Phases of Dormancy in Yam Tubers (Dioscorea rotundata)

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• Background and Aims The control of dormancy in yam (Dioscorea spp.) tubers is poorly understood and attempts to shorten the long dormant period (i.e. cause tubers to sprout or germinate much earlier) have been unsuccessful. The aim of this study was to identify and define the phases of dormancy in Dioscorea rotundata tubers, and to produce a framework within which dormancy can be more effectively studied.

• Methods Plants of 'TDr 131' derived from tissue culture were grown in a glasshouse simulating temperature and photoperiod at Ibadan (7°N), Nigeria to produce tubers. Tubers were sampled on four occasions: 30 d before shoot senescence (149 days after planting, DAP), at shoot senescence (179 DAP), and twice during storage at a constant 25°C (269 and 326 DAP). The development of the apical shoot bud was described from tissue sections. In addition, the responsiveness of shoot apical bud development to plant growth regulators (gibberellic acid, 2-chloroethanol and thiourea) applied to excised tuber sections was also examined 6 and 12 d after treatment.

• Key Results and Conclusions Three phases of tuber dormancy are proposed: Phase I, from tuber initiation to the appearance of the tuber germinating meristem; Phase II, from the tuber germinating meristem to initiation of foliar primordium; and Phase III, from foliar primordium to appearance of the shoot bud on the surface of the tuber. Phase I is the longest phase (approx. 220 d in 'TDr 131'), is not affected by PGRs and is proposed to be an endo-dormant phase. Phases II and III are shorter (<70 d in total), are influenced by PGRs and environmental conditions, and are therefore endo-eco-dormant phases. To manipulate dormancy to allow off-season planting and more than one generation per year requires that the duration of Phase I is shortened.

Key words: Dioscorea rotundata, yam, dormancy, phases of dormancy, plant growth regulator, primary thickening meristem, tuber germinating meristem, shoot apical meristem.

INTRODUCTION

Yams belong to the monocotyledonous family Dioscoreaceae and genus Dioscorea. They are grown for their tubers or storage organs, which may be subterranean (e.g. D. rotundata, D. alata) or aerial (e.g. D. bulbilfera), and serve a dual agricultural function as source of food and planting material (Coursey, 1967; Hahn, 1995). Yam tubers exhibit dormancy, which prevents precocious sprouting (germination), prolongs storability and maintains food quality. Yams are grown in regions on three continents: West Africa, South America and Asia (Coursey, 1967; Alexander and Coursey, 1969; Ayensu and Coursey, 1972). In West Africa yams are a major source of nourishment to millions of people, as well as being a crop of prestige and cultural importance (Coursey, 1967; Martin and Sadik, 1977). The most important species in West Africa are white yam (D. rotundata) and water yam (D. alata).

Yams are grown as annuals with tubers being planted between February (in the humid forest) and April (in the Guinea savanna) in West Africa. Harvesting is sometimes done 180 d after planting (DAP), i.e. in August in the humid forest agroecological zone, but mostly when the shoot senescence is about 180 to 270 d later in the Guinea savanna and humid forest, respectively (i.e. October and November, respectively). Harvested tubers remain dormant (i.e. incapable of developing an internal shoot bud or external shoot bud/sprout) for 30 to 150 d depending on date of harvest, species, and growing and storage environmental conditions (Passam, 1982; Orkwor and Ekanayake, 1998). Thus, only one crop cycle is possible per year, restricting supply (Olayide et al., 1972) and the rate of progress of crop improvement. Breaking or shortening dormancy in yam is a priority for yam breeders (Asiedu et al., 1998) but the control of dormancy is not well understood (Passam, 1982; Suttle, 1996).

Dormant yam tubers, uniquely and in contrast to potatoes (Solanum tuberosum), do not have any internal or external apical shoot buds or sprouts. Instead, dormant yam tubers (as observed after harvest/during storage) have a layer of meristematic cells below the surface of the tuber (Onwueme, 1973; Mathurin and Degras, 1978; Wickham et al., 1981). Onwueme (1973) and Wickham et al. (1981) have shown in D. rotundata and D. alata that at the resumption of active growth, shoot apical bud formation begins in this meristematic cell layer, long before any external shoot bud/sprout is visible on the tuber surface. The anatomical changes in the meristem that lead to shoot bud or sprout formation are described later.

There have been a number of studies of the effects of exogenous plant growth regulators (PGRs) on dormancy in yams (summarized in Passam, 1982; Degras, 1993; Craufurd et al., 2001; Ile, 2004) and potato (Suttle, 1996). Changes in concentration of endogenous PGRs during dormancy (i.e. after tuber harvest) and through its...
release (sprouting), have also been studied (Coleman and King, 1984; Ireland and Passam, 1985; Park et al., 2001). Most of the studies with PGRs have applied them to leaves shortly before harvest or to whole tubers at harvest or during storage. The most consistent effects have been observed with gibberellin, chloroethanol and thiourea (Passam, 1982; Degras, 1993; Craufurd et al., 2001). These studies have shown that PGRs can both shorten (chloroethanol, thiourea) and prolong (gibberellin) the duration of dormancy. However, their effects have been both inconsistent—the timing of application has not been related to any anatomical or physiological state of the tuber (Barker et al., 1999; Craufurd et al., 2001; Ile, 2004)—and small, ranging from 7 to 48 d and thus of little practical benefit (Craufurd et al., 2001; Ile, 2004). Hence in the absence of information on the anatomical or physiological state of dormancy, it is hard to draw any conclusion on the endogenous control of dormancy and develop protocols that can effectively shorten dormancy. We hypothesized that yam tubers are only receptive to PGRs (and other external stimuli) when tubers approach their natural sprouting time, i.e. PGRs cannot break dormancy, only hasten (or delay) the rate of shoot apical development.

Suttle (1996) has suggested that the earliest indication of the release of bud dormancy is a good point to start studies into the control of the release of dormancy. In potato, the first signs of the release of bud dormancy are manifested at the cellular level (i.e. mitosis preceding cell division and elongation) and these are evident long before bud growth is visible. Indeed, in potato the application of 2-chloroethanol resulted in cell division and elongation within 72 h of application (Rappaport and Wolf, 1969; Rylski et al., 1974), suggesting a possible technique to study dormancy in yam.

The objective of this paper was to identify and define the phases of dormancy in D. rotundata tubers and to produce a framework within which dormancy can be more effectively studied. To achieve this, changes in tuber anatomy during tuber growth (i.e. before harvest) and storage were examined and clear stages defined. PGRs (gibberellin, 2-chloroethanol, thiourea) were also applied to excised tuber portions during tuber growth and storage to examine whether PGRs had any short-term (6 to 12 d) effect on anatomical development and whether this varied with stage of development.

MATERIALS AND METHODS

Plantlet propagation

The yam variety Dioscorea rotundata Poir. ‘abi’ (‘TDr 131’) was chosen for this study because of its long tuber dormancy. Field experiments showed that tubers of this variety begin to sprout by late February to early March when harvested by November to December of the previous year. Plantlets were derived from shoot apical meristem cultures of D. rotundata ‘TDr 131’ as described by Ng (1984). This activity was carried out at the International Institute of Tropical Agriculture, (IITA), Ibadan, Nigeria. The plantlets were air-freighted to the UK where they were multiplied at the Plant Sciences Laboratories, The University of Reading, UK, by regular sub-culturing in yam regeneration medium (Ng, 1984).

Production of tubers and growing conditions in the glasshouse

Following sub-culturing, yam plantlets were transplanted into 25-cm diameter pots and grown in a temperature- and photoperiod-controlled glasshouse at the Plant Environment Laboratory, The University of Reading. There were three plantlets per pot. Each pot contained a mixture of sand, gravel, vermiculite and loam-less compost in a ratio of 4 : 2 : 4 : 1 (v/v), as well as 3 g L⁻¹ Osmocote Plus fertilizer. Osmocote Plus is a slow-release (90–120 d) fertilizer containing 15N + 11P₂O₅ + 13K₂O + 2MgO (Monro Horticulture, Goodwood, West Sussex, UK). Transplanting was done on 1 May, 2001 and plants grew under ambient conditions for 20 d. From 21 May 2001, plants were grown under a constant 32/22 °C day/night temperature regime. Photoperiod was changed every 7 d to simulate a June planting date at Ibadan, Nigeria. This meant that these received inductive, shortening day lengths during tuber formation. Plants were trained on canes to expose the leaves of the twining stem to solar radiation for efficient photosynthesis (Orkwor and Asadu, 1998). Pots were watered regularly as required until 15 October 2001 (169 days after planting, DAP). Thereafter, watering was stopped to allow vines to senescence and the tubers to mature (i.e. for the epidermis to darken in colour and thicken by way of suberization) before harvesting was done.

Harvest dates and post-harvest storage

Tubers were harvested twice; 30 tubers on 26 September 2001 (149 DAP) when the vine was still green, and 180 tubers on 25 October 2001 (179 DAP) as the vine began to senesce. A total of 210 clean tubers were then stored in a Saxcil growth cabinet. Two sets of 30 of tubers (representing tubers harvested at either 149 or 179 DAP) were stored for observation of sprouting date while a set of 150 tubers was stored for PGR treatment and anatomical studies. The growth cabinet was maintained at 28 °C, 80 % relative humidity. These conditions are favourable for sprouting (Mozie, 1984). White fluorescent tubes that provided a photon flux density of 0·017 mmol m⁻² s⁻¹ were used to provide illumination and photoperiod was maintained at 12 h.

Preparation of tubers for application of PGR treatments

At each treatment date, 30 tubers were randomly selected from those in storage. They were washed and allowed to stand in running water for about 10 min after which they were surface sterilized for 10 min in 5 % sodium-hypochloritate solution. Tubers were allowed to dry under a lamina flow hood and all subsequent activities were conducted aseptically.
TABLE 1. Plant growth regulator (PGR) treatments, concentration of aqueous solution used and duration of soaking of tubers

<table>
<thead>
<tr>
<th>PGR treatment</th>
<th>Concentration</th>
<th>Duration (mins)</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Deionized water</td>
<td>120</td>
<td>Control (H2O)</td>
</tr>
<tr>
<td>Gibberellic acid</td>
<td>150 mg L⁻¹</td>
<td>120</td>
<td>150 GA1</td>
</tr>
<tr>
<td>Gibberellic acid</td>
<td>1000 mg L⁻¹</td>
<td>120</td>
<td>1000 GA1</td>
</tr>
<tr>
<td>2-chloroethanol</td>
<td>40 mL L⁻¹</td>
<td>5</td>
<td>40 CLE</td>
</tr>
<tr>
<td>2-chloroethanol</td>
<td>60 mL L⁻¹</td>
<td>5</td>
<td>60 CLE</td>
</tr>
<tr>
<td>Thiourea</td>
<td>20 g L⁻¹</td>
<td>60</td>
<td>Thiourea</td>
</tr>
</tbody>
</table>

For treatment in PGR solutions, only the head or proximal region (region closest to the point of attachment of the tuber to the stem/vine) was used. This was done to minimize experimental error since different tuber regions are known to sprout at different rates (Passam et al., 1978). The head region of each tuber was split longitudinally into two halves. Each half was again split longitudinally into three parts, to give a total of six longitudinal portions per tuber head region. Portions were then randomly assigned to one of six PGR treatments. Treatments were chosen based on evidence from the reviews of Craufurd et al. (2001) and Ile (2004) that ethylene-producing PGRs (2-chloroethanol [CLE] and thiourea) and GA3 are the PGRs with the most consistent effects on whole-tuber dormancy. Treatments were applied by soaking the tuber portions in aqueous solution of the various PGRs (Table 1) containing seven drops of the surfactant Tween 20. This procedure resulted in minimal damage to the tuber tissues during treatment. After treatment, cut surfaces were treated against fungi by lightly dipping in a suspension of benomyl and allowed to dry. Treated tuber portions were then placed on a double layer of sterile filter paper on moistened sterile paper towel (to maintain humidity) in a transparent plastic storage box, and the box covers replaced. Boxes were then wrapped with foil paper to create uniform dark storage conditions.

Preparation of treated tuber portions for anatomical investigations

At 6 and 12 d after treatment, 15 tuber portions per treatment were randomly sampled. The healed surfaces of sampled tuber portions were removed and tuber portions of dimensions 1.0 × 0.5 × 0.5 cm (length × breadth × depth) were quickly taken. To limit variability, the length measurements were started from the tip of the head region. These portions were then fixed for 48 h in 3 mL Kew cocktail solution (http://www.plantsci.rdg.ac.uk/coshh.htm) to halt active cellular activities, then embedded in Paraplast wax. Prior to embedding, the portions were first dehydrated by transferring them sequentially through a series of increasing concentrations of ethanol (70 to 100 % absolute ethanol), then 100 % ethanol: histoclear (1 : 1), pure histoclear (each for 12 h); histoclear: Paraplast (1 : 1) solution for 24 h, molten Paraplast (melting point 60 °C) for 48 h, and finally embedded in freshly molten Paraplast.

To section and stain sections, nine embedded tuber portions per treatment were picked randomly. Twelve consecutive longitudinal sections of 18 μm thickness per tuber portion were cut on a disposable-blade rotary microtome (Bright-5030) at an angle of 5°. Sections were collected on slides, three sections per slide, and allowed to settle and dry for 48 h. Sections were then de-waxed in histoclear, hydrated gradually in decreasing concentrations of ethanol (from 100 to 30 %) and stained in Aalcian blue and Safranine in 50 % ethanol. Sections originating from the same tuber (tuber head region), irrespective of treatments, were stained at the same time to reduce experimental error during the staining procedure. After staining, sections were dehydrated in increasing concentrations of ethanol and then in histoclear before being mounted for observation.

Thus at each treatment date a total of 108 tissue sections per treatment were observed under a Reichert-Jung microscope (Bright-5030) at an angle of 5°. Sections of the tuber meristematic region. Stages observed for were: (1) development of a mass of cells; (2) formation of the tuber germinating meristem; and (3) formation of shoot apical meristem and foliar primordium. Light photomicrographs were taken on a Reichert Polyvar 2, Leitz Wetzlar D68232 light microscope attached to a Yashica 108 camera and a Reichert Trimag 654602 camera exposure control.

Experimental design and data analysis

The experiment was a 6 × 4 factorial experiment, analysed as a randomized complete-block design with three replicates. The factors were six PGR treatments and four treatment times (149, 179, 269 and 326 DAP). Treatment times were chosen based on the following: at 149 (30 d before senescence) and 179 DAP (senescence) tubers were expected to be dormant (no active meristem); at 269 DAP (in January) active cell division was expected to begin (but well before the appearance of sprouting loci, which may be occur in late February, about 300 DAP); and at 326 DAP when control tubers started sprouting. Following PGR treatment, sampling was done twice, at 6 and 12 d after treatment for observation of stages of the sprouting process.

The SAS GENMOD procedure logit link function was used to determine the effects of treatments and individual tubers on the development of the tuber germinating meristem and shoot apical meristem. This analysis treats stages of development as absent (0) or present (1) and estimates the probability of the occurrence of the stage of development. The ‘Odds Ratio Statistic’ (Collet, 2003) was used to estimate the chance of the presence of a tuber germinating meristem in a PGR treatment relative to that in the control. This statistic could not be calculated for a shoot apical meristem as no shoot apical meristem was observed in control tubers. A ratio of 1 implied equality, while <1 and >1 implied that the treatment had less and more chance, respectively, to reveal the presence of the observed response compared to the control.
RESULTS AND DISCUSSION

Date of sprouting

The first tubers among those stored only for visual observation of date of sprouting started sprouting 326 DAP. The average duration from harvest at vine senescence (179 DAP) to 50% sprouting was 160 d and tubers sprouted on 10 April 2002, i.e. at 339 DAP. Tubers harvested 30 d prior to vine senescence (149 DAP) sprouted 187 d later, on 7 April 2002, i.e. 336 DAP. Therefore, date of harvest had no effect on the date of 50% sprouting of these whole, untreated tubers.

Yam tubers are assumed to be dormant at or shortly before maturity, an ill-defined event characterized by senescence of the shoot rather than the physiological status of the tuber. Studies by Okoli (1980) and Swannell et al. (2003) clearly show that tubers are dormant well before shoot senescence, possibly very soon after initiation when tubers are growing. Burton’s (Burton et al., 1992) suggestion that the dormant period in potato should be considered from tuber initiation to tuber sprouting is therefore also applicable to yam.

Organogenesis of yam shoot apical bud

Based on observations from this study and supported mainly by the works of Onwueme (1973) and Wickham et al. (1981) this section describes stages in shoot bud formation. The stages observed in this study are similar to those reported earlier. However, this work differs from earlier work in that it reports the anatomy of growing tubers (i.e. prior to senescence). Also, it is the first study systematically designed to relate anatomical events leading to shoot bud formation to tuber age. It also relates the effects of PGRs on these events to duration of dormancy.

Figures 1–6 show the organogenesis of the shoot apical bud. The anatomy of tubers harvested at 149 DAP was the same as those harvested at 179 DAP. At 149 and 179 DAP, four major tissue regions were identified (Fig. 1): (1) the protective region: characterized by the presence of an outer layer of primary suberized cells and an inner layer of radially arranged suberized cork cells; (2) the cortex: which is beneath the protective region and containing parenchyma cells; (3) the meristematic region: 2–4 layers of small, flattened and stretched-out undifferentiated cells that lie beneath the cortex; and (4) the storage parenchyma: filled with starch grains and scattered vascular tissues. At these dates (i.e. up to harvest at 179 DAP), there is no sign of any active meristematic activity leading to apical shoot bud formation. Similar structures have been reported in tubers of many Dioscorea spp. (observed at harvest at vine senescence and during storage) and such tubers are said to be dormant (Onwueme, 1973; Mathurin and Degras, 1978; Wickham et al., 1981). Thus the anatomy of tubers harvested at 149 and 179 DAP clearly indicates that growing tubers are already dormant.

The first sign of shoot apical bud development, visible 6 d after treatment at 269 DAP, was active cell division.
and differentiation in the meristematic cell layer. This led to the formation of a localized mass of cells, called the primary thickening meristem (Wickham et al., 1981). These cells were small, either irregular or oblong in shape and arranged in a horizontal array. The primary thickening meristem in turn gave rise to the tuber germinating meristem (Fig. 2), which was distinguished from the primary thickening meristem by the particularly widespread nature of cell activity in the meristematic layer and the change in the shape of the cells from horizontal to a more vertical array. The tuber germinating meristem is typically 10–40 cell layers thick depending on the level of development and the area with the most activity.

The resumption of active cell division in the region of the meristem is known to mark the start of shoot bud genesis (Onwueme, 1973), and such activity is known to be preceded by the formation of the tuber-root, seen on the tuber surface as thin, short-lived roots (Wickham et al., 1981; Wilson et al., 1998). The tuber-roots observed in this study were similar to those reported by Wickham et al. (1981), being developed due to localized cell activity in the meristematic region (Fig. 3). However, since tuber-roots were seen to form in all treatments from 149 DAP (i.e. 30 d before vine senescence), it is suggested here that the development of tuber-roots does not necessarily herald the development of a shoot bud. Although the function of tuber-roots is still not known, the high humidity under which the current experiments were conducted may have supported their production, as observed by Wickham et al. (1981).

A developing (shoot) apical meristem formed as cells at the apex of the tuber germinating meristem organized (Fig. 4). This activity marked the progression into advanced stages of apical shoot bud formation, with the shoot apical meristem developing tangential to the tuber germinating meristem (Fig. 5). Foliar primordia were initiated from the peripheral cells of the shoot apical meristem and complete apical shoot buds were thereby formed (Fig. 6). These later stages all occurred after 269 DAP.

**Effect of PGRs on shoot apical development**

No PGR had any effect on shoot meristematic activity in tuber sections treated at 149 or 179 DAP. There was no evidence of any thickening of the meristematic cell layer to form a primary thickening meristem or tuber germinating meristem in any of the 54 sections examined at either 6 or 12 d after treatment with PGRs. The first tuber germinating meristem in the control tubers was observed at 269 DAP, but only in one replicate. In the same replicate (tuber), a more advanced tuber germinating meristem was observed following treatment with 60 CLÉ. No other PGR treatment had any effect at 269 DAP.

At the last treatment date (326 DAP), when a tuber germinating meristem was present in most control tubers, PGRs had a significant effect on shoot apical bud development. Six days after treatment, tissue sections from 54 sampled tuber portions showed that the probability of the presence of a tuber germinating meristem was
Tuber germinating meristem

<table>
<thead>
<tr>
<th>PGR treatment</th>
<th>Tuber germinating meristem</th>
<th>Shoot apical meristem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.89 ± 0.19</td>
<td>0.00† ± 0.00</td>
</tr>
<tr>
<td>150 GA₃</td>
<td>0.78 ± 0.30</td>
<td>0.88 ± 0.11</td>
</tr>
<tr>
<td>1000 GA₃</td>
<td>0.44 ± 0.53</td>
<td>0.50 ± 0.22</td>
</tr>
<tr>
<td>40 CLE</td>
<td>1.00 ± 0.40*</td>
<td>1.13 ± 0.67</td>
</tr>
<tr>
<td>60 CLE</td>
<td>0.89 ± 0.19</td>
<td>1.00 ± 0.67</td>
</tr>
<tr>
<td>Thiourea</td>
<td>0.80 ± 0.28</td>
<td>0.90 ± 0.33</td>
</tr>
</tbody>
</table>

* In 40 CLE, all sections had a tuber germinating meristem.
† In the control no section had a tuber germinating meristem.

Phases of dormancy in D. rotundata

On the basis of results reported here, and those of Wickham et al. (1981) and Onwueme (1973) in particular, we propose three phases of dormancy in white yam (Fig. 7).

Phase I: Tuber initiation to appearance of tuber germinating meristem. Tubers harvested at 149 DAP, 30 d before vine senescence and harvest, were clearly dormant, having the same anatomical structure as well as sprouting at the same time as those harvested at 179 DAP. As discussed previously, there is good evidence that dormancy starts much earlier than this (Okoli, 1980; Nwoke and Okonkwo, 1981; Swannell et al., 2003). We therefore consider that Phase I of dormancy should be defined as commencing from tuber initiation, as suggested by Burton et al. (1992) for potato.

Renewed active cell division and differentiation in the meristematic layer to form a tuber germinating meristem marks the first easily visible anatomical sign of shoot apical bud development. Most tubers sampled at 269 DAP, as well as those harvested at 149 and 179 DAP, did not have a tuber germinating meristem and were therefore dormant. Although the appearance of a tuber germinating meristem was preceded by that of a primary thickening meristem, it was not always easy to discriminate between the mass of cells that led to a root meristem rather than a shoot meristem, so the former marker (tuber germinating meristem) is preferred.

Therefore, Phase I of dormancy (Fig. 7) can be defined as that period during which no active meristematic activity (tuber germinating meristem) was observed and PGRs were unable to trigger tuber germinating meristem formation. This phase appears to correspond to deep factors.
dormancy or endo-dormancy as defined by Lang et al. (1987). In ‘TDr 131’, the average duration of this phase was at least 200 d, and typically 220 d (Fig. 7).

**Phase II: tuber germinating meristem to foliar primordium.** Phase II of dormancy starts with the appearance of the tuber germinating meristem (Fig. 7) and its duration in ‘TDr 131’ was about 35 d. Cooler temperatures and/or low relative humidity can extend this period by >20 d. PGRs did not induce the formation of a tuber germinating meristem, but they did influence tuber germinating meristem development (number of cell layers) and the rate/progression of shoot apical development. In *D. alata* protein and RNA contents have been shown to increase during this period (Jayakumar et al., 1993). This indicates a significant change in the status of dormancy; perhaps from one of endo-dormancy to one of endo-/eco-dormancy where factors such as endogenous and exogenous PGRs, air temperature and relative humidity can affect apical shoot bud development and hence the duration of this phase. This phase ends with the appearance of the foliar primordium.

**Phase III: Foliar primordium to sprouting.** Phase III of dormancy (see Fig. 7) is that period from the development of the complete shoot apical bud/foliar primodium to its eventual emergence on the tuber surface (as an external shoot bud or sprout). The duration of Phase III in ‘TDr 131’ was about 10 d, which is in agreement with the suggestion by Onwueme (1973) that sprouting occurs about 7 d after shoot bud formation. The duration of this phase, like Phase II, is influenced by temperature and relative humidity, and PGRs, notably GA.

**Conclusions**

We propose that there are three phases of dormancy in *D. rotundata* yams: Phase I (tuber initiation to tuber germinating meristem formation), Phase II (tuber germinating meristem to foliar primordium) and Phase III (foliar primordium to the appearance of shoot buds at the surface/sprouting loci). Phase I, which is the longest phase, is not influenced by external factors and is proposed to be an endo-dormant phase. Phases II and III are endo-/eco-dormant phases influenced by exogenous PGRs and environmental conditions. To manipulate dormancy to allow off-season planting and more than one generation per year requires that the duration of Phase I is shortened.

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**LITERATURE CITED**


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