content of these GAs in tubers exiting dormancy was essentially the same as that of deeply dormant tubers (Figure 2). Increases in endogenous GA content became evident only after sprout growth commenced. Furthermore, comparison of GA_1 content and dormancy in tubers of a wild-type and dwarf mutant of *S. tuberosum* ssp. *andigena* revealed a near-identical pattern of dormancy progression despite the absence of detectable levels of GA_1 in the dwarf sibling at any stage of dormancy. Subsequent sprout growth in dwarf tubers was severely reduced relative to that in the wild-type tubers, consistent with the known role of GA to promote shoot growth in most seed plants. Collectively, these 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.

CYTOKININS AND TUBER DORMANCY

Cytokinins are defined by their ability to stimulate cell division in hormone-depleted plant tissues by releasing a G-1 cell cycle block (Francis and Sorrell 2001). Given that growth inhibition in dormant tuber meristems is a result of the arrest of bud meristem cells in the G-1 phase of the cell cycle (Campbell et al. 1996), cytokinins are likely candidates for endogenous dormancy-terminating hormones. Hemberg (1970) demonstrated that both natural and synthetic cytokinins can break tuber dormancy. Similarly, tubers formed on potato plants that have been transformed with a cytokinin biosynthesis gene from *Agrobacterium tumefaciens* displayed a number of morphological abnormalities including sporadic precocious sprouting (Ooms and Lenton 1985). Early bioassay data suggested that increases in endogenous cytokinins accompanied dormancy break (van Staden and Brown 1979; Koda 1982; Banas et al. 1984). Endogenous cytokinins in seed plants are chemically diverse and readily interconvertible. As such, deriving useful information about cytokinin content from bioassays is difficult. Much more rigorous fractionation and detection methodologies are required to discern meaningful physiologically relevant relationships.

More recent studies using immunological techniques have confirmed these bioassay data, and an increase in total immuno-reactive cytokinins was detected in tubers exiting dormancy under both growth-permissive and -inhibiting temperatures (Sukhova et al. 1993; Turnbull and Hanke 1985b). These data were consistent with a role for endogenous cytokinins as cognate dormancy-terminating agents. However, the significance of these data is somewhat compromised by the fact that the cytokinins were measured in unfractionated extracts using polyclonal antibodies that recognized both active and inactive cytokinin metabolites. These issues were subsequently addressed in a study that determined the endogenous levels of eight individual cytokinins in tuber-apical bud/periderm extracts using side-chain specific monoclonal antibodies (Suttle 1998b). In this study, an increase in bioactive cytokinins was found to precede the onset of sprouting in tubers stored under growth-permissive conditions and in tubers held at 3 C (Figure 3). These results demonstrated that the increase in bioactive cytokinins was not a result of bud growth, but more likely was a cause of the re-initiation of meristematic activity. In addition to cytokinins of the *trans*-zeatin family, potatoes contain *cis*-zeatin derivatives that exhibit biological activity in a number of bioassays (Mauk and Langille 1978). Exogenous *cis*-zeatin was as effective as *trans*-zeatin in breaking tuber dormancy and endogenous levels of free *cis*-zeatin, but not its riboside, increased prior to the onset of sprout growth (Suttle and Banowetz 2000). Metabolic studies using [^{14}C]-*cis*-zeatin demonstrated only limited (ca. 10%) conversion of *cis*- to *trans*-zeatin in these tubers suggesting that *cis*-zeatin is also a potential regulator of tuber dormancy.

In addition to an increase in cytokinin content, dormancy progression is characterized by an increased sensitivity to cytokinins. Immediately after harvest and during early postharvest storage, tubers were insensitive to exogenous cytokinins

(Turnbull and Hanke 1985a; Suttle 2002). Thereafter, dormant tubers exhibited a time-dependent increase in cytokinin sensitivity. The increase in cytokinin sensitivity was not accompanied by changes in cytokinin metabolism, which suggested that elements of the cytokinin perception and/or signal transduction pathway were affected by dormancy status (Suttle 2002). These results suggest that endogenous cytokinins are natural dormancy-terminating agents in potato tubers.

OTHER GROWTH FACTORS AND TUBER DORMANCY

Phenolic compounds are a diverse class of natural products many of which exhibit growth-inhibiting activity in various bioassay systems. Potato periderm is a rich source of phenolics, and the original extracts assayed by Hemberg for inhibitory activity in his pioneering studies on dormancy control contained several phenolic acids (Holst 1971). More recent studies have demonstrated that the loss of tuber dormancy is accompanied by a reduction in phenolic acid content and an increase in phenolic conjugate levels (Cvikrová et al. 1994). Although these results are suggestive of a role for phenolic compounds in tuber dormancy regulation, they are, by no means, proof of such a relationship.

The onset of dormancy is considered to occur at the time of tuber initiation (Burton 1989). Tuberization is a photoperiodically sensitive developmental process that is stimulated under short days by leaf-derived factors (Ewing 1995). Current evidence suggests that one of these leaf factors is a jasmonic acid derivative given the trivial name tuberonic acid (Yoshihara et al. 1989). The question arises as to the role of jasmonates in tuber dormancy inception and control. Although endogenous contents of jasmonic acid have been measured in developing tubers and elongating sprouts (Abdala et al. 2000), the role of jasmonates in tuber dormancy has not been determined.

Brassinosteroids (BS) are an enigmatic class of endogenous plant growth substances and were originally isolated from rapeseed pollen as growth-promoting substances (see Clouse and Sasse 1998 for review). Since the original isolation, BS have been identified in over 21 families of seed plants and are most likely ubiquitous throughout the plant kingdom. Depending on the assay system, BS elicit a wide range of biological activities including both growth promotion and inhibition. Postharvest application of 2,4-epibrassinolide was reported to prolong tuber dormancy and increase ABA content and ethylene production (Korableva et al. 2002). The effects of dormancy status on BS content and activities have not been reported and, as such, the role of this interesting class of regulators in tuber dormancy remains speculative.

Potato tubers produce a number of volatile compounds, some of which contribute to the flavor and aroma of potato products. In addition to sensory value, several of these volatiles are potent growth inhibitors. Burton and Meigh (1971) first demonstrated that several sprout-inhibiting compounds accumulated in potato storage atmospheres. Subse-

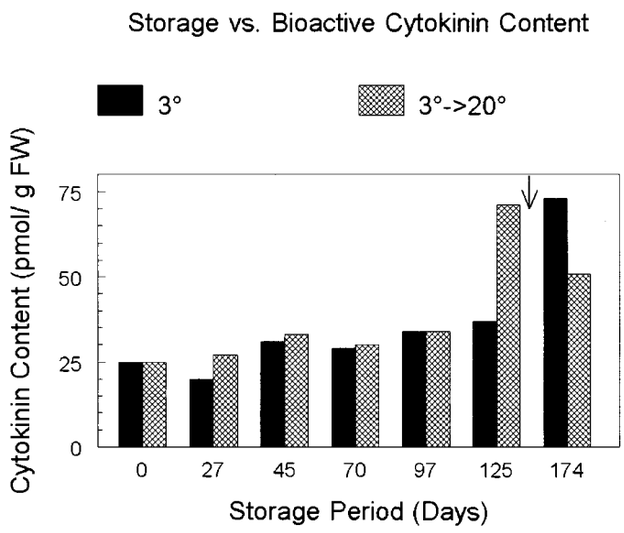

FIGURE 3.
Effects of postharvest storage on the endogenous contents of bioactive cytokinins. Tubers were either stored continuously at 3 C or were shifted from 3 C to 20 C seven days prior to analysis. Downward arrow indicates the ending of dormancy. Data adapted from Suttle 1998b.

quent studies identified several bioactive volatiles including the 1,4- and 1,6- isomers of dimethyl-naphthalene (Meigh et al. 1973). Application of these dimethyl-naphthalene derivatives results in a transient inhibition of sprout growth, and a commercial product containing these isomers has been marketed for postharvest sprout control (Lewis et al. 1997; Prange et al. 1997). Whether these compounds participate in tuber dormancy control or merely reinforce dormancy-imposed growth inhibition is unknown. Thus despite claims to the contrary, the actual role of these as cognate dormancy regulating substances remains unproven.

GENERAL SUMMARY

The current status of knowledge regarding the hormonal regulation of tuber dormancy is graphically summarized in Figure 4. Moving from left to right, as tubers are placed into storage they are highly dormant, dormancy weakens as storage continues, and ultimately the tubers exit dormancy and sprouting begins. Both ABA and ethylene are required for the initiation of tuber dormancy, but only ABA is needed to maintain the dormant state. Endogenous cytokinin levels are relatively low in highly dormant tubers and tubers are non-responsive to exogenous cytokinins. During dormancy, tubers actively metabolize both ABA and cytokinins to inactive products. As dormancy weakens, tuber ABA levels decline and tubers become increasingly sensitive to exogenous cytokinins. An increase in endogenous cytokinins slightly precedes or coincides with dormancy exit and the onset of sprout growth. Sprout growth is accompanied by increases in both endogenous IAA and GA. Thus although tuber dormancy progression and sprout growth require the concerted synthesis and action of many hormones, ABA and cytokinins appear to be the principal dormancy regulating hormones.

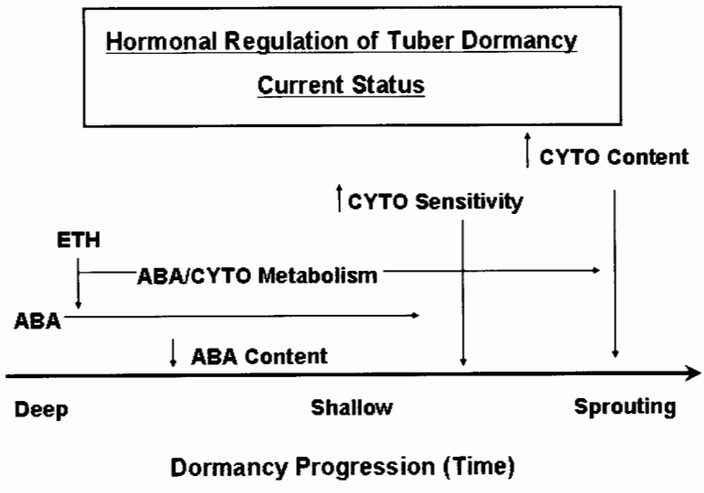

FIGURE 4.
Schematic overview of the roles of endogenous hormones in tuber dormancy progression. See text for complete explanation.

THE ROAD AHEAD

From the foregoing, it is clear that substantial progress has been made in the identification of endogenous regulators of tuber dormancy. However, the progress to date is only a starting point and much needs to be learned about the complex systems operative in tuber dormancy control.

In many respects plant hormone biology is still in its infancy and new endogenous regulators continue to be recognized. No doubt, some of these will be found to play a role in tuber dormancy regulation. Having identified some of the characters in this cast, the next task is to identify the biochemical processes regulating the biosynthesis and activity of these hormones. Some progress in this area has been made. The metabolic fate of cytokinins in tubers during dormancy progression has been studied and two potential metabolic control systems identified (Suttle 2002). Studies are underway in this laboratory to determine the effects of dormancy status on the expression of genes coding for proteins involved in ABA biosynthesis and cytokinin action.

With the exception of the GA-deficient dwarf mutants, physiologically defined genetic mutants to date have not been extensively used in tuber dormancy studies. The powerful tools of forward and reverse genetics also have not been employed to any great degree in tuber dormancy research. Together with more classical approaches, these newer techniques will be instrumental in assembling a coherent picture of the natural mechanisms of tuber dormancy control.

Once identified, these dormancy control processes can be exploited to develop improved

postharvest storage sprout-control technologies. The older empirical methods of sprout control chemistry R & D will be replaced with bio-rationale approaches that have been so successfully used by the pharmaceutical industry. Ultimately all segments of the potato industry from producers to consumers will benefit from this new knowledge.

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