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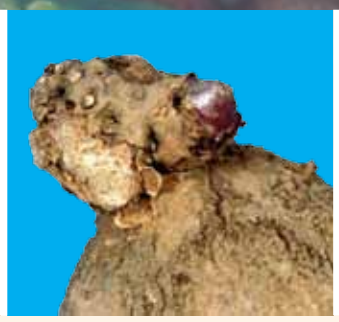
a framework for manipulation

Elsie I. Hamadina

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ISBN 978-978-50368-2-4

Correct citation: Elsie I. Hamadina. 2011. The control of yam tuber dormancy: a framework for manipulation. IITA, Ibadan, Nigeria. 60 pp.

Printed in Nigeria by IITA

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Preface

Yam (*Dioscorea* spp.) are monocotyledonous plants belonging to the family Dioscoreaceae and genus *Dioscorea*. Over 600 species are identified but only six are important in Africa, Southeast Asia, and South America. The economically important species are *D. rotundata, D. alata, D. cayenensis, D. bulbifera, D. dumetorum,* and *D. esculenta* (Hahn 1995).

Yam produce edible subterranean or aerial tubers that form the organ of economic importance. The tuber is important chiefly as a staple food, providing nourishment to people in the tropics and subtropics. It is particularly rich in carbohydrate, containing 50–80% starch/ dry weight. Other constituents of high nutritional values are vitamins C and B6, potassium, iron, manganese, and amino acids; contents of sodium and saturated fats are low. More than the daily adult requirement of vitamin C can be obtained from yam (even after losses from cooking have been subtracted) (Bell 1983). Also, the combination of high potassium and low sodium makes yam potentially important in protecting people against osteoporosis and heart-related diseases. Worldwide, as many as 5 million ha of land are put to yam cultivation and about 49 million t of the crop are produced with 94% of this value being grown in West and Central Africa (FAO 2005). In West Africa, consumption/capita/day ranges from 258 kcal (in Nigeria) to 364 kcal (in Bénin). Indeed, yam is so important that it has a place in festive occasions, rites, and taboos of the people. Agriculturally, the tuber is important as it is the source of planting material.

Cultivation is mainly by vegetative propagation using the whole tuber or pieces of it (setts). Planting is done between late January and April in West Africa coinciding with the start of the rains, although early plantings in November–December are known (see Annex A). Irrespective of when planting is done, vine emergence occurs about the month of February and beyond,. Tubers are initiated from 30 days after vine emergence and these are formed underground in most species including *D. rotundata*. However, some species, such as *D. alata,* produce aerial tubers. Flowering occurs 40 to 90 days after vine emergence (Ile et al. 2006) depending on the planting date. In yam, therefore, growth is determinate but tuber development commences during early growth.

Tubers become mature for harvest as early as 6 months after vine emergence, corresponding to about the month of August (see Annex A). Early harvested tubers have a very high moisture content and so are prone to deterioration from diseases. Also, they have a bland taste after being cooked.The main harvesting season falls between the months of November and January of the following year, coinciding with the onset of shoot senescence and the start of the dry season (see Annex A). These tubers are larger, morphologically more mature, have a higher dry matter content and lower moisture, a lower susceptibility to deterioration, and better cooking and nutritive qualities than those from an early harvest. After harvest and during storage, sprouting begins. Sprouting tends

to occur at a definite period of the year, coinciding with the onset of the rains. Hence, the duration to sprouting varies from 30 to 150 days, depending on harvest date, species, and storage conditions.Tubers harvested early in the season spend a longer time in storage before sprouting occurs. Though the onset of sprouting is welcomed by the farmer who desires to commence planting, it marks the start of physiologically and pathologically induced deterioration and eventually the loss of food quality. The period during which yam tubers will not grow, even if put under ideal conditions for growth, is referred to as the dormant period and such tubers are said to be dormant.

With an ever rapidly increasing population in the tropics and the attendant reduction in farmland, the demand for yam tubers is always higher than the supply, causing scarcity, particularly during the planting/growing season. Consequently, the price of tubers for food is often exorbitant and beyond the purchasing power of the masses. Furthermore, a high price of tubers leads to a high cost of planting material, which in turn leads to a high cost of production. Planting material alone accounts for half the cost of tuber production. This situation hinders production/productivity as poor farmers, who constitute the bulk of yam producers, can afford to cultivate only small pieces of land. The challenge for researchers is to come up with techniques that can increase the production and availability of healthy yam tubers as a source of food, particularly during the off-season, and of planting material without necessarily increasing crop land area. Research in crop physiology can contribute to achieving this goal.

The development of technologies that temporarily separate the dual function of the tuber, while improving agronomic methods of production, would increase the availability of yam for food and reduce the cost of purchasing tubers for planting or seed tubers (those put aside only for planting). In line with this view, efforts have been made to increase the availability of planting material. These include the traditional “double harvesting” technique and the development of the “miniset technology”. The minisett technology involves the setting aside of healthy tubers right after harvest to be cut into small portions (setts) of about 30–100 g for use during the planting season. The technology can help to improve the availability of planting material by increasing the tuber: planting material ratio from 1: 1–2 to about 1: 20–30 (Okoli et al. 1982; Asiedu et al. 1998). This technology, however, is poorly adopted by most farmers, and the few who accept it soon abandon it because of their inability to continue to retain healthy tubers for use as planting material when there is a high demand for the tubers for food and income (ANB-BIA 2003). Also, the technique is unattractive to farmers because the minisetts produce mini-tubers (50–200 g whole tubers) that can be used as seed tubers for ware tuber production only in the next season. The technique is also not attractive to breeders who wish to increase the pace of yam improvement because mini-tubers also express long dormancy. Thus, in spite of the potentials of these techniques, tubers are still scarce during the planting season, the cost of planting material is still high, and these facts together still constitute a major drawback to yam production (IITA 2004).

This book shows that the primary key to increased tuber productivity and all-year-round availability of seed tubers rests in success at preventing the initiation of dormancy and/or the ability to drastically break the long dormant period in whole tubers (and cause instantly the appearance of a sprout on the surface of the tuber). Shortening dormancy or preventing it would achieve the following:

- Encourage two or more planting and harvesting times/year.
- Increase the ability to manipulate planting time. The current inability to manipulate dormancy has meant that experiments requiring planting have to wait until the onset of natural sprouting. Also, the control of sprouting by artificial means would synchronize sprouting times among tubers of the same variety, which is at the moment highly variable. The timing of sprouting and the timing of vine emergence are important variables determining the uniformity of growth stages in growth analysis.
- Reduce the loss of important genotypes to pests and diseases during the compulsory storage period. The storage of seed yam would be avoided, the availability of tubers for planting material would be improved, and consequently tuber production would be increased (IITA 1995, 1997).
- Increase the pace at which desired hybrids are bred and released. More than one generation/year would be attained in conventional yam breeding programs.

In addition, this book is different from other books on yam for the following reasons.

1. It brings together information that highlight the presence of confusing definitions of dormancy and some terms associated with the timing of the start, duration, and end of dormancy. It shows the influence of such confusion on the breeders' persistent inability to drastically shorten seed tuber dormancy and redefines some of these terms.
2. It also provides some explanation for the minimal success achieved in the past at breaking whole tuber dormancy. To ensure a clear understanding of the content and facilitate follow-up studies, this material provides a glossary of terms and presents in some detail the experimental procedure and results of recent studies conducted by Ile (2004).
3. It ensures that the identified gaps in our understanding of the mechanism of control of yam dormancy are bridged by providing a potential technique for preventing tuber dormancy and a framework (based on the effects of plant growth regulators [PGRs] on dormancy) for effectively studying dormancy in yam.

This book would therefore be suitable for scientists,yam breeders, physiologists, and undergraduate/graduate students of agriculture and botany and related fields.

Acknowledgments

I wish to thank the Research Endowment Trust Fund of the University of Reading, UK, for their support and for funding the research work being published. I also thank IITA, Ibadan, Nigeria, for the training it provided to me before and throughout the fellowship with the University of Reading. Dr Peter Q. Craufurd and Prof. Nick H. Battey (University of Reading) gave me their immeasurable professional support during the course of this work and Dr M. Quin (IITA) encouraged its publication.

Many thanks are due to Dr R. Asiedu (IITA) for his earlier invaluable support and for reading the manuscript and providing important comments. I am also indebted to Rose Umelo (editor, IITA) for her work. In addition, I wish to thank Mrs Karina Lawal, Mr Christian Okonkwo, and other members of the staff of the Yam Breeding Program, IITA, for their assistance and friendly cooperation. Finally, I thank all the members of my family for their encouragement.

Acronyms and abbreviations

ABA	abscisic acid
ASB	appearance of shoot bud
AU	absorbance unit
CCC	2-chloroethyl-trimethylammonium chloride
CLE	2-chloroethanol
DAE	days after emergence
DAM	developing apical meristem
DAP	days after planting
DOY	day of year
EPGRs	endogenous plant growth regulators
FLU	Fluridon
FP	foliar primodium
FPP	farnesyl diphosphate
GA	Gibberellic acid
GS	Guinea savanna agroecology
HF	humid forest agroecology
HPLC	high performance liquid chromatography
PAR	photosynthetically active radiation
PDS	phytoene desaturase
PGRs	Plant growth regulators
PNC	primary nodal complex
PPO	protoporphyrinogen oxidase
PTM	primary thickening meristem
RH	relative humidity
SAM	shoot apical meristem
TGM	tuber geminating meristem
TS	Moist savanna/transition agroecology

Description of the yam tuber, definitions of dormancy, and implications of poorly defined terms on the understanding of yam tuber dormancy

This section describes the morphology of ware yam tubers, the definitions of dormancy in relation to yam, the anatomy of dormant tubers, the series of anatomical events that take place prior to the start of sprouting, and the morphology of sprouting tubers. This section also looks at the confusing definitions of terms associated with yam dormancy, *e.g*., tuber-head, primary nodal complex (PNC), and the consequences of such confusing definitions on the outcome of studies conducted to manipulate tuber dormancy in the past. The descriptions are based primarily on the work of Ile (2004) supported by other relevant published works (where necessary).

Morphology of intact ware yam tuber and agricultural importance of the tuber-head

Yam tubers are mostly almost cylindrical in shape with a brownish periderm and a firm, white flesh which consists of large ovoid and highly hydrated starch grains. They have no buds or “eyes” on the main body, no terminal buds on the proximal part of the tuber, no scale leaves on the tuber surface, and no root cap (Fig. 1).

The tuber can be divided into three regions: head, middle, and tail, based on their physiological and biochemical differences (i.e*.,* respiration, nutrient content, enzyme

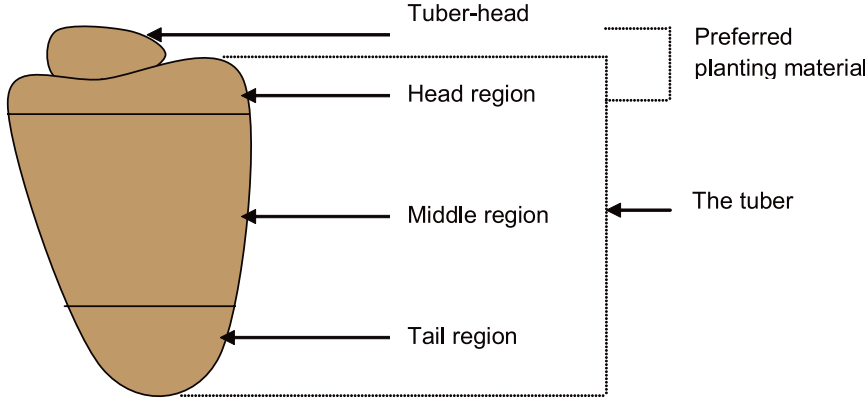


Figure 1. Schematic representation of dormant intact yam tuber.

present/activity) during and at the release of dormancy. Attached to the head region is a corm-like structure (Okonkwo 1985, Degras 1993), also called the tuber-head (Wilson et al. 1998), and tubers that have their tuber-head attached are referred to as intact tubers. In some literature the tuber-head is also referred to as the degenerate rhizome (Burkill 1960), the sympodial rootstock, the tuberous hypocotyl, and the tubercle (Sharma 1974, 1976, 1980, Okonkwo 1985).

An intact tuber is harvested by severing senescent vine(s) from the tuber-head (when harvesting is performed at the end of the growing season). Some tubers are devoid of tuber-heads as these have been detached in the course of harvesting; such tubers are referred to as headless tubers. Traditionally, the head region plus some part of the tuber-head is retained for use as planting material during the next planting season while the rest of the tuber is reserved for food. The head region, with or without the tuber-head or pieces of it, is always preferred because sprouting/germination occurs readily from the more proximal region. This phenomenon is termed proximal dominance (Onwueme 1984).

Definitions of dormancy

Generally, dormancy is defined in one of the following ways:

- a programmed inability to grow, i.e.,
  – absence of a visible growth process in plant structures possessing a meristem, e.g., apical and lateral shoot buds, root apices, embryos, and cambia,
- a state of rest
  – when metabolic activities are low, e.g., respiration, enzyme activity, starch and sugar metabolism, quantity/presence of endogenous growth inhibiting substances, etc.,
- according to its regulating mechanism(s)
  – endo-dormancy; controlled by factor(s) within the specific organ
  – para-dormancy; controlled by factor(s) external to the organ but within the plant, and
  – eco-dormancy; controlled by factor(s) external to the plant (the external environment).

Yam tuber dormancy, like dormancy in other tuber structures, can be defined in all of the ways above except for the absence of bud growth/ bud rest and para-dormancy. Bud dormancy ideally relates to the expression of the state of dormancy or the absence of growth in dormant shoot buds, e.g., bud dormancy in potato tubers, or lateral bud dormancy in some plant stems. Consequently, this definition does not adequately represent true tuber dormancy in yam because the tuber is devoid of buds during dormancy. Note, however, that this definition can be useful in defining dormancy that is induced after sprout emergence, such as when sprout growth is inhibited by temperature. Yam do not appear to exhibit para-dormancy. This is because dormant postharvest tubers

are already detached from their vines. During growth also, there are no plant factors known to exclusively cause dormancy in developing tubers.

The definition of yam tuber dormancy by its control mechanism is one aspect that has received little attention. Unfortunately, it is as crucial to the magnitude of success attainable in the manipulation of dormancy length as is the need to understand the mechanism(s) controlling the start and end of dormancy. Ile (2004) hypothesized that there are various phases of dormancy and that their control mechanisms vary. Results of extensive experimentation (field and laboratory studies) that verify the hypothesis are discussed in the relevant section. Prior to the work of Ile (2004), the duration of dormancy, which varied depending on the perceived start and end of dormancy, is simply considered to be under strong endogenous and/or environmental influences, suggesting that all the different developmental stages within any one definition of a dormant period are controlled by the same mechanism(s).

Anatomical structure of dormant yam tubers

Four major tissue regions are identifiable in dormant tubers (Fig. 2). These are (i) the protective region characterized by the presence of an outer layer of cork cells and an inner layer of radially arranged cork cells. The inner cork cells are associated with a cambial layer in *D. alata* and in mature tubers the outer cork cells are suberized, (ii) the cortex which is beneath the protective region contains cortical parenchyma cells, some tannin cells and idioblast cells, which contain raphide in *D. alata,* (iii) the meristematic region (mr) is 2–4 layers of small, flattened, and stretched out undifferentiated cells which lie beneath the cortex. In some species such as *D. alata*, there is no clear meristematic layer; rather there is an inner cortex made up of small differentiating cells (about five cells thick) and some idioblasts, which are found adjacent to the sclerenchyma band, and (iv) the storage parenchyma filled with starch grains and scattered vascular tissues.

The anatomy of dormant tubers of other *Dioscorea* spp. has been reported for mature tubers that were harvested at or after vine senescence or during storage and observed until sprouting (Onwueme 1973; Mathurin 1977; Mathurin and Degras 1978;and Wickham et al. 1981). Although the reports were based on observations covering a small proportion of the entire dormant period, they are similar to the anatomy of the dormant *D. rotundata* tuber.

Anatomical events leading to sprouting and the development of the PNC

The first signs of active cell division and differentiation occur in the meristematic region. This activity can lead to the formation of a localized mass of cells, called the primary thickening meristem (PTM) (Wickham et al. 1981) or the tuber germinating meristem

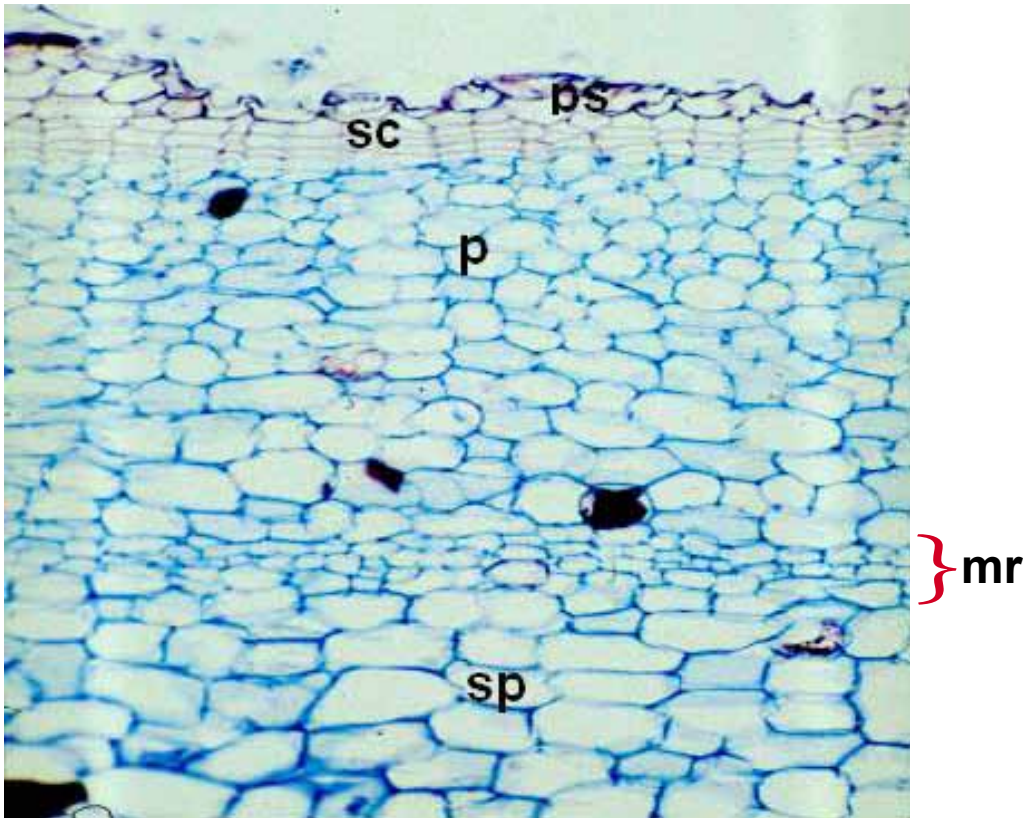


Figure 2. Longitudinal section of the head region of dormant *D. rotundata* tuber. Section taken from tubers at 179 DAP. Abbreviations: ic = inner cork cells; oc = outer cork cells; p = cortical parenchyma; mr = meristematic region; sp = storage parenchyma. Magnified 28X. Source: Ile (2004).

(TGM). The cells of the PTM are small, either irregular or oblong in shape, and arranged in a horizontal array. It is, however, unclear how the site for renewed growth is determined.

The TGM (Fig. 3), which is distinguished from the PTM by the particularly widespread nature of cell activity in the meristematic layer and the change in the shape of the cells from a horizontal to a more vertical array, is the first event leading to the formation of the shoot bud. The TGM is typically 10 to 40 cell layers thick, depending on the level of development and the area with the most activity (Wickham 1981).

A developing apical (shoot) meristem (DAM) is seen as an organized group of cells at the apex of the TGM (Fig. 4). This event marks the progression into advanced stages of apical shoot bud formation, with the shoot apical meristem (SAM) developing tangentially to the TGM (Fig. 5). Foliar primordia (FP) are initiated from the peripheral cells of the SAM marking the development of complete apical shoot buds (Fig. 6). So far, all of these events occur within the tuber with no external indications.

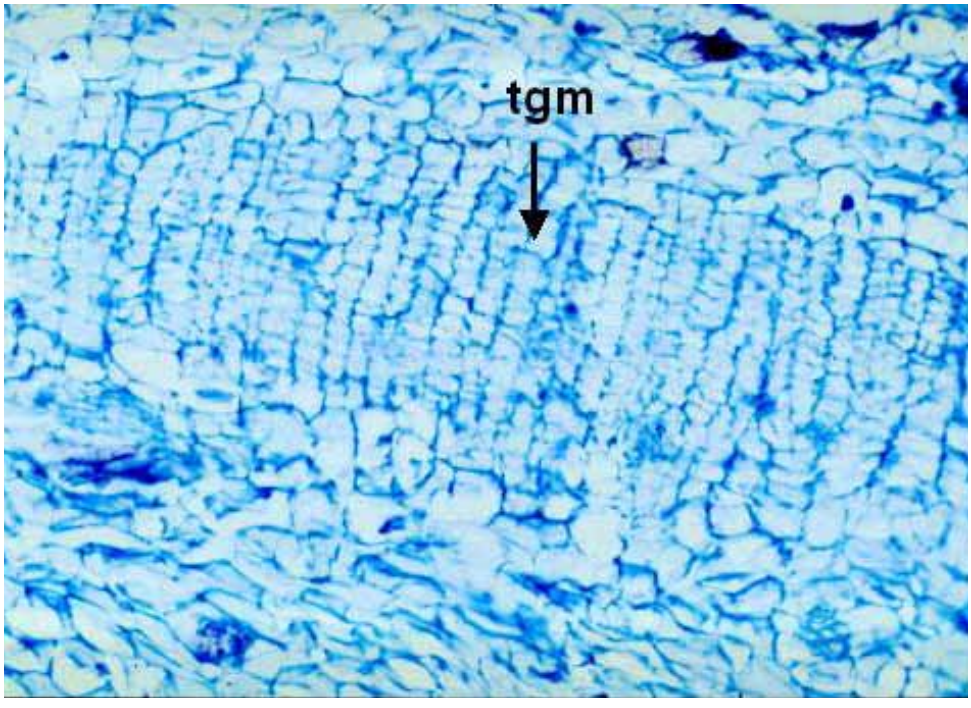


Figure 3. The tuber-germinating meristem (TGM) as revealed on longitudinal sections of the yam tuber-head region. Magnified 28X. Source: Ile (2004).

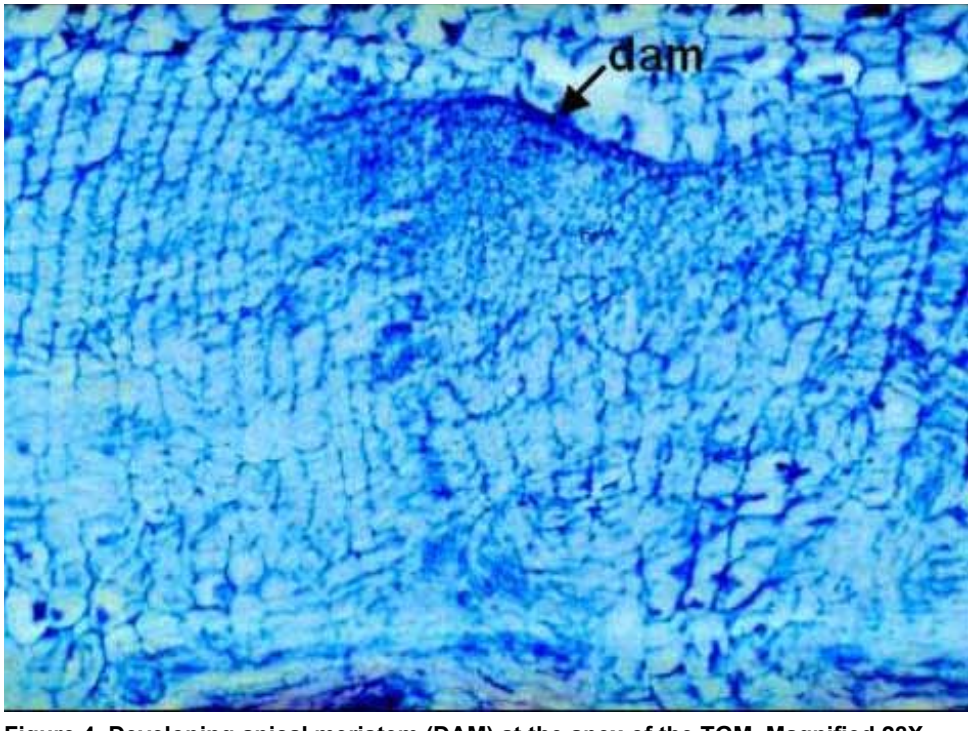


Figure 4. Developing apical meristem (DAM) at the apex of the TGM. Magnified 28X. Source: Ile (2004).

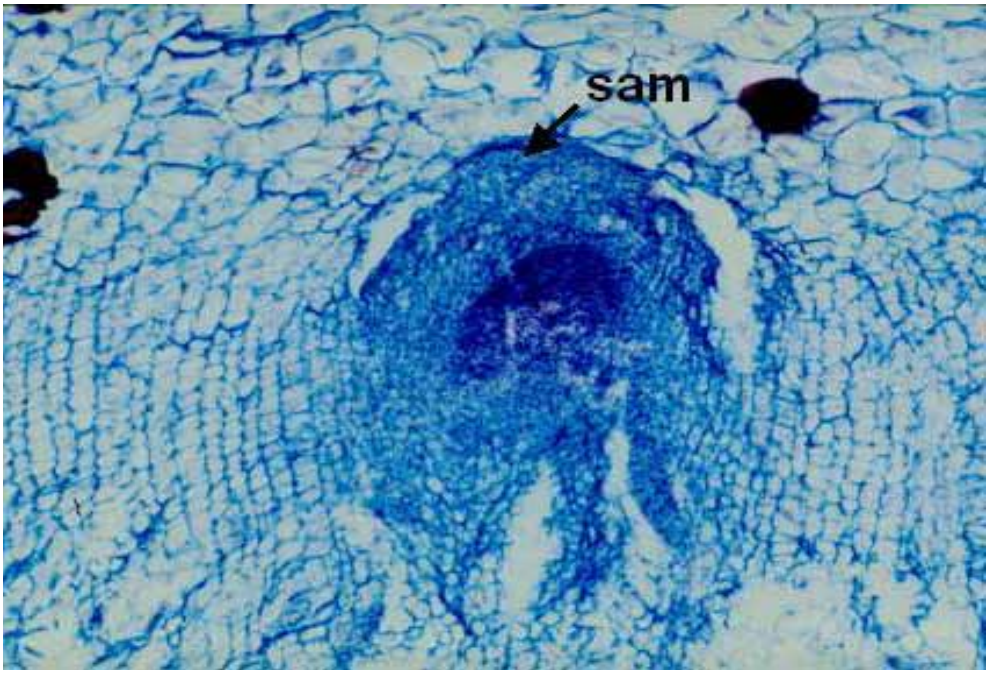


Figure 5. Formation of the shoot apical meristem (SAM) in *D. rotundata*. Magnified 28X.
Source: Ile (2004).

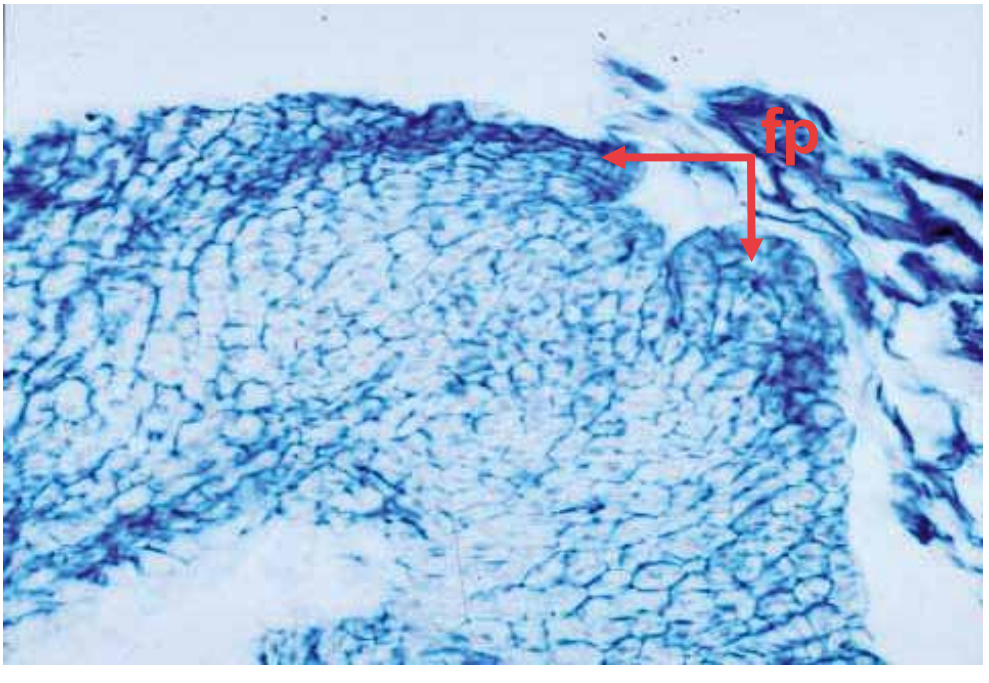


Figure 6. Development of foliar primordium (FP) in *D. rotundata*. Magnified 28X.
Source: Ile (2004).

Figure 7. External stages of the sprouting process: appearance of the sprouting locus on the tuber-head of an intact *D. rotundata* tuber. Source: Ile (2004).

Figure 8. External stages of the sprouting process: emergence of the shoot bud, through the sprouting locus, on to the surface of the tuber. Source: Ile (2004).

Further development of the complete shoot bud leads to the appearance of the shoot bud on the surface of the tuber. The complete shoot bud develops a calyptra which protects it as it grows outwards through the tuber cortex and dense cork layers to the surface. This growth causes a bulge on the surface of the tuber which eventually cracks open, slightly exposing the internal shoot bud as a whitish tissue. The exposed portion of the tuber is referred to as the sprouting locus (Fig. 7). Although the presence of the sprouting locus is the first external visible mark of the release of dormancy, the locus is sometimes too small to be recognized and thus is often unnoticed. Eventually, the internal shoot bud emerges/appears on the surface of the tuber, and is then referred to as an external shoot bud or sprout (Fig. 8). This event is termed sprouting. Although there are other variants of the definition of sprouting, the definition here is the most common first visible mark of the end/release of dormancy and the start of vegetative growth. The events from active meristematic activity which lead to TGM formation to sprouting are collectively referred to as the yam sprouting process.

The PNC is formed by the vascularization of the PNC meristem (Fig. 9), which is formed due to activity in the region of the first node of the calyptra and the TGM (Wickham et al 1981). The PNC is recognized externally by the thickening of the base of the sprout/external shoot bud (Wickham et al. 1981). Hence, the PNC will not be recognized at the microscopic level if observations are not made well after FP formation. It is for this reason that the studies of Onwueme (1973) and Ile (2004) did not observe the internal formation of the PNC. However, the manifestation of the

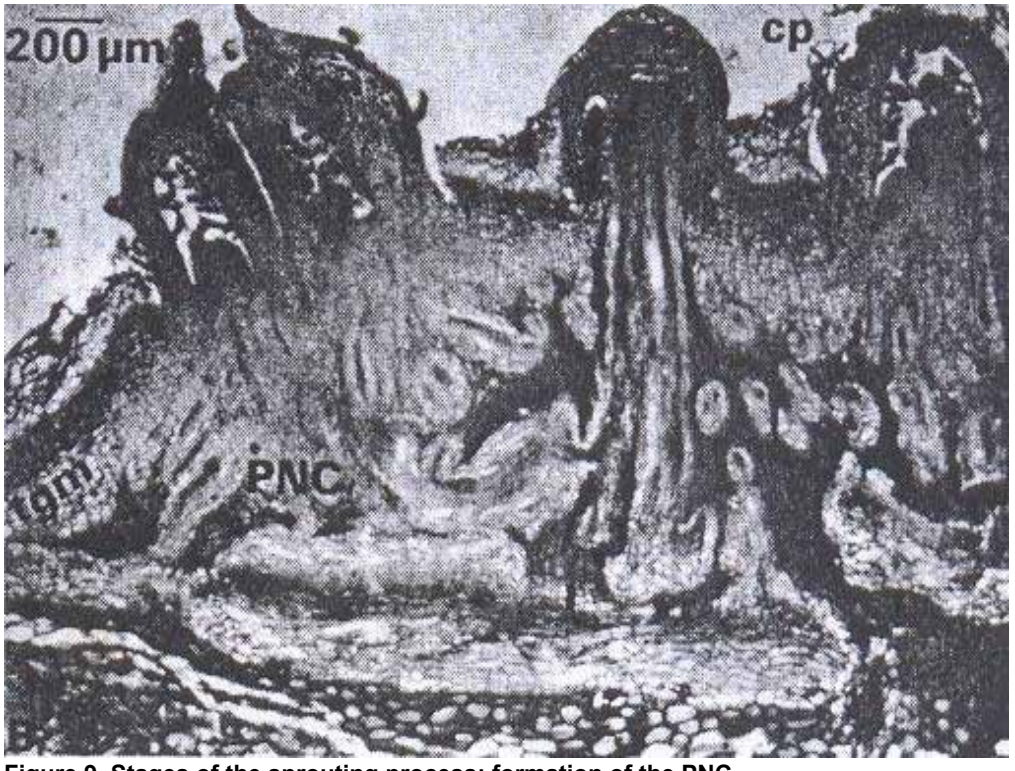


Figure 9. Stages of the sprouting process: formation of the PNC.
Source: Wickham et al. (1981).

development of the PNC (Fig. 10) was recognized externally in the study of intact whole *D. rotundata* tubers by Ile (2004).

The PNC functions as an organ that gives rise to the yam vine/stem and feeder roots (Fig. 11). It was first identified during seedling germination (Ferguson 1972; 1973) and has subsequently been recognized during the sprouting of headless tubers (Onwueme 1973; Wickham et al. 1981) and intact tubers (Ile et al. 2004), during the sprouting of stem cuttings (Wickham et al. 1982) and bulbils (Sharma 1974, 1980; Wickham et al. 1982) of many *Dioscorea* species.

In summary, it is clear that the resumption of active cell division that leads to TGM formation is the earliest mark of shoot bud genesis. The formation of the PTM leads to the formation of tuber-roots, which are seen on the tuber surface as thin, short-lived roots (Wickham et al. 1981, Wilson et al. 1998) but the formation of the PTM does not necessarily precede/herald shoot bud genesis. In the work of Ile (2004), similar tuber-roots were observed to develop due to localized cell activity in the meristematic region (Fig. 12), and they were found to be present in sections taken from even highly dormant tubers. The presence of tuber-roots is not indicative of nearness to shoot bud genesis or of the depth of dormancy but it may precede shoot bud genesis in tubers that are

Figure 10. Stages of the sprouting process: external manifestation of the formation of the PNC. Source: Ile (2004).

Figure 11. Stages of the sprouting process: emergence of vine and feeder roots from the PNC. Source: Ile (2004).

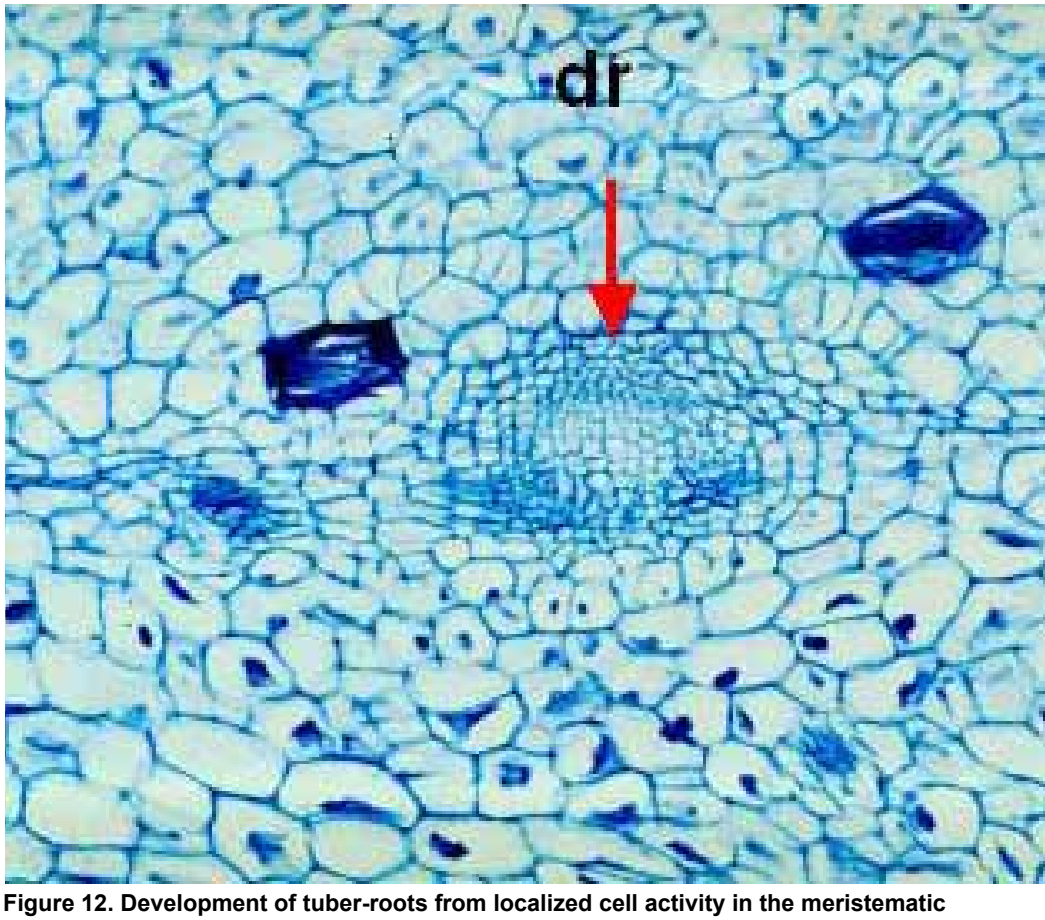


Figure 12. Development of tuber-roots from localized cell activity in the meristematic region. Abbreviations: dr = developing tuber-root. Magnified 28X. Source: Ile (2004).

near their natural sprouting time. The development of tuber-roots may be encouraged by humidity. When tuber portions were stored in dark boxes containing moistened paper towels, tuber-roots were observed on the surface of the tuber. Wickham et al. (1981) also recognize the relationship between the development of tuber-roots and humidity. The PNC is formed after sprouting and may constitute the organ of renewed vegetative growth.

Definitions of the tuber-head as “the organ of renewed vegetative growth and as the PNC”, and implications of the interchangeable use of terms

In spite of the clear definitions of the tuber-head and PNC above, it is common and confusing to find the tuber-head being referred to as the organ of renewed vegetative growth and the PNC. Wilson et al. (1998), for example, suggested that in intact tubers, the tuber-head that surmounts the tuber is the source of roots, shoot, and tubers during renewed growth. In other instances it is defined as the PNC (Ferguson 1972; Onwueme 1984; Wilson 1998). These definitions do imply that the tuber-heads of dormant intact tubers have the capacity to function as the organ/bud during sprouting, differentiating directly into roots, vines, and tubers. It also implies that the terms tuber-head and PNC refer to the same structure.

However, in view of the definitions of tuber-head and PNC in the sections above, it is apparent that they are different structures since: (1) the tuber-head is present and the PNC is absent during dormancy of intact tubers, (2) both structures are present during the renewed vegetative growth of intact tubers, and (3) the PNC is present during the renewed growth of headless tubers. Furthermore, the fact that the PNC (from which vines and feeder roots emerge) is always formed on the tuber surface of headless tubers or on the tuber-head of intact tubers indicates that vines and feeder roots are not differentiated directly from the tuber-head, and hence the tuber-head can neither be referred to as an “organ” nor can it function as the organ of renewed vegetative growth.

Continuous reference to the tuber-head as the PNC can have serious practical implications on the nature of research conducted and the extent to which the duration of dormancy is shortened or prolonged. For example, the manipulation of the tuber-head by detaching or cutting it in various ways and treating cut surfaces with growth-inhibiting plant growth regulators, as found in the work of Tschannan et al. (2003), was conducted because the tuber-head is considered the PNC.

In spite of the differences in the functions of the tuber-head and the PNC, it is possible that the fact that the PNC of a sprouting tuber eventually becomes the tuber-head of the tuber initiated during plant growth may have contributed also to the confusion of

terms. During renewed vegetative growth, the PNC of the sprout/external shoot bud differentiates, giving rise to the feeder roots and shoot(s). In *D. rotundata*, where tubers are produced underground, they are developed from a programmed site within the PNC (see the review by Craufurd et al. (2001) for the process of tuber initiation). By harvest time, the mature tuber remains attached to the “once-PNC”, which is now brownish in color, appears corky, and contains “eyes” that are indeed the points of attachment of feeder roots. In intact tubers, the tuber is harvested with the “once-PNC” still attached but it is detached in headless tubers. Thus the “once-PNC” becomes the tuber-head, the corm-like structure at the top of the tuber, the degenerate rhizome, etc. Therefore, Wilson et al. *(*1998) were in line to have stated that the tuber-head is formed *de novo* in headless tubers. However, since the PNC is also formed in the tuber-head of intact tubers and since the PNC eventually becomes the tuber-head of the harvested underground tuber, it is then necessary to add that the tuber-head is formed *de novo* also in intact tubers.

To limit any further misconception it is recommended that the term PNC be considered as the organ of renewed vegetative growth and should be used in the anatomical description of the process of renewed vegetative growth. The terms sprout or external shoot bud should be useful in the morphological description of the process of renewed vegetative growth. On the other hand, the terms tuber-head, rhizome, and sympodial rootstock should be used to refer to the corm-like structure of intact dormant or sprouting tubers.

II

Duration of yam tuber dormancy: paradigms on the start and end of dormancy and their implications for a successful manipulation of the duration of dormancy

Two broad paradigms on the start and end of dormancy can be identified. In paradigm A, dormancy commences late, by tuber maturity or by vine senescence/onset of the dry season and ends at sprouting (See Annex A). In contrast, in paradigm B, dormancy commences much earlier, such as during early tuber development, and ends with sprouting (See Annex A). This section discusses these paradigms and their effects on (1) the accuracy of and consistency in the duration of dormancy often presented, (2) the design of research conducted, (3) the timing of treatment application, and (4) the extent to which the length of the dormant period can be shortened. Also highlighted here are the effects of confused definitions of terms, such as those for tuber maturity, sprouting, and vine senescence, on the estimation of the duration of dormancy.

Paradigm A: dormancy commencing at vine senescence/ start of the dry season and ending at sprouting

Paradigm A (see Annex A) is consistent with the theory that dormancy is an adaptive mechanism developed for survival in adverse weather conditions, in this case, the dry season. Also in agreement with this paradigm are the results of published works that show that there is a slowing down of metabolic activities in tubers with the start of the dry season. For instance, tubers that are harvested at shoot senescence exhibit a reduced rate of respiration, and reduced starch and sugar metabolism. They contain high concentrations of growth-inhibiting substances, etc., with the reverse occurring at the end of dormancy/resumption of sprouting**.** It is important to note that in most of these studies, the experimental tubers were harvested at the attainment of tuber maturity or at best only a few days before this stage and the period covered is until the visible end of dormancy (sprouting). As such, the studies have provided information only on changes occurring from the defined time of harvest until sprouting.

Based on the definition in paradigm A, therefore, the duration of dormancy can range from 50 to 150 days, even for the same variety, being largely inconsistent. Some reasons for such wide variation relate to the ambiguous nature of the terms tuber maturity, vine senescence,

and sprouting, which consequently allows the use of varied dates of tuber harvest and varied signs of sprouting. Examples are discussed below of how these factors, as well as differences in species/varieties, and poorly stated/poor knowledge of environmental conditions in postharvest storage, can result in an inconsistent duration of dormancy.

Effect of harvest date on duration of dormancy

An important observation from early studies in Nigeria and in the Caribbean is that the relationship between the date of the tuber harvest and the duration of dormancy is negative and linear with the duration decreasing with later harvests. However, all tubers sprout at about the same time of the year. This relationship is true for *D. rotundata*, *D. alata,* and *D. esculenta* planted at the same time and stored under similar conditions. These indicate that (1) the duration of dormancy calculated using the harvest date as the reference start mark would always result in variations in duration to sprouting and that the dormant period referred to represents only a fraction of the true dormant period of a genotype, and (2) the ability to drastically shift the timing/date of sprouting is crucial to attaining the full benefits of shortening dormancy.

Effect of species on duration of dormancy

Yam species differ in their duration of dormancy. Much of this difference among species has been associated with adaptation to the agroecology of origin (Coursey 1976, Passam 1982) with durations decreasing as the duration of the marked dry season decreases from the drier savanna to the humid forest ecology. This hypothesis also supposes that species originate and can be grouped in relation to their agroecology of adaptation. For example, *D. elephantipes,* grown/originating in the semi-desert area, exhibits dormancy that is as long as the long dry period (Coursey 1967). From a general view also, it appears that the species tend to maintain their inherent long or short durations of dormancy even with changes in growing conditions (cultural practices and environmental conditions). Also *D. alata* originating from Asia is believed to exhibit a dormancy that is longer than that of *D. rotundata* originating from the savanna zone of West Africa, and with the shortest duration being expressed mostly by *D. cayenensis* originating from the humid forest agroecological zone of West Africa, which exhibits the shortest dry season (Martin and Sadik 1977, Passam 1982). Although this assertion can be assessed further, it appears from Table 1 that some varieties of *D. rotundata,* for example, exhibit dormancy that is at least as long as that of *D. alata* and variability within species is high.

These bring to the fore two fundamental questions. (1) Why is the variation within species so large? (2) Would broader understanding of the role of the agroecology of origin on the duration of dormancy come from studies at the varietal level? Furthermore, because most of these studies do not provide enough information about the date of harvest, date of sprouting, date of planting, date of vine emergence, and

Table 1. Durations of tuber dormancy (between harvest and sprouting) of three important yam species (modified from Orkwor and Ekanayake 1998).

Species	Duration (days)	Authors
D. alata	98 to112	Passam (1982)
	112	Campbell et al. (1962a)
	98 to 126	Hayward and Walker (1961), Burkill (1985)
	56	Nwoke and Okonkwo (1981)
	105 to 112	Coursey (1967)
D. rotundata	14 to 98	Burkill (1985)
	91	IITA (1976)
	56 to 112	Agbo (1992)
	63 to 112	Agbo (1992)
	105 to 112	Coursey (1967)
D. cayenensis	70 to 126	Passam (1982), Burkill (1985)
	28 to 56	Hayward and Walker (1961)

the environmental conditions experienced by the tubers during storage, it is difficult to explain why such differences in duration exist. The effect of storage environmental conditions on the duration of dormancy is discussed in a later section.

In conclusion, species differences influence the duration of dormancy. Nonetheless, a more realistic estimate of the duration of dormancy may be obtainable from experimentation that eliminates the effects of storage environmental conditions and tuber harvest date. With the incorporation of these factors, structured physiological studies can be conducted also to assess whether species differences in the duration of dormancy is a result of ontogenetic/phenological plasticity or true physiological adaptation (amelioration or tolerance) to the ecology of origin. Such studies may also involve growing and storing tubers in their ecology of origin and in contrasting agroecologies that support the growth and development of yam.

Effect of variety within a species on duration of dormancy

The duration of dormancy even within a yam species has long been known to vary. This difference in the date of sprouting/duration to sprouting can be as much as 45 days (Table 2) even when tubers are grown and stored under identical conditions. In spite of this difference, however, it is important to note that sprouting still occurs at a definite time of the year, which coincides with the season for planting yam in West Africa.

Effect of agroecology of origin on duration of dormancy

Ile (2004) determined whether the large variation in duration to sprouting /date of sprouting among varieties of *D. rotundata* (see Table 2 for a description of the landraces) is related to provenance or adaptation to the duration of the dry season at

Table 2. Variation in sprouting day of year (DOY) of *Dioscorea rotundata* landraces that were grown and stored in their respective agroecology of origin.

Landrace		Agro-ecology	Coordinates	Mean (DOY)	SE
Local name	Accession number				
Giwa	99-1	GS	9° 22'N;6° 18'E	54	1.73
Suba	99-2	GS	9° 05'N;6° 38'E	55	1.78
Akwuki	99-3	GS	9° 05'N;6° 38'E	58	1.64
Maisaki	99-4	GS	10° 85'N;7° 33'E	54	1.66
Kpakogi	99-5	GS	9° 18'N;6° 15'E	76	1.95
Yar-ganye	99-6	GS	10° 52'N;7° 34'E	60	1.63
Chikakwudu	99-7	GS	11° 08'N;7° 34'E	51	1.66
Lasirin	99-9	MS	7° 39'N;3° 39'E	51	2.39
Ajelanwa	99-10	MS	7° 39'N;3° 39'E	61	1.90
Ayin	99-11	MS	7° 40'N;3° 45'E	60	2.22
Ehuru	99-12	MS	7° 38'N;3° 40'E	54	1.99
Omi-efu	99-13	MS	7° 38'N;3° 40'E	55	1.75
Ekpe	99-14	HF	6° 20'N;6° 50'E	34	1.60
Adaka	99-15	HF	6° 20'N;6° 50'E	45	1.62
Nwopoko	99-16	HF	6° 40'N;7° 22'E	41	1.58
Abi	99-17	HF	6° 40'N;6° 48'E	61	1.57
Obiaturugo	99-18	HF	5° 49'N;7° 26'E	51	1.58
Azia	99-19	HF	4° 43'N;7° 18'E	39	1.58
Okom	99-20	HF	5° 19'N;7° 21'E	60	1.58
Bilazia	99-21	HF	4° 40'N;7° 23'E	48	1.57

- Coordinates indicate locations, in Nigeria, where landraces were collected.
- Landraces are known to be indigenous to the areas of collection.
- MS = moist savanna transition agroecological zone; HF = humid forest agroecological zone; GS = Guinea savanna agoecological zone; DOY = day of year

the respective ecology of origin. To achieve this, the provenances were grouped in one of the three distinct agroecologies within the yam-growing zone in Nigeria, the humid forest (HF), moist savanna or forest–savanna transition (MS), and Guinea savanna (GS).

In the first year of the study, the landraces were grown at a site in their respective provenances. Table 3 shows the dates (in DOY) of planting at sites representing each provenance, such as Abuja for GS landraces, Ibadan for MS landraces, and Onne for HF landraces. At harvest, tubers of each landrace were grouped in three lots by random selection with each part consisting of 100 whole and healthy tubers. Tubers in one of the three lots were stored in a barn at a site in their supposed agroecologies. The other two parts were each stored at a site in the other two agroecological zones. See Table

3 for dates (in DOY) of harvesting and storing of harvested tubers at a location in their agroecology of origin and two other locations as described above.

In the second year, only 11 of the 22 varieties were used in the study. At this time, the landraces were grown in their agroecology of origin as well as in the other two agroecological zones.

Dates of planting, harvesting, and storing of tubers at the different locations are shown (Table 3).

Table 3. Two-year provenance by storage experiment indicating dates (in DOY) of planting, harvesting, and storing of tubers at any of three locations representing three agroecologies of origin in Nigeria.

	Year 1			
		Date in DOY		
Provenance	Storage location	Planting	Harvesting	Storing
GS	Abuja	136	347	348
MS	Abuja	112	350	357
HF	Abuja	112	354	357
GS	Ibadan	136	347	351
MS	Ibadan	112	350	351
HF	Ibadan	112	354	357
GS	Onne	136	347	351
MS	Onne	112	350	351
HF	Onne	112	354	355
	Year 2			
Growing agroecology	Storage location	Planting	Harvesting	Storing
GS	Abuja	143	340	340
GS	Ibadan	143	340	348
GS	Onne	143	340	346
MS	Abuja	119	326	338
MS	Ibadan	119	326	326
MS	Onne	119	326	336
HF	Abuja	104	315	338
HF	Ibadan	104	315	325
HF	Onne	104	315	315

Table 4. Mean date (DOY) of sprouting of 11 landraces originating from GS (3 varieties), MS (4 varieties), and HF (4 varieties), grown in their respective ecology of origin and stored at sites in three agroecological zones (Abuja, Ibadan, and Onne) in Nigeria.

Provenance	Mean (DOY)	SE	Start of rainy season*	Storage location	Mean (DOY)	SE
GS	59	0.62	April	Abuja	63	0.62
MS	58	0.66	March	Ibadan	58	0.61
HF	57	0.51	February	Onne	53	0.57

Provenance = $P < 0.01$; storage = $P < 0.001$; *Jagtap 1993.

Table 5. Analysis of variance for the effects of provenance (Prov), and storage location (Storage loc.) on date of sprouting of 20 *D. rotundata* landraces in Year 1. ***= $P = 0.001$.

Source	DF	SS	Mean square	F Value
Storage location	2	67782.8	33891.4***	137.7
Provenance	2	8983.5	4491.8***	18.3
Storage location* Provenance	4	6535.1	1633.8***	6.6
Landrace (provenance)	17	269365.7	15845.0***	64.4
Storage loc. *Landrace (Prov.)	34	29379.2	864.1***	3.5

Findings suggest that (1) few tubers sprout in December–January. Sprouting occurs mostly between mid-February and April. This observation was true across landraces and storage locations, and (2) the ecology of origin *per se* may not play a strong role in determining the date of sprouting (Table 4). If the start of the rainy season at these agroecologies was the cue stimulating the start of sprouting, then the mean date of sprouting for landraces from the HF, for example, should be much earlier than those from the GS but this was not the case. Indeed, landraces from the HF were found to sprout only 1 day earlier than those from the MS and 2 days earlier, i.e., by 57 DOY, than those from the GS (after the effect of storage location was removed). This conclusion remained the same even when more landraces (all 20 landraces) are included in the data analysis (Table 5). Provenance contributed about the least (F value = 18.3) to the variation in date of sprouting (Table 5). The high contribution of landraces within provenance (landrace(provenance)) to the variation indicate that it is a more important (F value = 64.4) factor affecting the date of sprouting than provenance *per se*. Also, the high variation in landrace(provenance) indicate that both early and late sprouting landraces are present within a provenance.

In summary, the possibility of a role of adaptation to the agroecology of origin in determining the duration of dormancy/timing of sprouting in *D. rotundata* appears unlikely. Certainly, given that there are no known specialized internal structures in yam tubers for coping with the adverse dry season, and the internal structures of dormant tubers

originating from the different yam ecozones in Nigeria do not vary, there is no evidence to suggest the exhibition of amelioration; a response type indicative of physiological adaptation. Therefore, the association of dormancy with the slowing down of physiological activity during the dry season as well as the presence or absence of high or low quantities of biochemical element(s) may be correlative.

Therefore, it is proposed that the varieties that are “indigenous” to the agroecologies studied may indeed be the result of the farmers’ conscious selection for varieties that fit cultural preferences or for varieties with varying timing of sprouting (short and long durations to sprouting) to ensure the survival and availability of healthy tubers for different needs.

Effect of postharvest storage conditions on duration of dormancy

The effect of storage agroecology on the date of sprouting and duration to sprouting was determined in a multi-factorial experiment. For details of the experimental design and procedures, see subsection on the effect of agroecology of origin on the duration of dormancy above, as well as Ile (2004).

Observations show that the storage agroecology strongly affects the date of sprouting (< 20 days on average) with the effect being earlier and additive as the storage location moves from the GS (Abuja) to the HF (Onne). In the first year of the study, sprouting occurred by 53 DOY at Onne, 5 days later at Ibadan, and 10 days later at Abuja (see Table 4), indicating the additive nature of the effect of storage on the timing of sprouting at Onne. In the second year, sprouting occurred at 45 DOY at Onne (irrespective of growing agroecology), 8 days later at Ibadan, and 18 days later at Abuja. At Onne, the timing of sprouting varied in the two years by about 10 days, probably due to the significant additive effect of the inductive growing agroecology (i.e., at Onne). Thus, the effect may follow a predictable pattern (see the low F value for the interaction of storage location and landrace(provenance) in Table 4 as well as Fig. 14). The relationship is positive and linear with sprouting occurring later as storage location changed from the humid forest to the savanna. Thus, the effect of the storage environment must be strongly considered in dormancy studies.

A previous storage agroecology (two generations away or storage year (1) has no effect on the date of sprouting in the subsequent year (storage year 2). This suggests that the effect of a previous storage condition is transient and no significant memory of the effect is transferred to the next generation. The practical implication of this knowledge lies in the fact that landraces can be transported to other agroecologies with little or no fear of the transfer of a memory of the effects of a previous storage condition.

Note: only the effect of the storage environment just preceding growth is of consequence. Also, the effects of provenance are separated from the effects of the growing agroecology

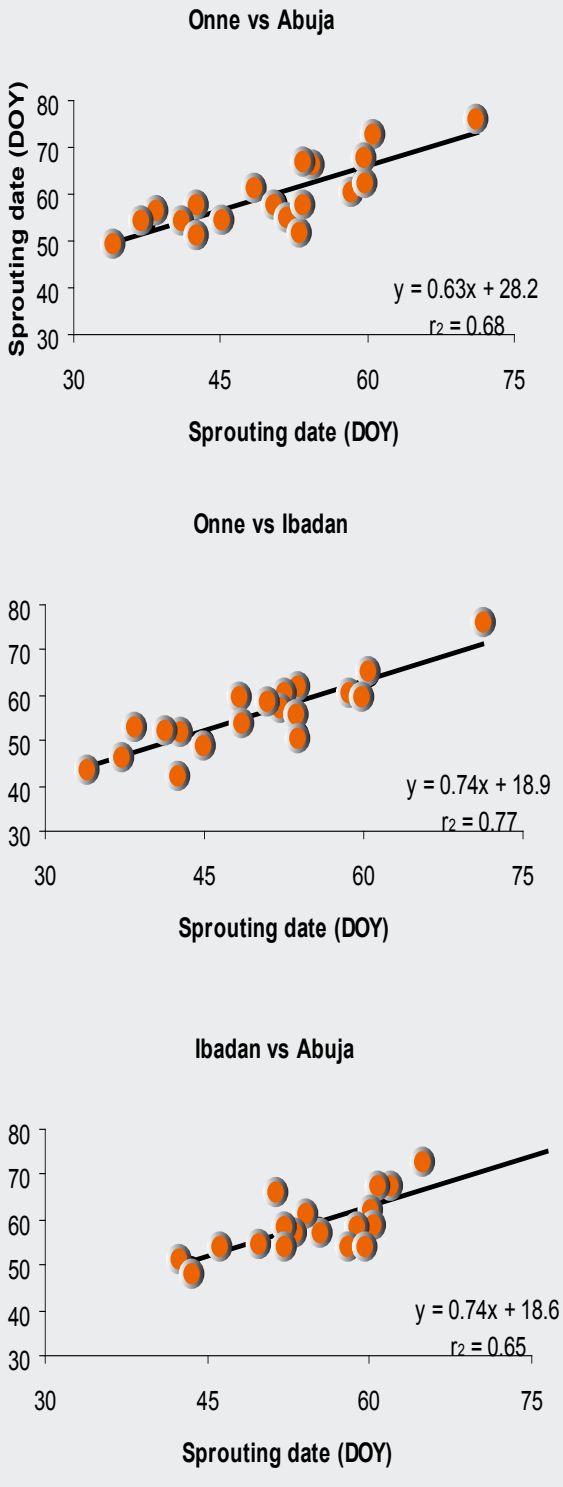


Figure 13. Relationships between dates of sprouting across sites located in three agroecological zones in Nigeria (at Onne, Ibadan, and Abuja). NB: x-axis vs. y-axis. Source: Ile (2004).

because landraces that are thought to originate from two diverse agroecologies, e.g., GS and HF, will respond alike when grown and stored under the same conditions.

Much is known of the effects of constant environmental conditions such as temperature (in particular), humidity, photoperiod, and light intensity on dormancy (see review by Craufurd et al. 2001). In summary, sprouting occurs a few days earlier as temperature increases up to its optimum for sprouting. Under saturated or unsaturated humidity, the optimum temperature for sprouting in tropical species ranges from 25 to 30 °C (Onwueme 1978) although exposure to a higher temperature (35 °C) has led to 85% sprouting after 95 days (Passam 1977). In contrast, low temperatures (15–16 °C) would prolong dormancy. At temperature regimes below 10 °C, rapid deterioration occurs as a result of chilling injury (Mozie 1984). Under natural storage conditions (i.e., in the yam barns), where the temperature fluctuates, sprouting also occurs progressively earlier in warmer conditions until the optimum. Among temperate species, on the other hand, the optimum temperature for sprouting is lower, ranging between 15 and 25 °C.

The effect of temperature on dormancy is suggested to relate to the effects of temperature on physiological activities, such as enzyme activity and respiration. It is, however, not clear whether the effects of temperature follow a simple count mechanism as it may appear. Generally, because in temperature-regulated plant processes, (1) the rate of progress of plant developmental events increases linearly with increasing temperature up to its optimum for the process, and (2) the expression of the effect of temperature in thermal time (°Cd) provides an adequate physiological explanation for the effects of small fluctuations in temperature, investigations were carried out to determine the relationship between storage temperature (in °Cd) and the date of sprouting.

The study was conducted in yam barns located at sites in Abuja (GS), Ibadan (MS), and Onne (HF), representing three of the agroecologies in Nigeria. Over the study period, the average temperature ranged from 25 to 27 °C across storage locations (Table 6) with the temperature at Onne (HF) being up to 2 °C higher than that at Abuja (GS). As with average temperature, average relative humidity followed the same trend.

Whether tubers developed during growth in the GS, MS, or HF, they always accumulated the lowest thermal time if stored at Onne compared with storage at Abuja or Ibadan and they were the earliest to sprout (Table 7). In contrast, although tubers stored at Abuja were the latest to sprout, they accumulated the highest thermal time only if grown in the HF. Thus, in spite of the clear correlative relationship between the date of sprouting (from harvest at vine senescence to sprouting) and storage location, the date of sprouting could not be explained by a linear function of date of sprouting (DOY) and thermal time (Figure not presented). This indicates that the sprouting date at these locations may not be controlled by a simple count mechanism driven by the average temperature (average thermal time) during storage.

Table 6. Temperature and relative humidity in the yam barns at Abuja, Ibadan, and Onne during the storage periods.

Storage location	Temperature (°C)			Average relative humidity (%)
	Minimum	Maximum	Average	
	Year I			
Abuja	14.6	35.9	26.3	42.0
Ibadan	17.4	36.1	27.1	54.7
Onne	19.9	36.7	27.1	NA
	Year 2			
Abuja	13.9	37.1	25.3	42.2
Ibadan	16.8	35.7	27.1	65.9
Onne	18.1	34.1	26.6	79.3

Table 7. Thermal time (in °Cd from date in storage to sprouting) and date of sprouting (in DOY) following storage of yam tubers in barns at three contrasting locations, Abuja, Ibadan, and Onne.

Growth agroecology	Storage location	Sprouting DOY	°Cd
GS	Abuja	66	1370
	Ibadan	57	1384
	Onne	51	1270
MS	Abuja	63	1536
	Ibadan	57	1627
	Onne	48	1448
HF	Abuja	60	1647
	Ibadan	46	1598
	Onne	36	1435

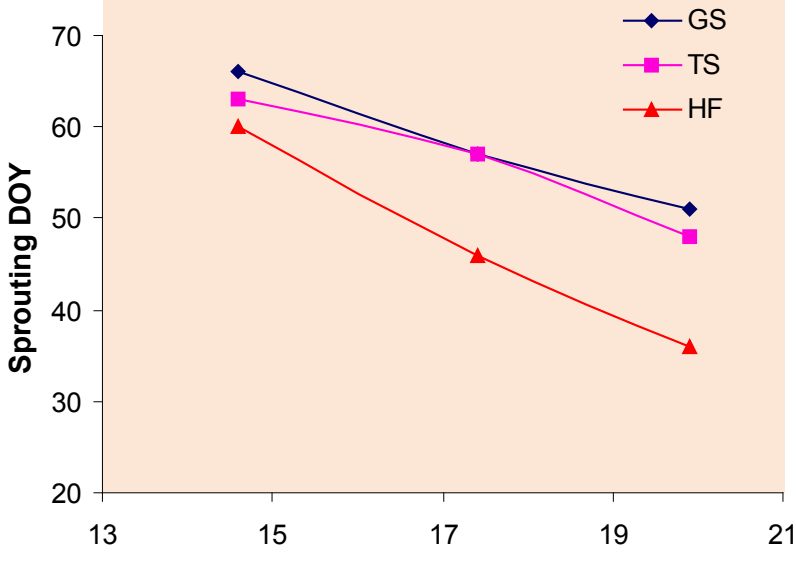


Figure 14. Relation between average minimum temperature at three storage locations (Abuja, Ibadan, and Onne) and sprouting DOY for tubers grown in three different agroecological zones (GS, MS, and HF).

It might, however, be important to investigate further whether the effect of temperature, under naturally fluctuating temperatures, is more related to the effects of night temperature. There is also a wider variability in night temperature than in day or average temperatures across locations. A preliminary analysis of the relation between night temperature at the storage locations (using temperature values for year I on Table 6) and sprouting date shows that a linear negative relation exists between night temperature during storage and sprouting DOY (Fig. 14). Tubers produced at any of the three agroecological zones (GS, MS, or HF) respond to storage conditions in the same manner, with sprouting DOY delayed

as the storage location shifts from Onne (high night temperature) to Abuja (lower night temperature). Also, it might be necessary to support this with an analysis of the relation between thermal time (using night temperatures) and sprouting date. Relative humidity might also contribute slightly to the timing of sprouting in yam.

Effect of growth-inhibiting plant growth regulators (PGRs) on dormancy

The possible role of endogenous growth-inhibiting substances in the control of yam dormancy was also considered within the context of paradigm A. Because many plant growth inhibitions are influenced by the concentration of endogenous growth inhibitory PGRs (Hemberg 1985), yam physiologists have sought to identify/isolate substances with growth inhibitory activities and determine their relationship with the maintenance of dormancy. Past studies have concentrated mainly on abscisic acid (ABA) and phenolic growth inhibitors, particularly batatasins. Batatasins belong to the phenolic class stillbenoids. They occur naturally in many plant species exhibiting dormancy. In *Dioscorea,* they have been isolated in *D. alata, D. cayenensis,* and *D. opposita* (Hashimoto et al. 1972; Ireland et al. 1981). They are more concentrated in the peel, (the region closest to the meristematic layer where sprouts originate) than in the pulp. Their growth inhibitory activity has also been reported in standard ABA bioassays such as the *Avena* and wheat coleoptile and lettuce hypocotyl extension tests (Ireland et al. 1981; Hashimoto and Tajima 1978). In Lino et al. (1978) they were also found to alter membrane properties *in-vitro*.

By isolating these compounds over time, it was clear that the concentration of batatasins increased from 150 days after planting, attaining a maximum at tuber maturity when tubers are declared dormant (Ireland and Passam 1984), and then declined gradually until sprouting (Hashimoto et al. 1972, Ireland et al. 1981; Ireland and Passam 1984). Exogenous application of batatasins I, II, III, IV, and V have inhibited the growth of shoot buds in potato and other plants, delayed the appearance of shoot buds in some yam spp., i.e*., D. alata, D. cayenensis,* and *D. esculenta* by about 15 days (Hashimoto et al. 1974; Hashimoto and Tajima 1978; Ireland and Passam 1984, 1985; Asahina et al. 1974,1998; Majumder and Pal 1992). Exogenous ABA has had no significant effect on the duration of dormancy in whole yam tubers.

In conclusion, therefore, the role of PGRs with growth inhibiting characteristics on the dormancy of whole yam tubers is not clear. What is clear is that the PGRs can inhibit bud dormancy, re-induce dormancy in sprouting buds, and their effect is slight on the duration of whole yam tuber dormancy (< 20). Some questions need clarification. (1) Are batatasins present or absent in developing tubers at stages earlier than 150 days after planting? (2) Would a similar correlation be observed in *D. rotundata*? (3) Would an apparent correlation imply a specific effect on the tuber rather than bud dormancy?

Effect of other PGRs on duration of dormancy

The role of endogenous and synthetic PGRs with growth-promoting properties has also been studied. Again, because of the wide acceptance of Paradigm A, virtually all studies aimed to manipulate the duration of dormancy using PGRs have begun at or after harvest at vine senescence. Recently, Craufurd et al. (2001) and Ile (2004) have extensively reviewed the effects of PGRs (ability to shorten or prolong dormancy) and degree of effects (number of days by which it was shortened or prolonged). See Annexes B–D.

From the review it was clear that:

- ethylene analogs were more likely to shorten dormancy and GA_3 was more likely to prolong it. Nonetheless, the effects of PGRs are inconsistent due to differences in tuber age at the time of PGR application,
- the effects of 2-chloroethanol, thiourea (ethylene analogs), and their recommended combination, which are potent in potato and other *Dioscorea* spp., have not been tested in *D. rotundata*,
- where studies are conducted, even much less success (0 to 10 days) is achievable in *D. rotundata,* the most important yam species,
- the application of PGRs to plant leaves just before senescence or to whole tubers after harvest induced sprouting to occur only up to 50 days earlier than the control,
- in many varieties, significant sprouting begins in February even when PGRs are applied just after harvest in November of the previous year,
- the achievement of up to 50 days earlier sprouting or even the occurrence of sprouting in November is not good enough to double yam tuber availability as well as to fulfil the wish of yam breeders desiring to have more than one generation/year in the breeding program. A more drastic shortening effect is needed. To achieve this, sprouting needs to be induced to occur in August–September.

From the above therefore, two major problems are clear: (1) the effects of PGRs on the duration of dormancy could not be explained adequately, and (2) the inability of PGRs to drastically shorten the duration of dormancy is a clear indication of poor understanding of the mechanism of dormancy. As discussed in Section II, these problems can be overcome by relating the effect of PGRs on dormancy to the progress in some anatomical events occurring during the release of dormancy.

Effects of poorly defined terms on duration of dormancy

The duration of dormancy presented is often inconsistent, even for the same variety. A major reason is the ambiguity in the definitions of the indices relating to the start and end of dormancy. One example is the use of the term ”tuber maturity”. Often the reader has to infer whether reference is being made to agronomic maturity or physiological maturity/ readiness for sprouting. Because both maturity types define two distinct stages of tuber development, durations will vary when calculated with these as the start indices. Another term that leads to inconsistency in the duration of dormancy is “senescence”. It must be clear whether reference is made to vine or leaf senescence. Because leaf senescence commences before vine senescence, tubers harvested at these stages are at different ages (with the latter being nearer the sprouting time than the former) and hence their durations to sprouting would vary. Furthermore, the index for leaf senescence varies from the appearance of the first senescing leaf to 20, 25, 50, or even 75% leaf senescence, and these differences can lead to irreproducible results on the duration to sprouting.

The terms that denote the end of dormancy have also contributed to the observed inconsistencies in duration to sprouting. The term ”sprouting” is often used to mark the end of dormancy or what is referred to as the end of visible dormancy in this book. In some studies, sprouting is considered to have occurred when shoot bud(s) appear on the surface of the tuber, i.e., what is referred to as the appearance of the shoot bud (ASB) in this book. In some cases, it is marked by the presence of sprouts, or sprouts up to 2.5 mm long, while in others, it is associated with the emergence of sprouts above soil level (or what will be more appropriately referred to as vine emergence). Thus, with such varied definitions, the duration of dormancy (in days from a defined start to the end) would always differ, even for the same variety.

For the sake of clarity and ease of comparing results it is important that the terms related to dormancy are clearly defined. Preferably, ASB, the appearance of the sprouting locus (though more difficult to recognize), should mark the end of visible dormancy (endo-dormancy, discussed in section III) while sprouting marks the end of bud dormancy.

Summary on Paradigm A

1. The duration of dormancy is long and highly variable. The variability in the duration of dormancy highlights the need for researchers to define terms clearly and describe all conditions experienced by tubers during storage and the growing season.
2. It is doubtful whether the variability in the duration of dormancy within varieties of *D. rotundata* “indigenous” to distinct agroecological zones in Nigeria, is due to inherent adaptation to their agroecology of origin/latitude of origin. Tubers, in spite of perceived differences in their agroecology of origin, will sprout at about the same time if grown and stored in similar environmental conditions.

3. The growing and storage conditions/agroecologies are important factors affecting the duration of dormancy with the effects being as long as 20 days.
4. Based on the effects of exogenous PGRs on the duration of whole tuber dormancy as well as the effects of physical and environmental factors, it is clear that whole tuber dormancy, in the context of paradigm A, can be shortened only by about 30 days.

Paradigm B: dormancy commencing early during tuber development and terminating at sprouting

As early as the 1980s, some researchers hypothesized that tuber dormancy does not begin when tubers reach agronomic maturity or leaf/vine senescence but rather much earlier during early tuber development (see Annex A). This school of thought holds that dormancy begins some time during tuber development and ends at sprouting (Okoli 1980; Passam et al. 1982). A second group suggests that there is a 'true" dormancy period that starts during tuber development and ends well before sprouting, being marked by the onset of activity in the meristematic region that leads to the formation of the internal shoot bud (Onwueme 1973; Ile 2004).

Only a few studies have been carried out within the context of paradigm B. Although the reason for this is not clear, it is supposed that paradigm B has been unattractive, probably due to the fact that it implies that actively growing and developing tubers exhibit dormancy. Another reason may be because it implies that yam tuber dormancy (observed in whole harvested tubers) may not arise simply due to the effects of adaptation to a prevalent or impending adverse environmental condition (such as the advent of cold periods in temperate regions and the dry season in tropical regions.). The consequence of limited research in this area has meant that the factors that affect the initiation and duration of dormancy are not clearly understood and evidence that elucidates its control mechanism(s) is rare.

The discussion in the subsections below therefore shows how the use of different dates for the start and end of dormancy can affect the consistency and accuracy of the duration of dormancy, the design of experiments, and the effect of using Paradigm B on the rate of success in shortening the duration of dormancy.

Effect of harvest date on the duration of dormancy

The works of Okoli (1980) and Passam et al. (1982) were the first few to show the linear negative relationship between the date of the yam tuber harvest (in DAE or DAP) and the duration of dormancy. By harvesting tubers of four varieties of *D. rotundata* every seven days from as early as 98 DAP to 252 DAP and recording the date of sprouting, Okoli (1980) showed that the duration of dormancy was progressively shorter as the date of tuber harvest was delayed. Subsequent studies with *D. rotundata* and *D. alata* have also shown this relationship (Wickham et al. 1984; Swanell et al. 2003).

These results clearly show that tubers are dormant by 98 DAP and certainly well before harvest at vine senescence (agronomic maturity). Also, they imply that the duration of dormancy would be inconsistent and irreproducible where the duration from a harvest date to sprouting is presented as the total length of dormancy of a variety or species. Note that the tuber age in DAE provides a better indication about the closeness of tubers to the time of sprouting than DAP. However, a harvest date in calendar months (without a mention of planting or emergence date) has no definite association with the date of tuber initiation, date of vine emergence, or date of planting tuber age, nor does it provide an indication about how close tubers are to sprouting.

Effect of growing environmental conditions on dormancy

One implication of dormancy commencing at tuber initiation or earlier during tuber development is that growing conditions during tuber initiation and development may affect the duration of dormancy. To investigate this, a field study was conducted involving the growth of 11 landraces in contrasting agroecological zones in Nigeria. For details about experimental design and procedure, see the subsection above on “the effect of postharvest storage condition on duration of dormancy” above as well as Ile (2004). To complement the field data, a controlled environment study was conducted to determine the effects on the duration of dormancy of the specific variables of a growing environment, such as soil fertility, air temperature, and photoperiod. The photoperiod regime imposed simulated a June planting at Abuja and Ibadan (Fig. 15). Day and night temperatures represented the average maximum and minimum temperatures at the two locations. Two levels of soil fertility were achieved by applying a slow release fertilizer, Osmocote Plus (15 N + 11 P_2O_5 + 13 K_2O + 2 MgO) at two levels (Table 8). Planting and tuber harvesting operations

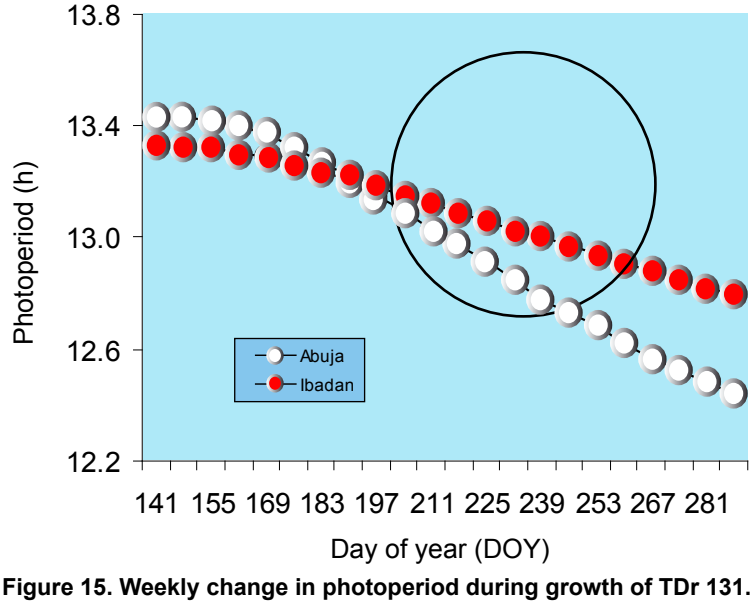


Figure 15. Weekly change in photoperiod during growth of TDr 131.

Table 8. Photoperiod, constant day and night temperatures, and soil fertility treatments experienced during growth.

Photoperiod	Day temperature (°C)	Night temperature (°C)	Fertility (slow release) (g)
Ibadan	32	27	3
Abuja	32	27	3
Ibadan (control)	32	22	3
Ibadan	32	22	1

Table 9. Sprouting date (DOY) in relation to growing and subsequent storage agroecology.

Growing location	Storage location						Growing location	
	Abuja	SE	Ibadan	SE	Onne	SE	Mean	SE
GS	66	1.03	57	0.90	51	0.91	58	0.55
MS	63	0.91	57	0.83	48	0.83	56	0.49
HF	60	0.01	46	0.86	36	0.84	47	0.53
Mean	63	0.57	53	0.50	45	0.50		

were done on the same date across treatments (see Ile 2004 for details). Because the date of sprouting is recorded during storage, all tubers were stored under uniform and favorable conditions for sprouting (constant 28 °C, 80% relative humidity [RH], and 12-hour photoperiod).

From the field study, it is clear that date of sprouting is affected by growing agroecology (Table 9) and the effect is additive if both storage and subsequent growing operations are carried out in inductive agroecologies. On average, sprouting occurred at 47 DOY (i.e., in early February) if landraces were grown at Onne (HF) but growing the same landraces at Abuja (GS) led to sprouting 11 days later. The interaction between the growing agroecology and the subsequent storage environment indicates clearly that the HF environment (at Onne) is more suitable for stimulating early sprouting than conditions at Abuja (GS) or Ibadan (MS) with sprouting occurring earlier (in an additive manner) if both growing and storage operations were carried out at Onne (36 DOY) rather than either of the operations alone.

Clearly, therefore, it is a unique finding that favorable conditions during growth and storage can shorten the timing of sprouting by about < 20 days and that their effect is additive where growing and storage operations are carried out consecutively under inductive agroecology (i.e., at Onne). It suggests that the duration of dormancy is a plastic response to the environmental conditions for growing and storage.

Table 10. Effects of photoperiod, temperature, and soil fertility during plant growth and tuber development on the date of sprouting (DOY), and thermal time (°Cd) from planting to harvest and thermal time from harvest to sprouting in TDr 131. T_b = 10 °C.

Photoperiod	Day temp. (°C)	Night temp. (°C)	Fertility (g)	Sprouting date (DOY)	°Cd (planting* to harvest)	°Cd (harvest to sprouting)
Ibadan	32	22	1	91 ± 1.76	3026	2528
Ibadan	32	27	3	88 ± 1.69	3471	2480
Ibadan	32	22	3	94 ± 1.76	3026	2576
Abuja	32	27	3	88 ± 1.84	3471	2480

*Tissue culture derived plantlets were grown.

The study showed that variations in photoperiod and soil fertility during growth do not significantly affect the duration of yam tuber dormancy (Table 10). One significant (P = 0.05) variable affecting the duration of dormancy is the night temperature, where a 5 °C higher night temperature resulted in earlier (by 6 days) sprouting compared with the control (22 °C night temperature). This effect is similar to that observed from field studies, i.e., 10 days in the growing agroecology study, and suggests that the effect of the growing agroecology on the duration of yam tuber dormancy relates to differences in the night temperature.

Because temperature often affects many plant growth and developmental processes by affecting the rate of development (expressed in thermal time), data analysis was carried out to determine the relationship between thermal time accumulated during growth, tuber storage, or the total period from planting to sprouting, and the date of sprouting. From Table 10 it is clear that sprouting is earlier as the thermal time accumulated during the growth period (between planting and harvest) increases (r^2 = 0.82). Considering that the daytime temperature is constant for all treatments, the result suggests that the effect of temperature on tuber dormancy relates indeed to the effects of the nighttime temperature. It also confirms that the effect of the nighttime temperature follows a predictable count mechanism. Nonetheless, it is doubtful whether the results imply that temperature can be used to manipulate dormancy in such a way that it would be possible to prevent the initiation of dormancy or to break it drastically. This would be discussed further in Section IV.

Effect of growth-inhibiting PGRs on dormancy

In a pilot study, the relationship was investigated between changes in free phenolic substances of the stillbenoid class and the start and end of tuber dormancy in *D. rotundata.* Samples were collected and analyzed on four dates: at 127 DAP (tubers harvested while plants were still green), 176 DAP (at vine senescence/tuber maturity), during tuber storage at 246 DAP, and 303 DAP (when sprouting had begun) with n = 7 tubers at each date. The samples were freeze-dried and total free phenolics were

Table 11. Changes in mean total free phenolics (AU units/g dry wt.) over sampling dates.

Sampling date (DAP)	Mean (AU units/g dry wt.)	SE
127	2.457	0.69
176	1.797	0.30
246	1.554	0.29
303	1.635	0.30

n = 7 tubers/date.

quantified from crude extract using High Performance Liquid Chromatography (HPLC). The instrument used was a Watter 600 multi-solvent delivery system fitted with a Watter 994 photodiode array detector. The column was a Watter Bondapak Phenyl C18 of dimension 4 mm internal diameter (ID) × 30 cm. To separate compounds in extract, a reverse phase gradient program was used with UV detection at 264 and 272 nm and the diode array scan was over the range of 200 to 400 nm [see Ile (2004) for more details]. The pattern of change of free phenolics over the study period suggests the following.

1. Dormancy commences well before vine senescence in *D. rotundata.*
2. There is little evidence to support the idea that phenolic growth substances regulate the start of yam dormancy or that dormancy begins at vine senescence (Table 11). Hence, the data contradict the hypothesis proposed by Ireland and Passam (1984) that dormancy is initiated at vine senescence or tuber maturity when a threshold concentration of batatasins is attained. This is because both the mean concentration of individual phenolic compounds [see Ile (2004) for table showing changes in concentration of individual compounds] and mean total free phenolics were higher (2.46 AU units/g dry wt) in tubers that were harvested before vine senescence than at or after vine senescence (< 1.79 AU units/g dry wt). The lower concentrations of batatasins observed by Ireland et al. (1981) during the early stages of tuber development than at tuber maturity may perhaps relate to lower dry matter content (Ketitu and Oyenuga 1973) and/or the presence of thin un-suberized skin, more consistent with the early stages of tuber development than at tuber maturity.
3. The role of phenolics in the end or release of dormancy is not clear. The absence of a significant decline in total free phenolics between harvest at 176 DAP and sprouting at 303 DAP (see Table 8) suggests that free phenolics may not have a role in controlling the end of tuber dormancy in *D. rotundata.* However, the trend in two compounds suggested that they might be broken down to allow sprouting [data available in Ile (2004)]. More research is needed to verify the role of phenolics in the ending or release of dormancy.

Effect of other PGRs on the duration of dormancy

The rationale for applying PGRs during early tuber development is based on the hypothesis that dormancy will be shortened drastically if PGRs are applied earlier, during tuber development, i.e., prior to or just after tuber formation, rather than later, at tuber maturity. Hence, the role of PGRs in the control of yam tuber dormancy was investigated by (1) applying test PGRs to the growth medium prior to tuber formation (results are discussed in Section III), (2) applying PGRs exogenously on whole tubers (results are discussed in Section IV), and (3) observing anatomically, the effects of PGRs on the genesis and development of the shoot apical bud, which is an early indication of the release of dormancy (results are discussed in Section IV). The findings from these studies are included in the summary of Paradigm B.

Summary on Paradigm B

- Dormancy commences much earlier, during tuber initiation and development, rather than later.
- The duration of this dormancy is much longer than its estimation under Paradigm A and covers a larger part if not all of the period of dormancy.
- The difference in the duration of dormancy/timing of sprouting among landraces of *D. rotundata* is not related simply to provenance/adaptation to the agroecology of origin, i.e., durations of the dry or rainy season, but instead the duration of dormancy is plastic, depending on growing and storage conditions.
- Inductive environmental and endogenous factors, such as air temperature, photoperiod, relative humidity, and exogenously applied/endogenous PGRs, etc., can slightly shorten the duration of dormancy

III

Effects of plant growth regulators on tuber development and the induction and duration of yam tuber dormancy

Based on the conclusion in Section II, the study presented in this section is aimed at providing a better understanding of the effects of PGRs in the initiation of tubers and tuber dormancy. The hypothesis was that dormancy begins during tuber initiation and development and PGRs regulate the initiation of tubers and tuber dormancy.

The protocol

Plantlet propagation

Plantlets were derived from apical shoot meristems of *D rotundata* var. TDr 131. The shoot meristems were cultured in a yam meristem medium, which was prepared as described by Ng (1984). Plantlets were multiplied by regular subculturing (every 40 to 46 days) in a yam regeneration medium and grown under uniform conditions (Ng 1984,1986). Plantlets were 44 to 58 days old by the start of the experiments. The species TDr 131 was chosen because the tubers exhibit prolonged dormancy.

Plant growth regulators treatments

The PGRs tested were ABA, gibberellic acid (GA_3) 2-chloroethylphosphonic acid (ethylene source) and their inhibitors fluridon (FLU), 2-chloroethyl-trimethylammonium chloride (CCC) and silver nitrate ($AgNO_3$) (Table 12). Empirical evidence shows that these PGRs control, fairly consistently, the dormancy of mature underground tubers and bulbils. When applied just after harvest at agronomic maturity, GA_3 most often prolongs the dormancy of mature bulbils and underground tubers; ethylene analogs most likely shorten dormancy; and ABA most likely induces strong growth inhibitory responses. However, the effects of ABA in *D. rotundata* are scarcely known and ABA has had little or no effect in *D. opposita* bulbils *(*Hashimoto and Tamura 1969), *D. alata and D. esculenta* (Wickham et al. 1984), and *D. composita* (Gupta et al. 1979). The relative consistency of the effects of these PGRs makes them target PGRs in this study.

This study was conducted *in-vitro*. The *in-vitro* system is recognized as a powerful tool in the study of the complex mechanisms of tuber dormancy, which are rather difficult to understand from studies carried out under field conditions (Suttle and Hultstrand 1994; Coleman et al. 2001). Another advantage of this system over field conditions rests

Table 12. PGR treatments and concentrations tested in two *in-vitro* studies.

Treatment	Concentration
Control	
Abscisic acid	5 µM
Abscisic acid	50 µM
FLU	10 µM
FLU	30 µM
Gibberellic acid	5 mg L^{-1}
Gibberellic acid	150 mg L^{-1}
CCC	500 mg L^{-1}
CCC	2000 mg L^{-1}
Ethephon	100 mg L^{-1}
Ethephon	500 mg L^{-1}
Silver nitrate	25 µM
Silver nitrate	50 µM

CCC= 2-chloroethyl-trimethylammonium chloride.

in the fact that problems such as the uncertainty of the physiological age of tubers are removed since the date of tuber initiation can be recognized. More specifically, it is argued that it removes the inconclusiveness of results from exogenous PGR treatments, i.e., the possibility that test PGRS are not absorbed by the tubers or PGRS are absorbed in varying quantities and the possibility of differences in the mode of actions of synthetic and endogenous PGRs. It therefore provides a logical method for investigating the role of specific PGRs on dormancy, since the biosynthesis or action of such endogenous PGRs can be blocked with known antagonists when absorbed during plantlet growth. The micro-tubers produced under such conditions are deficient in the specific endogenous PGR. This provides a more conclusive system for manipulating endogenous levels of a PGR and evaluating the effect of its level or deficiency on dormancy (Suttle and Hulstrand 1994).

The PGRs were tested at two concentrations (see Table 12). The choice of test concentrations was based on their effectiveness in previous studies at the whole tuber level as well as their effectiveness and nonphytotoxic effect in yam and potato tissue culture for rapid plantlet and micro-tuber production. Thus, there were 13 treatments; 12 PGR treatments, plus a control. Due to the large number of treatments involved in this study and the constraints of time and facility (space), it was impossible to include more, *i.e,.* reversal treatments consistent with studies involving growth inhibitors. However, this study supposes that the uptake of FLU leads to a decline in ABA levels in yam tissues and that this effect can be reversed by the application of ABA as reported consistently in potato and other crops (Hole et al. 1989; Le Page-Degivry and Garello1992; Suttle and Hulstrand1994).

The study began with the culturing of nodal explants from young, actively growing vines of plantlets in 350 mL jars containing 50 mL yam tuberization medium (Ng 1988) (control) or yam tuberization medium plus a test PGR. A one-L yam tuberization medium was composed of 4.43 g Murashige and Skoog (MS) basal medium, 100 mg Myo-inositol (meso-inositol; I-inositol), 60 g sucrose, 0.5 mg Kinetin (6-furfurylaminopurine) dissolved in HCl, and 20 mg L-cysteine (C_3 H_7 NO_2 S) dissolved in NaOH. In this study, fairly solid media were used (i.e., 5 g/ L agar). In PGR treatments, compounds were added to the yam tuberization medium prior to autoclaving. However, because autoclaving conditions destroy the chemical integrity of CCC, ethephon (2-chloroethylphosphonic acid), and FLU (1-methyl-3-phenyl-5-3(trifluoromethyl)phenyl-4(1H)-pyridinone), filtered and sterilized concentrations of these compounds were added after autoclaving. Ethephon and CCC were dissolved in sterile distilled water and FLU was dissolved in ethanol, as advised by the manufacturers (see Cornell University Chemical Fact Sheet No. 81, 1999- http:/pmep.cce.cornell.edu; ChemService Material Safety Data Sheet). After subculturing, all jars were placed in darkness for 1 day in a growth cabinet at 24 ^{o}C prior to the start of the experiments.

Growth conditions of plantlets and experimental design

Two experiments were conducted, one in a growth cabinet (Experiment I) and the other in a tissue culture room (Experiment II). In Experiment I there were 13 treatments and each consisted of 20 jars (one explant/jar) with each jar being a replicate. The light source was cool white 160 W Sylvania florescent tubes and the tubes were positioned horizontally along the length of the growth cabinet (2340 V.Fm.Ro model, Sanya Gallenkamp). The temperature was maintained at 28 ^{o}C in the day and 24 ^{o}C at night and the photoperiod was at a constant 12 h cycle. A spectroradiometer was used to measure the amount of photosynthetically active radiation (PAR) produced by the fluorescent tubes. The PAR level at the jar lid level was 11.7% of total radiation. The photon flux density at the jar lid level was 420 µmol m^{-2} d^{-1}. The temperature, photoperiod, and irradiance levels used in this study have successfully produced micro-tubers in the past (Ng 1988). However, the irradiance was increased to 720 µmol m^{-2} d^{-1} at 142 days after culturing to enhance the growth rate. In Experiment II, there were also 13 treatments and each treatment consisted of 10 jars (one explant /jar) with each jar being a replicate. The light source, white Philips TLD 36 W/35 fluorescent tube, was located above the shelf on which jars were placed horizontally along the length of the shelf. Temperature was maintained at 22 ± 2 ^{o}C and photoperiod at a constant 16 h cycle. The PAR intercepted at the jar lid was 12.4% of total radiation. The photon density at the same level was 720 µmol m^{-2} d^{-1}.

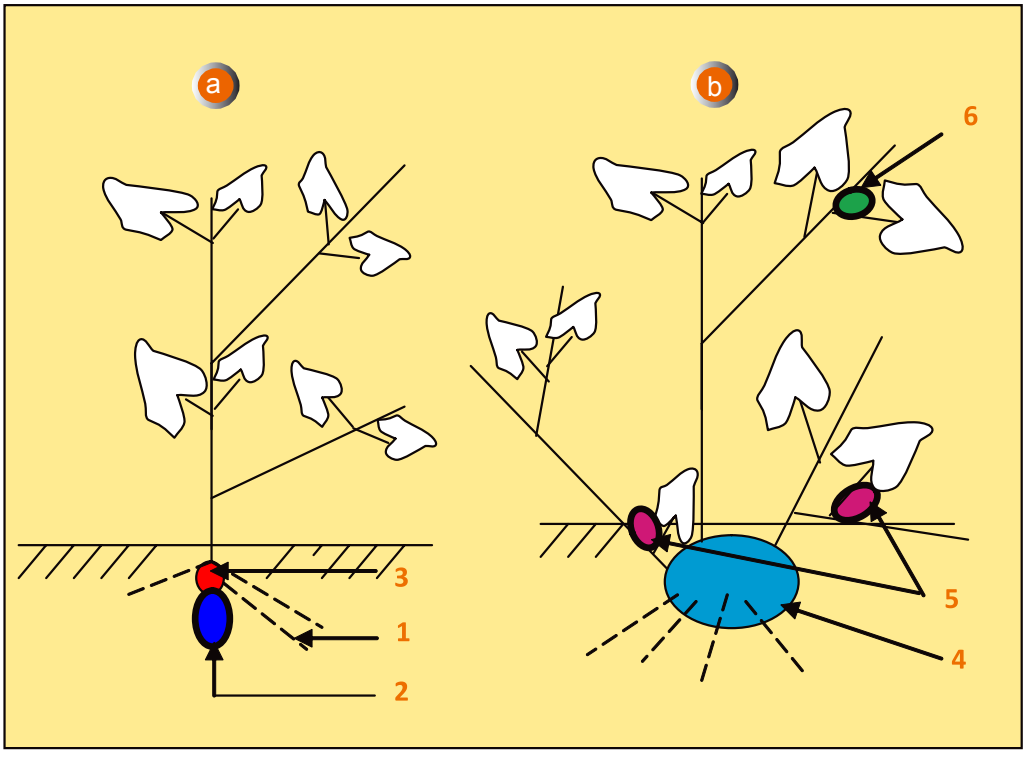


Figure 16. Schematic representation of tuber and root origins in plantlets. a. shows origin of feeder roots (1) and basal micro-tubers (2) attached to a small mass of cells at base of stem (3). b. shows origin of stems and feeder roots from a callus (4) and the development of micro-tubers from lower leaf axils (5) and upper leaf axils (6).

Micro-tuber initiation, harvest, storage conditions, and data analysis

Experiments commenced 5–6 March 2002. Micro-tuber initiation was marked by the emergence of a small mass of cells at the base of the main vine and/or from a node on a lateral branch (Fig.16). A tuber was ready to be harvested when more than 60% of its surface had changed from whitish or greenish white to a reddish brown or brownish color. After harvest, the weight of the micro-tuber was recorded and observed for external signs of renewed growth, i.e., sprouting/appearance of the ASB. Thereafter, micro-tubers were rinsed in sterile distilled water, left to dry, and then put in labeled sterile test tubes (one micro-tuber/test tube). All micro-tubers were stored in a growth cabinet in the dark at day and night temperatures of 28 ^{o}C and 24 ^{o}C and 80% RH. During storage, micro-tubers were observed every 7 days for the presence of sprout(s) and the date of such an occurrence was recorded.

The duration of dormancy was calculated as the difference, in days, from the date of micro-tuber initiation to the date of ASB. The effects of treatments on dormancy were analyzed using the non-parametric survival data analysis tool (Collet 2003) run on SAS v8 computer software.

Findings

Effects of PGRs on shoot development and tuber origin

With treatment in FLU, stems/vines and feeder roots emerged from a callus and the stem and leaves were bleached but this bleaching effect wore off by the later stages of growth. In the controls and other PGR treatments, there were no bleached vines and leaves, and all the micro-tubers produced exhibited dormancy. Generally, a nodal explant developed into a plantlet with one main vine, and micro-tubers developed from a small whitish mass of cells at the base of the vine that also gave rise to feeder roots (see Fig. 16). In a few plantlets, however, more than one green vine was produced from a callus and micro-tubers were produced from the axils of lateral leaf nodes around the upper region of the stem.

Micro-tubers emerged mostly from the first two nodes of a vine or the first two nodes of a branch emerging from the first two nodes (see Fig.16). These micro-tubers are hereafter referred to as micro-tuber initiated from “lower nodes”. The presence of numerous stems, branches, and feeder and tuber roots (roots emerging from the tuber) resulted in the formation of a dense cover of roots around the lower portion of plantlets making it difficult to observe the date of sprouting. A number of micro-tubers also formed in the upper nodes towards the shoot tip: these were developed late during growth and exhibited dormancy. All micro-tubers were similar to underground tubers. The relationship between the origin of micro-tubers and the state of dormancy expressed (non-dormant or dormant) is unclear. Although it is known that the nodes of *Dioscorea* spp. maintain the capacity to differentiate into a branch, flower, leaf, and/or tuber, the formation of micro-tubers from leaf axils is not common in *D. rotundata.* The formation of late, dormant upper node tubers may be related to a decline in FLU levels in the upper nodes (observed as the return of color in the leaves and stems).

Effects of FLU on dormancy and tuber initiation

In the controls and most PGR treatments, sprouting was observed after February 2003, i.e., about 360 days after explant culture. In the FLU treatments, all micro-tubers emerging from lower nodes were already sprouting (with some possessing vine(s) and leaves) by August 2002 in both experiments, i.e., 120 to 180 days earlier than the control. The number of sprouting and non-sprouting micro-tubers observed at harvest and their location of origin on the plantlet are presented in Table 13. In 30 µM FLU, 85% of the micro-tubers were produced from the lower nodes in Experiment I and 100% in Experiment II. At a lower concentration of FLU, i.e., 10 µM FLU, 46% of micro-tubers were produced from the lower nodes in Experiment I and 69% in Experiment II. The few micro-tubers emerging from the base of the stem and leaf axils exhibited dormancy.

Table 13. Effects of 10 and 30 µM FLU on the number of micro-tubers originating at three positions and the percentage germination (in parentheses) at harvest in Experiments I and II.

Treatment	Position		
	Lower nodes	Base of stem	Upper nodes
Experiment I			
FLU 10 µM	17 (100%)	4 (0%)	16 (0%)
FLU 30 µM	57 (100%)	0	9 (0%)
Experiment II			
FLU 10 µM	11 (100%)	6 (0%)	0
FLU 30 µM	7 (100%)	0	0

The production of very small lower node micro-tubers (< 0.5 g) in FLU treatments compared with other PGR treatments and the control is suggested to relate to the fact that the micro-tubers sprouted soon after initiation with too little starch from which to draw. In addition, the long length of vines (up to 10 cm in some tubers) suggests that a considerable amount of stored energy in the tubers had been used for growth. Therefore, the possibility that FLU may have a direct, negative effect on tuber weight is doubtful.

Possible role of ABA in yam tuber dormancy

The role of ABA in yam dormancy and the mechanism of action of FLU on yam tuber dormancy are unclear and cannot be explained adequately because of insufficient data. However, it is clear that endogenous ABA content increases in yam tubers during development and attains a maximum at vine senescence, and that dormant tubers are high in ABA content. It is known also that FLU causes early sprouting in maize seeds (Hole et al. 1989), the sunflower (*Helianthus annuus*) embryo (Le Page-Degivry and Garello, 1992), potato micro-tubers (Suttle and Hultstrand 1994) and in the bulb of lily (Kim et al. 1994**)**. Suttle and Hultstrand (1994) showed that 44% of potato tubers sprout 21 days after culture in 10 µM FLU, while sprouting occurred 63 days after culture in the control. Reversal studies have also shown that the effect of FLU can be reversed following the exogenous application of ABA (Hole et al. 1989; Le Page-Degivry and Garello 1992; Suttle and Hultstrand 1994; Yamazaki et al. 1999). Evidence from molecular studies also supports that FLU acts via the inhibition of ABA biosynthesis (Sanderman and Boger 1989; Sandmann and Mitchell 2001; Srivastava 2002; Liondgren et al. 2003).

The possibility that ABA is directly produced from farnesyl diphosphate (FPP) via 1-deoxy-ABA pathway has been discredited by the work of Creelman and Zeevaart (1984) cf Srivasrava (2002). Another reason why FLU may be thought to act through a completely different pathway or at least that it induces significant adverse side-effects on plant performance arises from its bleaching effect on leaves and stems. Although there is a

dearth of information on this with regard to yam, there is ample evidence to support that FLU inhibits enzymes in the carotenoid pathway, such as the inhibition of the enzyme phytoene desaturase (PDS), which catalyzes the conversion of phytoene to carotenoids rather than the inhibition of the enzymes in the chlorophyll biosynthetic pathway such as protoporphyrinogen oxidase (PPO). PPO catalyzes the conversion of protoporphyrinogen-IX to protoporphyrin-IX, a photo-sensitizer whose activity leads to the oxidative degradation of lipids in cell membranes, hence causing damage to cellular constituents, such as the chloroplast. Nevertheless, there is a need to confirm a lack of the chlorophyll biosynthetic pathway of action of FLU in yam. One such research should involve the use of mutants of chlorophyll to test the effect of FLU on the ABA/carotenoid level (Mulwa and Nwanza 2006).

In yam, therefore, there is the possibility that FLU prevents the initiation of dormancy through the inhibition of the biosynthesis of ABA, the dormancy-promoting endogenous PGR. Further work is required to validate this assertion. The efficiency of a potent dormancy-shortening PGR depends on the timing of application. Dormancy can be prevented if its initiation is inhibited during tuber initiation.

Effects of other PGRs on yam tuber initiation and dormancy

The duration from culturing to micro-tuber initiation in the control was 176 days in Experiment I and 76 days in Experiment 2. This delay in tuber initiation reflects the observed slower growth rate in Experiment I. Despite this difference in growth between experiments, PGRs generally had very similar effects (to delay or hasten) on the time to initiation. $AgNO_3$ had no effect on the time of micro-tuber initiation in either experiment compared to the control, whereas 50 µM ABA and CCC delayed initiation by 23 to 45 days. GA_3, however, caused very early initiation relative to the control in Experiment I (83 cf 176 days) but had no effect in Experiment II.

ABA, CCC, and $AgNO_3$ had consistent, but only minimal effects on dormancy with sprouting occurring at about the same time of the year (Table 14). The effects of ethephon and GA_3 on dormancy are still not clear because ethephon does not appear to support shoot growth and hence tuberization (except for three plantlets in ethephon 100 mg L^{-1} in Experiment II which initiated three minute tubers) and GA_3 supports growth and tuberization too poorly. With GA_3, micro-tubers were initiated very early compared with the control in Experiment I (83 cf 176 days) but had no effect in Experiment II and though the micro-tubers were apparently normal, they were very small and most of them shrivelled in storage. The inhibitory effects of ethephon on growth and tuber initiation have been shown in many studies with potato involving much lower concentrations of ethephon (< 2.0 µL/ L of ethylene gas and 0.5 to 50 M ethephon) (Rylski et al*.* 1974; Hussey and Stacey 1984**)**. Similarly, the negative effect of GA_3 in potato shoot growth and tuberization are recognized at even lower concentrations (10^{-7} to $5x10^{-5}$ M and 0.1 to 1 mg/L) (Garcia

Table 14. Effect of PGRs on the 50th percentile duration from tissue culture to sprouting and on the date of 50% sprouting in two different *in-vitro* studies. Explants were cultured on 5 to 8 March 2002 in both studies.

	Study I				Study II			
	50th percentile durations (d)		50th percentile duration of total crop cycle and date of sprouting (2003)		50th percentile durations (days)		50th percentile duration of total crop cycle and date of sprouting (2003)	
Treatments	Culture to micro-tuber initiation	Micro-tuber initiation to sprouting	Duration (d)	Date	Culture to micro-tuber initiation	Micro-tuber initiation to sprouting	Duration (days)	Date
Control	176	246	409	17 Apr	76	275	353	20 Feb
ABA 5 µM	176	277	†	†	82	263	352	19 Feb
ABA 50 µM	199	210	408	16 Apr	102	NA	NA	NA
FLU 10 µM	220	†	†	†	107	NA	NA	NA
FLU 30 µM	220	193	409	17 Apr	NA	NA	NA	NA
CCC 500 mg L^{-1}	209	†	†	†	99	270	366	05 Mar
CCC 2000 mg L^{-1}	221	213	422	30 Apr	100	257	366	05 Mar
$AgNO_3$ 25 µM	192	233	422	30 Apr	83	262	343	10 Feb
$AgNO_3$ 50 µM	185	232	402	10 Apr	76	262	346	13 Feb

Study I (total crop duration): Log-Rank Test = 24.0; DF = 8; pr > Chi Square = 0.002; † = Not estimable.
Study II (total crop duration: Log-Rank Test = 8.31; DF = 5; pr > Chi Square = 0.140; NA = Not analyzed.

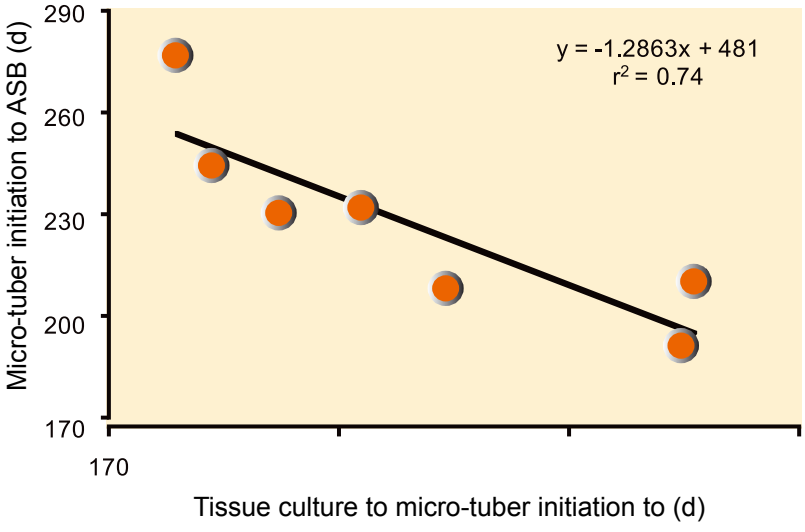


Figure 17. Relationship between the durations from tissue culture to micro-tuber initiation and from tuber initiation to the appearance of an ASB, in 8 PGR treatments plus a control in Experiment I (in a growth chamber).

and Gomez-Campo 1973; Koda and Okazawa 1983; Hussey and Stacey 1984; Fondong et al. 1994). The average duration from micro-tuber initiation to sprouting, i.e., dormancy, was 232 days in Experiment I and 264 days in Experiment II, a comparatively small (32 day) difference given that the average difference in the time of micro-tuber initiation between experiments was 100 days. In Experiment I, the control micro-tubers sprouted 246 days after initiation; CCC and 50 µM ABA shortened this period by about 30 days, whereas 5 µM ABA prolonged dormancy by about 30 days. In Experiment II, the control micro-tubers sprouted 275 days after initiation (a difference of only 29 days from Experiment I). Durations varied by only 18 days and PGRs had no significant effects on dormancy. Generally, durations from culturing to sprouting averaged 418 days in Experiment I and 354 days in Experiment II. The above effects of PGRs on the duration are therefore in the order of ± 5 to 10% only.

The study also shows that where the PGRs prolong the duration from culturing to tuber initiation of dormant tubers, they shorten the duration from tuber initiation to sprouting (Fig. 17) with the relationship being inverse and linear. Recall also that the data from field (growing and storage agroecology) and controlled environment studies also showed that there is an inverse relationship between the duration from planting to harvest and the duration from harvest to sprouting. Hence, it is proposed that, in tubers, the durations from culturing to tuber initiation and from tuber initiation to sprouting are always balanced out to allow sprouting to occur at a specific period of the year, which may be programmed at tuber initiation.

IV

Phases of dormancy, durations, and framework for effective shortening of the duration of yam tuber dormancy

From the preceding sections it is clear that: (1) the total period of yam tuber dormancy may consist of different phases that are associated with different control mechanisms, (2) PGRs are more effective at shortening the duration of dormancy in whole field tubers that are approaching their natural sprouting time than in those at their mid-stage of dormancy, and (3) PGRs can regulate the initiation of dormancy at tuber initiation.

This section presents the definitions and durations of phases of yam tuber dormancy including a definition of yam dormancy by its potential control mechanism. It also provides and discusses a framework for studying, analyzing, and effectively manipulating dormancy in yam. The conclusions are based mainly on results from anatomical studies showing the effects of PGRs on different stages of dormancy and the genesis and development of the shoot apical bud, also on results from experiments on the effects of exogenous PGRs on the duration of whole tuber dormancy as well as other published studies already reported in this book. The bases for the methodology used in this work are briefly discussed below; however, details can be found in Ile (2004).

In potato, the first signs of the release of bud dormancy are manifested at the cellular level (i.e., mitoses preceding cell division and elongation) and these are evident long before visible bud growth is observed. In yam tubers, buds are absent during dormancy and their appearance on the surface of the tuber is the most common (visible) indication of the release of dormancy. The genesis of shoot buds, observed at microscopic levels, occurs long before the buds emerge on the surface of the tuber. These early indications of the onset of vegetative growth are stronger indicators of the release of dormancy than the visible indicators, and hence, represent a good point from which to start studies into the control of the release of dormancy. Indeed, in potato the application of 2-chloroethanol resulted in cell division and elongation within 72 hours of application (Rappaport and Wolf 1969; Rylski et al. 1974). In yam, however, there is a dearth of information on the effect of PGRs on the genesis and development of shoot apical buds. To clearly explain the effects of PGRs (gibberellin, 2-chloroethanol, thiourea: each at two concentrations) on anatomical development and how this varied with the stage of development, the anatomical changes occurring in the tuber from dormancy through shoot bud formation were determined. The results also provide some explanation for the minimal effect of PGRs on the duration of whole tuber dormancy.

Mini-tubers were harvested at various stages of the life cycle of the tuber (149 and 179 DAP; during tuber growth but prior to vine senescence, and during tuber storage (269 and 326 DAP). At each harvest time, 10 tubers were washed and sterilized and six tuber portions were cut (under aseptic conditions) from the head regions of each tuber. Each tuber portion/ tuber was labeled and given one of six treatments (Table 14). After treatment, the portions were allowed to dry out and then stored in a humid dark box [see Ile (2004) for more details] for 6–12 days. Tissue sections were cut from the tuber portions (using a rotary microtome) at 6 and 12 days after a treatment. PGR treatments were applied only at times when tubers were still visibly dormant (absence of obvious sprouting loci or external shoot bud/sprout on the tuber surface). The PGRs tested were selected based on the inference that they would be more likely to prolong whole tuber dormancy (duration to sprouting) or to shorten it rather than to do both [see recent review on the effects of PGRs on whole tuber dormancy by Craufurd et al. (2001) and Ile (2004)].

Effect of PGRs on shoot apical bud development

Observations at 6 or 12 days after PGR treatment at 149 DAP (30 days before vine senescence) and at 179 DAP (vine senescence) show that the anatomical structures were similar to those in Figure 2. This implies that tubers that are harvested as early as 149 DAP are dormant and PGRs were unable to break their dormancy by stimulating activity in the meristematic layer to form a TGM or SAM in any of the 54 sections examined.

The first manifestation of a TGM was recognized at 269 DAP in the control tubers but only in one replicate. In the same replicate (tuber), a more advanced TGM was observed following treatment with 60 ml L^{-1} 2-chloroethanol (CLE). No other PGR treatment had any effect at 269 DAP.

At the last treatment date (326 DAP), when a TGM 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 TGM was significantly (P<0.001) affected by the PGR treatment (Table 15). The mean predicted probability of a TGM in tissue sections from the control, CLE, and thiourea treatments was 0.8 to 1.0, i.e., most sections had a TGM. In contrast, treatment with 1000 mg L^{-1} GA_3 significantly reduced the probability of a TGM being present. Given that 6 days after treatment most control tuber sections had a TGM, 1000 mg L^{-1} GA_3 may have reduced the probability of a TGM by slowing down the rate of cell differentiation or by de-differentiating these meristematic cells.

More advanced stages of SAM were also observed at 326 DAP, and there were significant effects (P < 0.001) of PGRs on the probability of a SAM being present (Table 15). In the control tuber portions no sections had advanced stages of shoot apical bud

Table 15. Effects of GA3, CLE, and thiourea on the probability of the presence of the (TGM) and an advanced stage of shoot bud development (SAM) in tissue sections at 6 days after treatment at 326 DAP.

	Predicted probability of the presence of				
	TGM			SAM	
PGR treatments	Mean	SD	Odds Ratio	Mean	SD
Control	0.89	0.19		0.00‡	0.00
150 mg L^{-1} GA_3	0.78	0.30	0.88	0.11	0.15
1000 mg L^{-1} GA_3	0.44	0.53	0.50	0.22	0.23
40 ml L^{-1}CLE	1.00	0.00*	1.13	0.67	0.39
60 ml L^{-1} CLE	0.89	0.19	1.00	0.67	0.39
Thiourea 20 g l^{-1}	0.80	0.28	0.90	0.33	0.28

* In 40 CLE sections, all had a TGM. ‡ In the control, no section had a SAM.

development and therefore Odds Ratios could not be calculated to compare PGR treatments with the control. However, treatments with CLE clearly increased the probability ($P < 0.001$) of a SAM being present (0.67 in both treatments), compared with the control (0.00), GA_3 (0.11 to 0.22), or thiourea (0.33).

With whole tubers, the effect of PGRs on the appearance of a shoot bud (ASB; external shoot bud) on the surface of the tuber was determined by soaking the whole tubers, for defined periods of time, in eight PGR treatments at four different dates (183, 214, 269, and 331 DAP). There were two controls, untreated control (i.e., tubers that received no water or PGR treatments) and treated control (sets of tubers soaked in water at each treatment date). The total duration from planting to 50% ASB was 331 days in the untreated control. Thus, prior to treatment at 331 DAP, all sprouts were removed.

The effect of treatments on ASB is shown in Figure 18. Ethylene-related PGRs were more likely to lead to earlier ASB (by shortening the duration from treatment to ASB) and synchronized the timing of ASB; GA_3 tends to prolong ASB. The tendency for ethylene-based treatments to shorten the duration is higher if PGRs are applied early (at 183 or 214 DAP); they would be most likely to prolong the duration when applied later (at 269 and 331 DAP). The response to a low concentration of GA_3 is similar to those of ethylene-based PGRs when applied early. Furthermore, the degree to which PGRs either shortened or prolonged the duration to ASB was minimal. Ethephon, the most effective ethylene-related PGR in this study, shortened the duration to ASB by just over 20 days and 1000 mg L^{-1} GA_3 prolonged the duration to ASB by the same length of time. In addition, in all treatments and irrespective of tuber age at the time of treatment, 50% ASB occurred at about the same month of the year (i.e., from 26 March to 9 April) and within the usual sprouting band in *Dioscorea* spp. (from February to April).

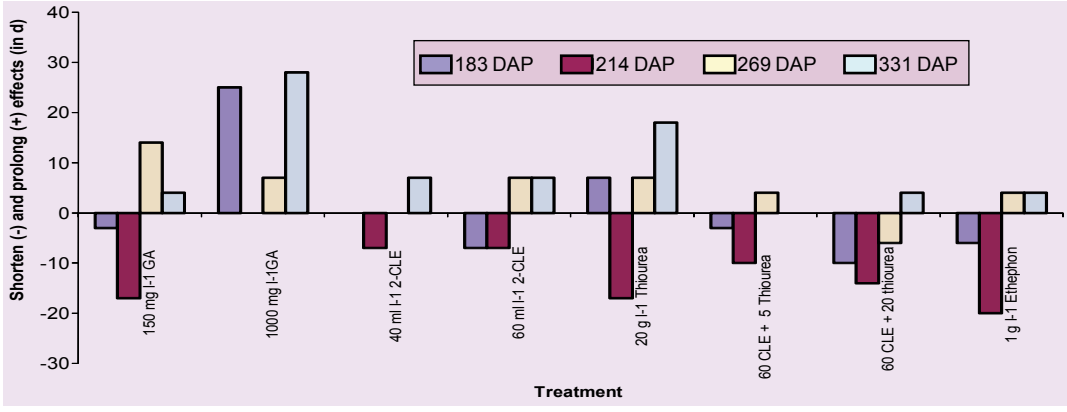


Figure 18. The effect of PGRs on duration from treatment at 183, 214, 269, and 331 DAP to ASB in *D. rotundata* tubers. Treatments were:

(1) 150 mg l-1 GA, (2) 1000 mg l-1 GA, (3) 40 ml l-1 2-chloroethanol (2-CLE), (4) 60 ml l-1 2-chloroethanol, (5) 20 g l-1 thiourea, (6) 60 ml l-1 2-chloroethanol + 5 g l-1 thiourea, (7) 60 ml l-1 2-chloroethanol + 20 g l-1 thiourea.

Generally, ethylene-producing compounds have been reported to slightly hasten sprouting *(*i.e., to shorten the time to the emergence of the external shoot bud); GA_3 delays sprouting and re-imposes bud dormancy in sprouting tubers (summarized in Passam 1982; Degras 1993; Craufurd et al. 2001; Ile 2004). Gibberellin antagonists have also been reported to hasten sprouting (Shiwachi et al. 2003), suggesting an important role for GA_3 in the control of dormancy in yam. These effects of GA_3 are in marked contrast to those in potato and in dormant seeds, where GA_3 usually breaks dormancy (Suttle 1996). In general, exogenous applications of PGRs have hastened sprouting by only about 33 days (see Passam 1982 and Ile 2004 for examples). Likewise, variability in storage environment causes sprouting to vary by only up to 30 days (Shiwachi et al. 2003). This lack of a major effect on duration to sprouting is interpreted to be caused by the inability of PGRs and environmental treatments to induce shoot apical development (i.e*.,* TGM formation). In var TDr 131 in this study, the TGM appears about >75% of the way through the period from tuber initiation to sprouting, leaving a relatively small proportion of the remaining period to sprouting that can be shortened by PGRs and the storage environment.

Phases of yam tuber dormancy and their potential control mechanisms

Phase I of dormancy and control: This phase begins at tuber initiation and ends with TGM formation. It is unaffected by many sprout-inhibiting and -promoting PGRs (Fig. 19). It appears to correspond to the deep dormancy, endo-dormancy, defined by Lang et al. (1987). This phase of yam tuber dormancy is proposed to be controlled by an intrinsic “clock”, which is unaffected by changes in temperature and/or photoperiod as happens with dormancy in seeds of *Mesembryanthemum* spp. (Leopold 1996). It is therefore termed the endo-dormant/ true dormant phase of yam tuber dormancy. The assertion is based on the following:

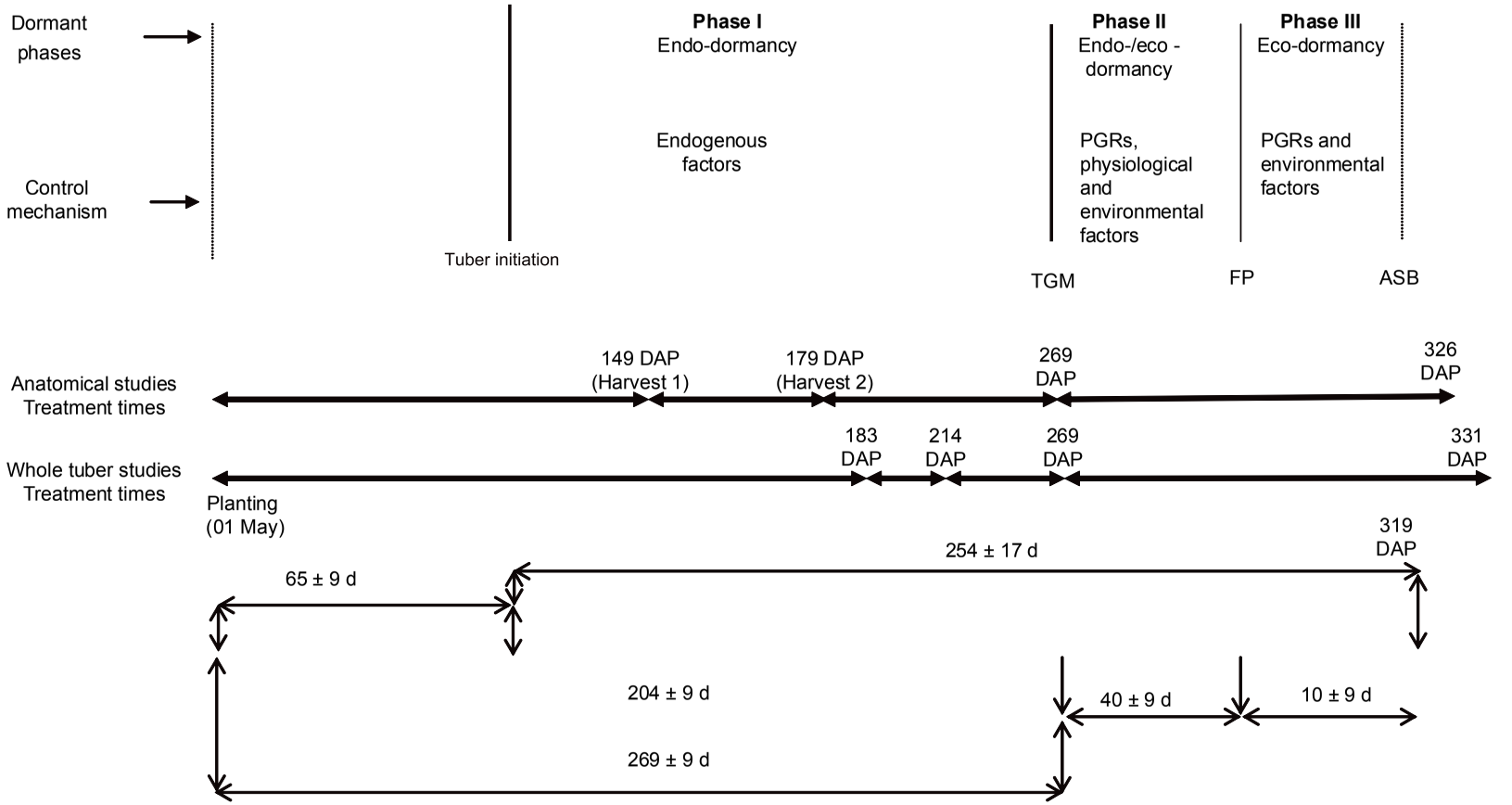


Figure 19. Presentation of phases of *D. rotundata* tuber dormancy, durations, and mechanism of control.

1. the inability of PGRs to induce the end of Phase I of dormancy,
2. the inability of exogenous PGRs to drastically shorten the duration of dormancy even if applied very early, prior to vine senescence,
3. the inability of a change in growth agroecology, within or across continents, to drastically affect the duration to sprouting or have an effect on sprouting time [(Passam et al. (1982); Ile (2004)],
4. the inability of agroecological conditions in natural, fluctuating storage to drastically affect the duration to sprouting (Ile 2004),
5. the inability of a constant, favorable temperature, photoperiod regimes, and different soil fertility levels (imposed early during growth or later during storage) to greatly shorten the duration to sprouting,
6. the supposition in potato that dormancy also begins early during tuber initiation rather than later (Burton et al. 1992), and that true dormancy ends well before the earliest signs of shoot bud differentiation are recognized (Jayakumar et al. 1993).

***Phase II of dormancy and control*:** This phase of dormancy begins at TGM and ends at the formation of the FP/shoot apical bud (Fig. 19). At this phase, PGRs can affect the progress towards sprouting. Because this phase occurs after the month of November in Nigeria, which coincides with the main tuber harvest and storage periods, and because most studies relating to the effects of changes in endogenous factors and environmental factors on the timing of sprouting fall within this phase, it is logical to infer that such effects are indeed effects on Phase II of dormancy rather than on the total dormant period.

Hence, the fact that the TGM appears about 85% of the way through the period from tuber initiation to sprouting, leaving only a relatively small proportion of the total period (Fig. 19) that is affected by PGRs and environmental factors, etc., explains why only a small gain in the earliness is achieved when tubers are treated well after harvest at vine senescence.

***Phase III of dormancy and control*:** This phase of dormancy begins from FP to ASB. The manifestation of one or more complete shoot apical bud(s) (FP) is known to coincide with the appearance of sprouting loci on the surface of the tuber. This event therefore marks the start of another significant stage: from the development of shoot apical bud(s) within the tuber to emergence on the surface of the tuber as sprout(s)/external shoot bud(s). Although this phase should ideally not be referred to as a phase of dormancy (since the appearance of a sprouting locus marks the end of visible dormancy), it is defined as such for two reasons: (1) because the sprouting locus is often not easily recognized and so many of such tubers are still being considered as dormant, (2) sprouting is widely used to mark the end of dormancy in many studies (see Annex A), perhaps due to ease of recognition. During this phase, further growth and development of the sprout are affected greatly by the environmental factors with an impact on it, e.g., temperature and the direct effect of

exogenous PGRs. Thus, like Phase II, Phase III of dormancy is controlled by exogenous PGRs, notably GA_3, which can affect sprout development directly through the inhibition of sprout growth, and by environmental conditions, such as air temperature and RH. Hence, Phase III of yam tuber dormancy can be considered mainly as an eco-dormant phase.

Durations of phases of dormancy and yam growth stages

The duration of the three phases of dormancy below are defined based on results from both anatomical and whole tuber studies (Fig. 19).

Duration of Phase I of dormancy: This phase begins at tuber initiation and ends with TGM formation. With TGM occurring by 269 DAP, the length of this phase is estimated to be 204 ± 9 days, i.e., 269 DAP minus 65 DAP.

Duration of Phase II of dormancy: This phase begins at TGM and ends at complete shoot apical bud (FP) formation. With the first ASB occurring at 319 DAP, the average duration of Phase II was estimated at 40 days; (319–269)–10 (number of days from FP to ASB). Generally, however, the duration of this phase may vary, even under natural conditions, by about 17 days. Thus, for the set of nonsprouting tubers treated at 326 DAP, the phase lasted 57 days (i.e., 326 DAP – 269 DAP).

Duration of Phase III of dormancy: This phase begins at FP and ends at ASB. With the earliest indication of ASB occurring at 319 DAP, the duration of Phase III is about 10 days (i.e., 319–269–40 DAP). This is in agreement with the work of Onwueme (1973) where sprout formation/ASB occurred 7 days after the appearance of sprouting loci/ FP in *D. rotundata* and 10 days afterwards in *D. alata* varieties.

Below are estimates of (1) duration of total crop cycle, (2) duration from planting to tuber initiation, and (3) duration from tuber initiation to sprouting. The estimates are average values derived from data presented in this book and other publications.

***Total crop cycle*:** The average duration from planting or culturing (single nodal explant tissue culture) to sprouting ranges from 274 to 353 days with an average of 314 ± 56 days (Fig. 19). The presence of large variability in duration represents differences in species/ varieties, environmental conditions for storage and growing, mark of sprouting (ASB or length of sprout), chemical/PGR treatments, etc. Values obtained in past field studies (Okoli 1980b, Swanell et al. 2003, Shiwachi et al. 2003, etc.) are within the range presented above.

***From planting to tuber initiation*:** In two *in-vitro* studies with varying temperature and photoperiod conditions (details of method in Section III), the durations from culturing to micro-tuber initiation were 68 and 76 days in the controls. In a glasshouse study, small whitish tubers weighing about 2 g and 10 g were observed by 76 days, indicating that the tubers must have been initiated earlier and are within the range observed for micro-tubers.

Data from other published works show that the duration from planting to tuber initiation ranges from 53 to 74 days, irrespective of the differences in field conditions and the varieties of *D. rotundata,* (including TDr 131) grown (Njoku et al. 1973; Onwueme 1975; Trouslot 1978; Swanell et al. 2003). In these field studies, planting was done soon after sprouting or at about sprouting time. The average duration from planting to tuber initiation is estimated as 65 ± 9 days (see Fig. 19).

***From tuber initiation to ASB*:** On average, this duration is 258 ± 14 days (Fig. 19). This is derived from results of three *in-vitro* studies where the durations were 246, 275, and 254 days. At the moment, estimates of this duration under field conditions are scarce and difficult to assess.

In summary, in spite of the fact that all tubers experienced close to uniform conditions, the duration of Phase II to Phase III varied by < 20 days and the difference between the first ASB and 50% ASB was 12 days. Results from other field experiments and controlled environment studies show that the total duration from planting to ASB could vary from 274 to 353 days with an average of 314 days. Values that fall within this range have also been reported by other workers (Okoli 1980b; Swanell et al. 2003; Shiwachi et al. (2003). It is estimated, therefore, that there will be a wider variation in the duration of Phases II and III under field conditions, up to 70 days, depending on the effects of factors controlling the progress of each of the two phases. Variations in the duration of the entire crop cycle (the most commonly measured variable) will range from 274 to 353 days with an average of 314 days due to differences in (1) the effects of factors that influence the duration from planting to tuber initiation (including the age/phase of dormancy of the plant material), (2) the chosen mark of the end of visible dormancy, such as the appearance of sprouting loci, ASB, a sprout of a defined length, etc., (3) differences in species/varieties, and (4) the durations of Phases II and III of dormancy. In contrast, the duration of Phase I of dormancy is somewhat fixed, at about 200 days, being constitutively maintained and unaffected specifically by external factors.

Practical implications of the identified phases of dormancy

The identification of the phases of yam tuber dormancy and other growth stages, their durations, and potential control mechanisms provides a useful framework for effectively studying and manipulating dormancy in *Dioscorea* species.

When the objective of a study is to enhance the synchrony of sprouting or to induce only a small shortening of dormancy without drastically altering the cropping cycle, the tubers may be harvested at the end of the main growing season and subjected to inductive conditions for sprout formation. Earlier applications are also recommended (at 189 and 214 DAP in particular) rather than later (at 269 or 331 DAP). It is important to note that the recommendation of an early PGR treatment does not imply that PGRs affect Phase I of dormancy (even though 189 and 214 DAP fall within Phase I of dormancy). Recall that

(1) in the absence of a TGM, which is the situation during Phase I of dormancy, PGR applications do not lead to TGM formation, (2) anatomical observations of tuber sections taken about 30 days after treatment at 214 DAP (i.e., tubers treated with ethephon) showed no signs of TGM formation, (3) the presence of numerous bumps and extensive shrivelling in tubers treated with ethephon by 214 DAP did not imply the presence of a shoot apical meristem; sections revealed no TGM or SAM, and (4) PGRs are effective in altering the duration of Phases II and III. Hence the often greater effects of an early application of PGRs may be due to (1) better permeability of the skin of young whole tubers to PGRs compared with older tubers, and (2) the concentration of PGRs at target structures (for ethylene-based PGRs, a high concentration just before TGM formation appears to shorten dormancy and when applied after the formation of the FP it appears to prolong/re-induce dormancy. Although the permeability of the yam tuber periderm by PGRs has not been well investigated, the presence of a thin whitish periderm in young tubers rather than in older ones and the absence of waxy suberized cork cells suggest a higher potential for PGR absorption. Follow-up studies are recommended that verify the permeability of the tuber periderms and the concentrations of PGRs taken up over the various phases of dormancy. Also recommended are studies that determine whether PGRs maintain their nature during the waiting period in the tuber.

With this framework, it is easy to see why the PGRs and other environmental factors tested in the past have only slightly shortened the duration to sprouting in whole yam dormancy. This lack of a major effect framework on the duration to sprouting is due to the inability of PGRs and environmental treatments to induce shoot apical development (i.e*.,* TGM formation) during Phase I of dormancy.

With the framework, it is now possible to estimate reasonably the degree to which the duration to sprouting is affected by any exogenous treatments. A treatment may be said to have broken dormancy (i.e*.,* Phase 1 of dormancy) if it brings about ASB in the first 180–210 days after planting in February or vine emergence in February, or if treatment induces the occurrence of ASB 90 or more days earlier than the control.

It would now be much easier to relate the effects of treatments on dormancy to specific physiological states (phases of dormancy). In the past, conclusions on the control of yam tuber dormancy were difficult because of the inability to relate the effects of PGRs, etc., to any physiological state.

The findings reported in this book would stimulate the establishment of more in-depth explanations of the mechanism controlling tuber dormancy, e.g., the effects of PGRs on subcellular activities relating to the progress towards ASB.

The framework can also form a base for effectively studying and analyzing dormancy in other yam species and other root and tuber crops exhibiting dormancy.

V

Conclusion

It is interpreted that the inability of temperature, PGRs, etc., to shorten the dormant period by more than 50 days is not indicative of their inability to break Phase I of dormancy but rather that they act by influencing the duration of the pre-tuber growth period and the rate of progress towards ASB (i.e., Phases II and III of dormancy). Furthermore, the observed inverse relationship between the duration from culturing to micro-tuber initiation and the duration from micro-tuber initiation to sprouting suggests that the duration of the former is memorized and used to determine the duration of the latter so as to ensure that ASB occurs at about the same period of the year.

The initiation of nondormant micro-tubers from lower whitish vine nodes suggests that they are initiated from nodes that are void of or low in carotenoids and as such, low in ABA, the dormancy-promoting PGR. Hence, ABA may regulate the initiation of dormancy at tuber initiation and development. Also, the formation of tubers at locations other than at the base of main stems may be a survival mechanism, which may bear little or no relationship to the state of dormancy. Yam have not been known to sprout in August–September, hence the occurrence of ASB at this time in FLU treatments has a huge potential significance in agriculture. This finding can serve as a springboard for (1) developing protocols that break endo-dormancy in underground tubers, (2) developing protocols of preventing dormancy in seed and clonal yam tubers, which will make planting time more flexible and hence help to increase the pace of breeding for improved yam varieties and indeed increase total annual yam production, and (3) the development of techniques for producing seed tubers from small sprouting micro-tubers. This would increase the supply of planting material and, in the long run, contribute to the doubling of tuber production and availability for food and planting material. One important question that needs to be addressed is the nature of the mode of action of FLU on yam tuber dormancy—is the effect temporary or permanent?

References

Agbo, F.M. 1992. IITA/ NRCRI Root Crop Research Technology Transfer Course Manual. National Root and Crop Research Institute, Umudike, Nigeria.

ANB-BIA. 2003. West Africa: Improving Yam Production Technology. African News Bulletin-Bulletin d'Information Supplement, Issue/Edition Nr 463-01/10/2003. http://ospiti.peacelink.it/anb-bia/nr463/nr463.html

Asahina, H., R. Yoshikawa, and Y. Shuto. 1998. Effects of batatasin III and its analogs on gibberellic acid-dependent alpa A_1 Induction in embroyo-less barley seeds and on cress growth. Bioscience, Biotechnology, Biochemistry 62**:** 1619–1620.

Asiedu, R., S.Y.C. Ng, K.V. Bai, I.J. Ekanayake, and N.M. Wanyera.1998. Genetic Improvement. Pages 63–104 *in:* Food Yams: Advances in Research, edited by G.C. Orkwor, R. Asiedu, and I.J. Ekanayake, NRCRI and IITA, Ibadan, Nigeria.

Barker, D.J., J.D.H. Keatinge, and R. Asiedu.1999. Yam dormancy: potential mechanisms for its manipulation. Tropical Science 39: 168–177.

Bell, A. 1983. Mineral content of yam tubers: raw, boiled, and as flour. Pages 157–160 *in*: Tropical Root Crops. Production and uses in Africa. Proceedings of the second Triennial symposium of the International Society for Tropical Roots Crops, AB, Douala, Cameroon, 14–19 August 1983.

Burkill, H.M. 1960. Organography and evolution of Dioscoreacea, the family of yams. Botanical Journal of the Linnaean Society 64: 319–412.

Burkill, H.M. 1985. The Useful Plants of West Tropical Africa. Vol. 1. Families A–D. 2nd edition. Royal Botanic Gardens, Kew, UK.

Burton, W.K., A. Van Es, and J.K. Hartmans.1992. The physics and physiology of storage. Pages 608–727 *in*:The Potato Crop edited by P.M. Harris, Chapman and Hall, London, UK.

Campbell, J.S., V.O. Chukwueke, F.A. Teriba, and H.V.S. Ho-A-Shu. 1962. Some physiological investigations into white Lisbon yam (*Dioscorea alata* L.) I. The breakage of the rest period in tubers by chemical means. Empire Journal of Experimental Agriculture 30**:** 108–114.

Cibes, H.R. and J. Adsuar. 1966. Effects of chloroethanol and thiourea on the germination and relative yield of the yam (*Dioscorea alata*). The Journal of Agriculture of the University of Puerto Rico 50: 201–208.

Coleman, W.K., D.J. Donnelly, and S.E. Coleman. 2001. Potato microtubers as research tools: A review. American Journal of Potato Research 78: 47–55.

Collet, D. 2003. Modelling Binary Data. 2nd edition. Chapman and Hall, London, UK

Coursey, D.G. 1976. The Origins and Domestication of Yams in Africa. Pages 383–408 *in*: Origins of African Plant Domestication, edited by J.R. Harlan. Mouton, The Hague, the Netherlands.

Coursey, D.G. 1967. Yams. Longman, Green and Co. Ltd, London.

Craufurd, P.Q., R.J. Summerfield, R. Asiedu, and P.V. Vara Prasad. 2001. Dormancy in yams (*Dioscorea* spp.). Experimental Agriculture 37: 147–181.

Degras, L. 1993. The Yam: A Tropical Root Crop*,* edited by R. Costo. Macmillan, London, UK

FAO (Food and Agriculture Organization). 2005. FAO production year, Rome, Italy.

Ferguson, T.U. 1972. The propagation of *Dioscorea* spp. by vine cuttings: A critical review. Tropical Root Crops Newsletter 5:4–7.

Ferguson, T.U. 1973. Tuber Development in Yams: Physiological and agronomic implications. Pages 72–77 *I i*: Proceedings of the Third International Symposium of International Society for Tropical Root Crops held at IITA, Ibadan, Nigeria, edited by C.L.A. Leakery. IITA, Ibadan, Nigeria.

Fondong, V.N., C. Martin, and F.S. Nana. 1994. Effect of GA_3 on the in vitro growth and development of four potato (*Solanum tuberosum* L.) genotypes. Pages 145–148 *in:* Proceedings of the Fifth Symposium of the International Society of Tropical Root Crops—Africa Branch. ISTRC.

Garcia-Torres, L. and C. Gomez-Campo. 1973. In vitro tuberization of potato sprouts as affected by ethrel and gibberellic acid. Potato Research 16: 73–79.

Girardin, O., Z. Farah, C. Nindjin, D. Otokore, P. Zaoungrana, P. Stamp, and D. Escher. 1998. Use of gibberellic acid to prolong dormancy and reduce losses during traditional storage of yams. Journal of Science of Food and Agriculture 77: 172–178.

Gupta, S., S.N. Sobti, and C.K. Atal. 1979. Tuber dormancy in *Dioscorea composita* Hemsl. Effect of growth regulators. Indian Journal of Experimental Biology17: 612–614.

Gyansa-Ameyaw, C.E. 1987. Microsett and slip propagation of *Dioscorea rotundata* seed yam. PhD thesis, Department of Crop Science submitted to the Faculty of Agriculture, University of Ghana.

Hahn, S.K. 1995. Yams: *Dioscorea s*pp. (*Dioscoreaceae*). Pages 112–120 *in*: Evolution of Crop Plants, edited by J. Smartt and N.W. Simmonds. Longman Scientific and Technical, UK.

Hasegawa, K. and T. Hashimoto. 1974. Gibberellin-induced dormancy and batatasin content in yam bulbils. Plant Cell Physiology 15**:** 1–6.

Hashimoto, T. and S. Tamura. 1969. Effects of abscisic acid on sprouting of aerial tubers of *Begonia evansiana* and *Dioscorea batatas*. Botanical Magazine Tokyo, 82: 69–75.

Hashimoto, T. and M. Tajima. 1978. Structures and synthesis of the growth inhibitors batatasins IV and V, and their physiological activities. Phytochemistry 17: 1179–1184.

Hashimoto, T., K. Hasegawa, and A. Kawarada. 1972. Batatasin: new dormancy-inducing substances of yam bulbils. Planta 108:368–374.

Hashimoto, T., K. Hasegawa, H. Yamaguchi, M. Saito, and S. Ishimoto. 1974. Structures and synthesis of batatasins, dormancy-inducing substances of yam bulbils. Phytochemistry 13: 2849–2852.

Hayward, L.A. and H.M. Walker.1961. The Effect of Pre-harvest Foliar Spray with Maleic Hydrazide on the Storage of Yams. Pages 107–115 *in*: Report of the West African Stored Products Research Unit. Federal Ministry of Commerce and Industry, Abuja, Nigeria.

Hemberg, T. 1985. Potato Rest. Pages 353–388 *in*: Potato Physiology, edited by P.H. Li. Academic Press, New York, USA.

Hole, D.J., J.D. Smith, and B.G. Cobb. 1989. Regulation of embryo dormancy by manipulation of abscisic acid in kernels and associated cob tissue of *Zea mays* L. cultured *in vitro*. Plant Physiology 91: 101–105.

Hussey, G. and N. Stacey. 1984. Factors affecting the formation of in vitro tubers of potato (*Solanum tuberosum* L.). Annals of Botany 53: 565–578.

IITA. 2004. Project 5- Improvement of Yam-based Systems. Medium-term Plan, IITA, Ibadan, Nigeria.

IITA. 1995. Background Documentation Workshop on Roots and Tuber Research in the CGIAR. IITA, Ibadan. Nigeria.
IITA. 1997. Project 13- Improvement of Yam-based Systems. Annual Report 1997. IITA Ibadan, Nigeria.
IITA. 1979. Root and Tuber Improvement Program Annual Report 1979. IITA, Ibadan, Nigeria.
IITA. 1976. Annual Report. IITA, Ibadan, Nigeria.
Ile, E.I. 2004. Control of Tuber Dormancy and Flowering in Yam *(Dioscorea rotundata Poir.)* tuber. PhD thesis, The University of Reading, Reading, UK.
Ile, E.I., P.Q. Craufurd, N.H. Battey, and R. Asiedu. 2006. Phases of tuber dormancy in yam (*Dioscorea rotundata* Poir.). Annals of Botany 97: 497–504.
Ile, E.I., P.Q. Craufurd, R. Asiedu, and N.H. Battey. 2004. Is the yam (*Dioscorea* spp.) tuber-head the primary nodal complex (PNC) and the origin of the vine, feeder root and tuber? A mini-review. Pages 235–238 *in*: Proceedings of the Ninth Triennial Symposium of the International Society for Tropical Root Crops–Africa Branch, held in Kenya, 31 October to 5 November 2004. Plant Physiology Session.
Ireland, C.R. and H.C. Passam. 1984. The level and distribution of phenolic plant growth inhibitors in yam tubers during dormancy. New Phytologist 233–242.
Ireland, C.R., W.W.E. Schwabe, and D.G. Coursey. 1981. The occurrence of batatasins in the *Dioscoreaceae*. Phytochemistry 20*:* 1569–1571.
Ireland, C.R. and H.C. Passam. 1985. Effect of exogenous batatasin, batatasin analogues and gibberellins on the dormancy of stored yam tubers. Tropical Agriculture 62: 41–46.
Jagtap, S.S. 1993. Climate Soils Agro-ecological Characteristics at Breeding Sites. (Draft for CID internal review). IITA, Ibadan, Nigeria.
Jayakumar, M., M. Eyini, and S. Pannirselvam. 1993. Changes in protein and RNA during dormancy of yam tuber tissues. Journal of Phytological Research 6: 63–66.
Ketitu, A.O. and U.A. Oyenuga. 1973. Changes in the carbohydrate constituents of yam tuber during growth. Journal of Science, Food and Agriculture 24:367–373.
Kim, K.S., E. Davelaar, and G.J. De Klerk. 1994. Abscisic acid controls dormancy development and bulb formation in lily plantlets regenerated in vitro. Plant Physiology 90: 59–64.
Koda, Y. and Y. Okazawa. 1983. Influences of environmental, hormonal and nutritional factors on potato tuberisation. Japan Journal of Crop Science 52: 582–591.
Kumar, D.A., P. Indira, and B. Nambisan.1998. Effect of light and growth regulators on sprouting of *Amorphophallus* tubers. Tropical Science: 187–189.
Lang, G.A., J.D. Early, G.C. Martin, and R. Darnell. 1987. Endo-, para-, and ecodormancy: physiological terminology and classifications for dormancy research. HortScience 22: 371–377.
Leopold, C.A. 1996. Natural History of Seed Dormancy. Pages 2–16 *in*: Plant Dormancy: Physiology, Biochemistry and Molecular Biology, edited by G.A. Lang, CAB International, Wallingford, UK.
Le-Page-Degivry, M.T.H. and G. Garello. 1992. In situ abscisic acid synthesis: A requirement for induction of embryo dormancy in *Helianthus annuus*. Plant Physiology 98: 1386–1390.

Lindgren, L.O., K.G. Stalberg, and A. Hoglund. 2003. Seed-specific over-expression of endogenous Arabidopsis Phytoene synthase gene results in delayed germination and increased levels of carotenoids, chorophyll, and abscisic acid. Plant Physiology 132: 779–785.

Lino, M., T. Hashimoto, and U. Heber. 1978. Inhibition of photosynthesis and respiration by batatasins. Planta 138: 167–172.

Majumder, P.L. and S. Pal. 1992. Rotundatin, a new 9, 10-dihydrophenanthrene derivative *from Dendrobium rotundatum*. Phytochemistry 31: 3225–3228.

Martin, F.W. 1977. Prolonging the storage life of yams by removal of shoots and by treatment with gibberellic acid and waxes. Tropical Root and Tuber Crop Newsletter 10: 39–44.

Martin, F.W. and E. Cabanillas. 1976. Stimulating the sprouting of yam tubers with ethephon. Journal of the University of Puerto Rico 60: 592–595.

Mathurin, P. 1977. Anatomy of the Tuber, Fragmentation and Germination Activation Trial. Thesis for degree in Agricultural Engineering, Dijon. cf. Degras (1993) (edited by R. Costo). Macmillan, London, UK.

Mathurin, P. and L. Degras. 1978. Anatomy of the Tuber as an Aid in Yam Biology Study. Pages 319–333 i*n*: 15th Annual Meeting of the Caribbean Food Crop Society Surinam, edited by R. Costo. The Caribbean Food Crop Society, Surinam.

Mozie, O. 1984. Influence of ventilation and humidity during storage on weight and quality changes of white yam tubers *Dioscorea rotundata* Poir. Journal of the University of Puerto Rico 68: 341–348.

Mulwa, R.M.S. and L.M. Nwanza. 2006. Biotechnology approaches to developing herbicide tolerance/selectivity in crops. African Journal of Biotechnology 5: 396–404.

Ng, S.Y.C. 1984. Meristem Culture and Multiplication. Pages 133–134 *in*: IITA Annual Report 1983. IITA, Ibadan, Nigeria.

Ng, S.Y.C. 1986. Yam Micro Tuber Production in Tissue Culture for International Distribution. *in*: IITA 1986 Annual Report and Research Highlights. IITA, Ibadan, Nigeria.

Ng, S.Y.C. 1988. In vitro tuberisation in white yam (*Dioscorea rotundata* Poir.). Plant Cell, Tissue and Organ Culture 14: 121–128.

Njoku, E., C. Oyolu, S.N.C. Okonkwo, and F.I.O. Nwoke. 1973. The Pattern of Growth and Development in *Dioscorea rotundata* Poir. I: Third Internal Symposium on Tropical Root Crops, IITA, Ibadan, Nigeria.

Nnodu, E.C. and S.O. Alozie. 1992. Using gibberellic acid to control sprouting of yam tubers. Tropical Agriculture 69: 329–333.

Nwoke, F.I.O. and S.N.C. Okonkwo. 1981. Length of tuber dormancy in yam (*Dioscorea* spp.). Nigeria Journal of Agricultural Science 3**:** 153–155.

Okagami, N. and N. Tanno. 1977. Dormancy in Dioscorea: generality of gibberellin-induced dormancy in asexual dormant organs. Plant Cell Physiology 18: 309–316.

Okoli, O.O. 1980. Dry matter accumulation and tuber sprouting in yams *Dioscorea* spp.). Experimental Agriculture 16: 161–167.

Okoli, O.O., M.C. Igbokwe, L.S.O. Ene, and J.U. Nwokoye. 1982. Rapid multiplication of yam by minisett technique. National Root Crops Research Institute, Umudike. Nigeria Research Bulletin 2: 1–12.

Okonkwo, S.N.C. 1985. The Botany of the Yam Plant and its Exploitation in Enhanced Productivity of the Crop. Pages 3–29 *in*: Advances in Yam Research, the Biochemistry and Technology of the Yam Tuber (edited by G.C. Osuji), Biochemical Society of Nigeria and Anambra State University of Technology, Enugu, Nigeria.

Onwueme, I.C. 1973. The sprouting process in yam, *Dioscorea* spp. tuber pieces. Journal of Agricultural Science 8: 11375–11379.

Onwueme, I.C. 1975. Influence of storage time on earliness of sprouting and tubering in *Disocorea rotundata* yam. Journal of Agricultural Science 84**:** 503–506.

Onwueme, I.C. 1978. The Tropical Tuber Crops: Yams, Cassava, Sweet potato*,* Cocoyams. John Wiley and Sons*,* Ltd, Chichester, UK.

Onwueme, I.C. 1984. Yam. Pages 569–585 *in*: The Physiology of Tropical Field Crops edited by P.R. Goldsworthy and N.M. Fisher. John Wiley and Sons Ltd, London, UK.

Orkwor, G.C. and I.J. Ekanayake. 1998. Growth and Development. Pages 39–62 *in:* Food Yams: Advances in Research, edited by G.C. Orkwor, R. Asiedu, and I.J. Ekanayake. NRCRI and IITA, Ibadan, Nigeria.

Passam, H.C. 1977 Sprouting and apical dominance of yam tuber. Tropical Science 19: 29–39.

Passam, H.C. 1982. Dormancy of Yams in Relation to Storage. Pages 285–293 *in*: Yams–Ignames, edited by J. Miege and N. Lyonga. OUP, Oxford, UK.

Passam, H.C., L.D. Wickham, and L.A. Wilson. 1982. A note on the relationship between maturity and dormancy in tubers of *Dioscorea alata* L. Tropical Science: 47–51.

Rao, M.M. and C. George 1990. Studies to extend the dormancy of white yam (*Dioscorea alata* L.). The Journal of Agriculture of the University of Puerto Rico 74**:** 213–219.

Rappaport, L. and N. Wolf. 1969. Regulation of Bud Rest in Tubers of Potato (*Solanum tuberosum* L. III. Nucleic Acid Synthesis Induced by Bud Excision and Ethylene Chlorohydrin. Pages 79–88 *in*: International Symposium on Plant Growth Substances*,* Calcutta, India.

Rylski, I., L. Rappaport, and H.K. Praitt. 1974. Dual effects of ethylene on potato dormancy and sprouting growth. Plant Physiology 53**:** 657–662.

Sanderman, G. and P. Boger. 1989. Inhibition of Carotenoid Biosynthesis by Herbicides. Pages 25–44 *in*: Target Sites of Herbicide Action, edited by P. Boger and G. Sanderman, CRC Press, Boca Raton, FL, USA.

Sandmann, G. and P. Mitchell. 2001. In vitro inhibition studies of phytoene desaturase by bleaching ketomorpholine derivatives. Journal of Agricultural Food Chemistry 49: 138–141.

Sharma, O.P. 1974. Anatomy, origin, and development of tuber of *Dioscorea glabra.* Phytomorphologist 24**:** 297–305.

Sharma, O.P. 1976. Tuber versus bulbil of *Dioscorea glabra*. Phytomorphologist 26**:** 87–96.

Sharma, O.P. 1980. Ontogeny and morphology of bulbil and its seedling tuber in *Dioscorea floribunda*. Proceedings of the Indian Academy of Science: 47–55.

Shiwachi, H., T. Ayankanmi, R. Asiedu, and M. Onjo. 2003. Induction of germination in dormant yam (*Dioscorea* spp.) tubers with inhibitors of gibberellins. Experimental Agriculture 39: 209–217.

Srivastava, L.M. 2002. Gibberellins. Page 175 *in*: Plant Growth and Development-Hormones and Environment. Academic Press, Amsterdam, The Netherlands.

Suttle, J.C. 1996. Dormancy in Tuberous Organs: Problems and Perspectives. Pages 133–146 *in:* Plant Dormancy: Physiology, Biochemistry, and Molecular Biology, edited by G.A. Lang, CAB International, Wallingford, UK.

Suttle, J.C. and J.F. Hultstrand. 1994. Role of endogenous abscisic acid in potato microtuber dormancy. Plant Physiology 105**:** 891–896.

Swanell, M.C., T.R. Wheeler, R.Asiedu, and P.Q. Craufurd. 2003. Effect of harvest date on the dormancy period of yam (*Dioscorea rotundata*). Tropical Science 43: 103–107.

Trouslot, M.F. 1978. Croissance et tuberisation chez quelques CVs de *Dioscorea-cayenensis* Lamk. (Growth and tuberisation of some *Dioscorea-cayenensis* Lamk. Cvs). cf. Degras 1993 edited by R. Costo.

Tschannan, A.B., O. Girardin, C. Nindjin, D. Dauda, Z. Farah, P. Stamp, and P. Escher. 2003. Improving the application of GA_3 to prolong dormancy of yam tuber (*Dioscorea* spp.). Journal of the Science of Food and Agriculture 83: 787–796.

Wickham, L.D., L.A, Wilson, and H.C. Passam. 1981. Tuber germination and early growth in four edible *Dioscorea* species. Annals of Botany 47: 87–95.

Wickham, L.D., L.A. Wilson, and H.C. Passam. 1982. The origin, development and germination of bulbils in two *Dioscorea* species. Annals of Botany 50: 621–627.

Wickham, L.D., D.H.C. Passam, and L.A. Wilson. 1984. Tuber development, storage and germination in yams (*Dioscorea* spp.) in response to pre-harvest application of plant growth regulators. Journal of Agricultural Science 102: 437–442.

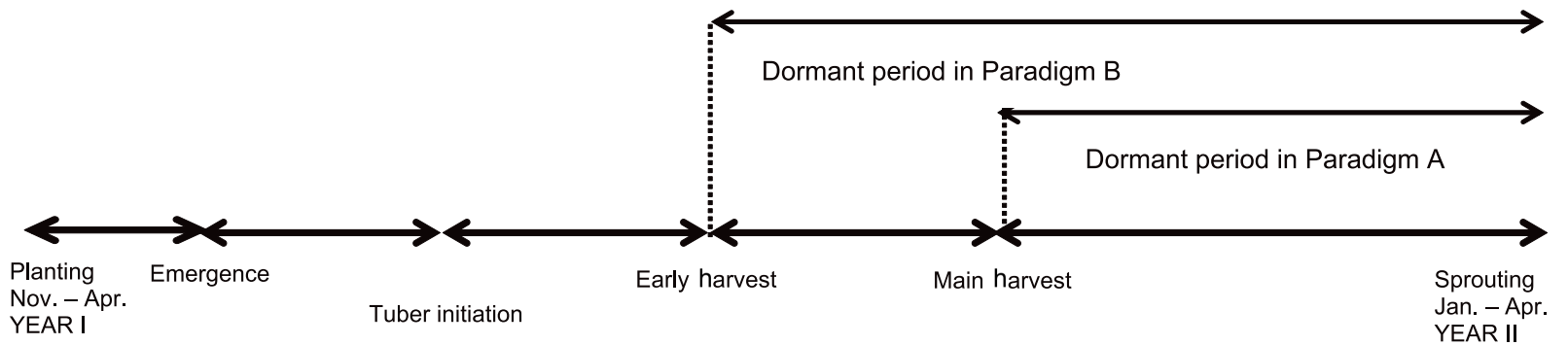
Wickham, L.D. 1988. Extension of dormancy in cush-cush yams (*Dioscorea trifida)* by treatment with gibberellic acid. Tropical Science 28: 75–77.

Wilson, L.A., L.D. Wickham, and T. Ferguson. 1998. Alternative manifestations in origin, form and function of the primary nodal complex of yams (*Dioscorea* spp.): A review. Tropical Agriculture, Trinidad 75: 77–83.

Yamazaki, H., T. Nishijima, Y. Yamato, M. Hamano, and H. Miura. 1999. Involvement of abscisic acid in bulb dormancy of *Allium wakegi* Araki. II. A comparison between dormant and non-dormant cultivars. Plant Growth Regulation 29: 195–200.

Annexes

Annex A. Diagrammatical presentation of major growth activities with calendar months and commonly defined periods of yam tuber dormancy.



Annex B. The effect and degree to which exogenous application of plant growth regulators (PGRs) have shortened (S), prolonged (P) or had no effect (N) on the duration to sprouting of whole tubers of *D. rotundata.*

PGR	Effect	Degree of effect of PGR (in days, compared to control)	Author
Shorten dormancy			
Ethephon	N	0	Passam (1977)
Ethephon	S	No data	IITA (1978)
Ethephon	N, S	0 or 10.5	Shiwachi et al (2004) (pers. com.)
Thiourea	N	0	Passam (1977)
Cystein	N	0	Passam (1977)
GA_3	S	No data	IITA (1979)
CCC	S	No data	IITA (1978)
Prolong dormancy			
GA_3	P	No data	IITA (1978)
GA_3	N	0	IITA (1979)
GA_3 (50 to 150 mg L^{-1})	N	0	Ireland and Passam (1985)
GA_3 (75 to 525 mg L^{-1})	P	18 to 23	Girardin et al. (1998)
GA_3 (150 mg L^{-1})	P	45	Nnodu and Alozie (1992)
GA_3	N	0	Passam (1977)
GA_3 (150 mg kg^{-1})	N	0	Tschannen et al. (2003)
Uniconazole-P	P, N	0 to 30	Shiwachi et al. (2003)
Prohexadione-calcium	P, N	0 to 40	Shiwachi et al. (2003)

Key: GA_3 = Gibberellic acid; CCC = 2-chloroethyltrimethyl-ammonium chloride, a GA_3 inhibitor; Uniconazole-P and Prohexadione-calcium = GA_3 inhibitors.

Annex C. The effect and degree to which exogenous application of plant growth regulators (PGR) have shortened (S), prolonged (P) or had no effect (N) on the duration to sprouting of whole tubers of *D. alata.*

PGR	Effect	Degree of effect of PGR (in d, or % sprouting) compared to control	Author
Shorten dormancy			
2-chloroethanol	S	48% sprouting vs 0% in control	Campbell et al. (1962a)
2-chloroethanol	N	0	Ireland and Passam (1984)
2-chloroethanol + thiourea	S	16	Martin and Cabanillas (1976)
2-chloroethanol + thiourea	S	48	Cibes and Adsuar (1966)
Ethephon	S	13	Martin and Cabanillas (1976)
Uniconazole-P	S	35	Shiwachi et al. (2003)
Prolong dormancy			
GA_3 (20 to 100 mg L^{-1})	N	0	Wickham et al. (1984c)
GA_3 (50 to 150 mg L^{-1})	P	12 to 38	Ireland and Passam (1985)
GA_3 (150 mg L^{-1})	P	28	Ireland and Passam (1984)
GA_3	P	25	Martin (1977)
GA_3 (1000 mg L^{-1})	P	123	Rao and George (1990)
Ethephon	N, P	0 or 10.5	Shiwashi et al. (2004) (Pers. Com.)
Uniconazole-P	P	Up to 21	Shiwachi et al. (2003)
Prohexadione-calcium	P, N	0 to 14	Shiwachi et al. (2003)

Key: See Annex B.

Annex D. The effect and degree to which exogenous application of plant growth regulators (PGR) have shortened (S), prolonged (P) or had no effect (N) on the duration to sprouting in whole tubers of other *Dioscorea species*.

Yam species	PGR	Effect	Degree of effect of PGR (in days or % sprouting)	Author
Shorten dormancy				
D. esculenta	2-chloroethanol	S	18 days	Ireland and Passam (1984)
D. amorphophallus	Ethephon (100 to 1000 mg L^{-1})	S	15 days	Kumar et al. (1998)
D. amorphophallus	Thiourea (50-1000 mg L^{-1})	S	15 days	Kumar et al. (1998)
D. opposita	CCC	S	45–65% spr.	Hasegawa and Hashimoto (1974)
D. opposita	CCC	S	60% spr.	Okagami and Tanno (1977)
D. amorphophallus	GA_3 (50 to 100 mg L^{-1})	S	15 days	Kumar et al. (1998)
D. opposita	Uniconazole	S	40% spr.	Tanno et al. (1995)
D. opposita	Prohexadione	S	10% spr.	Tanno et al. (1995)
Prolong dormancy				
D. opposita	GA_3	P	10% spr	Hasegawa and Hashimoto (1974)
D. opposita	GA_3 (0.03 to 300 µM)	P	0–35% spr	Okagami and Tanno (1977)
D. esculenta	GA_3 (20 to 100 mg L^{-1})	P	37–71 days	Wickham et al. (1984b)
D. esculenta	GA_3 (50 t0 150 mg L^{-1})	P	12–23 days	Ireland and Passam (1985)
D. esculenta	GA_3 (150 mg L^{-1})	P	20 days	Ireland and Passam (1984)
D. trifida	GA_3 (150 mg L^{-1})	P	35 days	Wickham (1988)

Key: See Annex B

Glossary

Tuber morphology

Headless tubers: tubers with detached tuber-head/ corm

Intact tuber/head tuber: tubers carrying a tuber-head/ corm

Mini-tubers/seed yam: small tubers (> 200 g) (mostly used as planting material) produced either by vegetative propagation of small tuber portions or tubers from a second harvest

Tuber head, corm, and rhizome: the corm-like structure attached to the proximal end of the main tuber

Yam tuber: the main storage organ of the yam plant, which serves as source of food and planting material

Tuber anatomy

Meristematic region: thin region (mostly 2 to 4 cells thick during dormancy) of small, flattened, or stretched out (i.e., oblong horizontally) slowly differentiating cells, which lie beneath the cortex

Primary nodal complex: formed after sprout appearance on tuber surface; externally recognized as the swelling of the base of the sprout

Shoot bud genesis: the onset of shoot bud development, seen at the cellular level and occurring long before sprout appearance

Tuber germinating meristem: The TGM is recognized by the large number (10 to 35 cells thick, depending on the area with the most activity) of oblong cells that are arranged vertically on top of one another. It is formed in the meristematic region due to renewed active cell division and differentiation at the end of endo-dormancy

Tuber dormancy

Agronomical maturity: tubers that have reached maturity for food and are usually harvested at the end of the growing season. Such tubers are dormant and are not usually ready to grow. (see Gyansa-Ameyaw 1987). Morphological attributes of mature tubers include the presence of well-formed periderm or skin; usually dark brown in color at main harvest **(**Passam et al. 1982**)**

Appearance of shoot bud on tuber surface (ASB): emergence of internal shoot bud on the surface of the tuber, which occurs after dormancy

Break of dormancy: to bring the dormant period to an end by artificial means

De-bud or de-sprout: whole tubers in which the sprout or external shoot bud has been detached

Duration of dormancy/dormant period: Length of visible dormancy–from planting or better from still tuber initiation to ASB. In the past, it has been calculated as duration from tuber harvest to ASB, from the start of an experiment to ASB, from planting date (during the natural growing season) to ASB and from planting to sprouting (early stages of sprout elongation)

Endogenous plant growth regulators (EPGRs)/(plant hormones): plant growth–regulating chemicals occurring naturally in the tuber and functioning as hormones *in-vivo*.

Extend dormancy: to maintain the dormant state by artificial means

Harvest date: the calendar day when harvesting is done. Harvest date alone tells too little about true tuber age because tubers may be harvested on the same date but planted on different dates

Inhibit sprouting: hinder the sprouting process or re-induce visible dormancy in already sprouting tubers

Landrace: yam varieties/species originating from or associated with particular agroecological zones or geographical locations. Ecotypic separation of varieties is an indication of adaptation to particular climatic conditions

Micro-tubers: small whole tubers produced *in vitro* from tissue culture plantlets

Physiological age/physiological state of readiness: age of the tuber in terms of a physiological state, i.e., phase of dormancy. A tuber may be ready to commence the process of shoot bud formation at or after TGM formation

Physiological maturity: when tubers are ready to grow as marked by end of endo-dormancy

Plant growth regulators (PGRs): chemicals and synthetic analogues of naturally occurring PGRs that regulate plant growth and development. Plant hormones are PGRs but not all growth regulators are plant hormones

Release of dormancy: the end of visible dormancy, resulting from the gradual natural process of dormancy loss

Sprout: the visible shoot bud that emerges on tuber surface

Sprouting: appearance of external shoot bud/ASB and its growth and development

Tuber age: the period, in days, that the tuber has existed at time t. Measurable if the dates of planting, vine emergence, or better still, tuber initiation are known

Tuber initiation: visible manifestation of cell differentiation into the organ, tuber

Vine emergence: emergence of yam vine (shoot) above the soil surface