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DORMANCY IN YAMS

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SUMMARY

The tubers of yam, principally those of *Dioscorea rotundata* (white Guinea yam) and *D. alata* (water or greater yam), are important staple foods and sources of carbohydrate in West Africa. Yams are grown in diverse environments – from the high-rainfall forest zone on the coast to the seasonally arid savannas of West Africa, that is in situations in which the duration and the timing of the onset of the growing season vary appreciably. Dormancy in both underground and aerial tubers of the *Dioscoreaceae* is an important adaptive mechanism that helps to maintain organoleptic quality during storage and also ensures that tubers germinate at the start of the growing season. Plant breeders are especially keen to manipulate the duration of the dormant period in order to synchronize growth periods and, therefore, to produce more than one generation per year. The control of tuber dormancy, however, is poorly understood. This review examines critically those factors that affect tuber initiation, dormancy and sprouting, and makes recommendations for future priorities in research.

INTRODUCTION

Origin and distribution

The family *Dioscoreaceae* is one of the oldest groups of angiosperms. It appears to have arisen in Southeast Asia about 3500 years before present (YBP) (Burkhill, 1960). The Asiatic yam, *Dioscorea alata*, originated in tropical Myanmar and Thailand, whereas, *D. rotundata*, *D. cayenensis* and *D. dumetorum* are believed to have originated in eastern Nigeria and from land tracts adjoining the Niger and Benue Rivers in West Africa (Coursey, 1967). There has been no migration of African species to Asia (Coursey, 1976) until very recent times, for example the introduction of *D. rotundata* from the International Institute for Tropical Agriculture (IITA), Nigeria into India (Nair *et al.*, 1987; Abraham *et al.*, 1989; Sen and Das, 1991).

Dioscorea alata spread from Southeast Asia to India and across the Pacific Ocean to reach the east coast of Africa about 2000 YBP. Later, during the time of the slave trade, both *D. alata* and *D. rotundata* were taken from West Africa to the Caribbean and the Americas where they are now established as important food crops.

Taxonomy and classification

Yams belong to the family *Dioscoreaceae*, and the genus *Dioscorea*. This genus includes about 600 species of which 50–60 are cultivated, or at least gathered, for food or pharmaceutical purposes (Norman *et al.*, 1995). There are, however, only about 12 species of economic significance as foods (Coursey, 1976). The more important food species are: *D. rotundata* (white Guinea yam), *D. alata* (water yam, winged yam or greater yam), *D. cayenensis* (yellow yam or yellow Guinea yam), *D. esculenta* (lesser yam, potato yam or Chinese yam), *D. dumetorum* (bitter yam or trifoliolate yam), *D. bulbifera* (aerial potato yam), *D. trifida* (cush-cush yam), *D. opposita* also known as *D. japonica* (cinnamon yam). *D. rotundata* and *D. alata* are by far the most important, together making up about 90% of world production of food yams (Alexander and Coursey, 1969).

Production and economic importance

Worldwide, the area of yams harvested in 1998 was estimated at 3.8×10^6 ha with a total production of 36 Mt (FAO, 1998). The average yield (fresh weight) is about 8 to 10 t ha^{-1}. Almost 90% of yams are produced in Africa, mostly from an area known as the West African Yam Belt (Table 1); this stretches from the west of the Cameroon mountains to the Bandama River in central Cote d'Ivoire (Hahn *et al.*, 1987). It includes Nigeria, the Republic of Benin, Togo, Ghana, Cameroon and Côte d'Ivoire.

Utilization

Yams are an important staple food and source of carbohydrate throughout West Africa. Also, they are important medicinally and have ritual and socio-cultural significance (Hahn *et al.*, 1987).

A versatile vegetable, yams can be boiled, roasted, grilled or fried and served sliced, as balls, mashed, chipped and flaked. Fresh tubers can be peeled, chipped, dried and milled into flour.

Typically, yam tubers contain (% fresh weight) 60–80% moisture, 15–38% carbohydrate, 1.0–3.8% crude protein, and 0.03–1.2% lipid, and important

Table 1. Estimated global area harvested and production statistics for yam in 1998.

Region	Country	Area harvested (10^6 ha)	Production (Mt)
World		3.79	36.04
Africa		3.64	31.31
	Nigeria	2.63	24.77
	Côte d'Ivoire	0.27	2.92
	Ghana	0.21	0.14
	Benin	0.14	1.58

Source: FAO (1998).

quantities of amino acids (aspartic acid, glutamic acid, alanine and phenylalanine), minerals (calcium, phosphorus and magnesium) and vitamins (ascorbic acid, beta carotene, thiamin and riboflavin). The tubers also contain alkaloids (sapogenins) which have genuine medicinal value and are used in many pharmaceutical preparations (Degras, 1993).

Genetic improvement

The principal objectives for genetic improvement of yams include increased tuber yield per unit area and unit time, resistance to diseases (e.g. anthracnose, viruses, tuber rots) and pests (e.g. nematodes), as well as various tuber characteristics that facilitate harvesting and are valued by consumers (e.g. size, shape, culinary quality, storability) (Asiedu *et al*., 1998). For most programmes the improvement scheme begins with an evaluation of germplasm from various sources in order to identify genotypes with desirable traits as parents for hybridization. Botanic seeds are generated in polycross fields or through biparental crosses among selected genotypes. Resultant seedlings are evaluated in nurseries. Plants selected from the nurseries progress through a series of clonal trials leading to the identification of superior genotypes as potential new varieties. Broad-based populations targeting major yam cultivation zones and populations developed for specific traits (such as disease resistance) are improved over successive years, principally through recurrent selection.

GROWTH AND DEVELOPMENT

Yams are annual or perennial vines and, botanically, are indeterminate climbers with annual or perennial underground and/or aerial tubers. Most are cultivated as annuals. Monoecious, dioecious, hermaphrodite and non-flowering forms occur (Bai and Ekanayake, 1998). Traditionally yams are propagated vegetatively from whole tubers (seed yams), large tuber pieces (setts) or, increasingly, from minisetts (Otoo *et al*., 1985). They can also be propagated from true-seeds though this practice is largely limited to breeding programmes.

Growth phases

The literature on growth, development and factors that affect patterns of growth has been reviewed recently by Orkwor and Ekanayake (1998) and the growth phases of food yams, principally *D. alata* and *D. rotundata*, have been described by Sobulo (1972), Ferguson (1977), Trouslot (1982) and Njoku *et al*. (1984).

Yams exhibit the sigmoidal growth pattern common to most annual plants. A period of slow growth during establishment is followed by a phase of rapid exponential growth as the canopy reaches maximum area and, finally, growth rates decline as the canopy senesces (Fig. 1). In brief, following the breaking of dormancy (sprouting), four distinct phases of development are commonly recognized (Fig. 1 and 2).

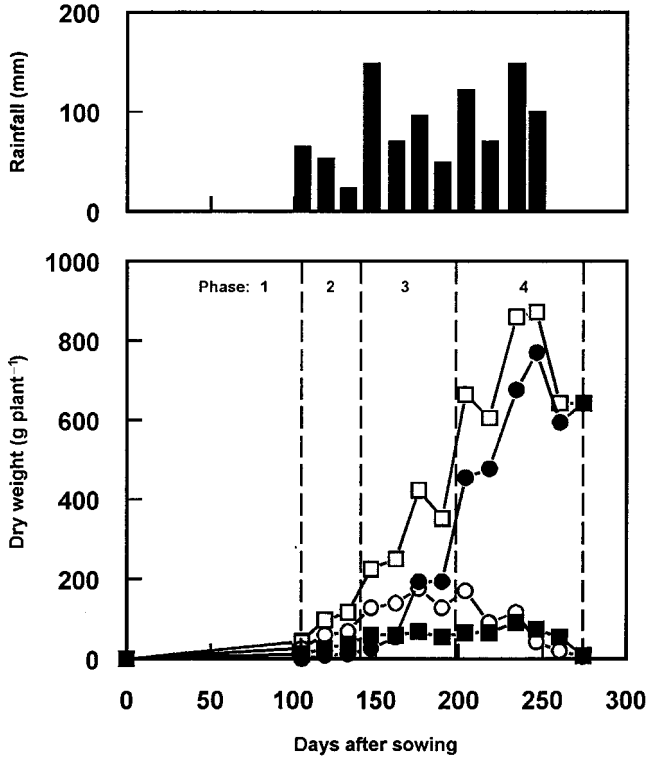

Figure 1. Total dry weight and partitioning of dry matter to tubers, leaves and petioles, and stems of *D. rotundata* cv Atoja grown at Ilora in Nigeria. Rainfall totals for successive 14-day periods are also shown. See text for explanation of Phases. Key: □ whole plant; ● tuber; ○ leaves and petioles; ■ stem. Redrawn from Sobulo (1972).

Phase 1: Tuber germination and sprout emergence. Dormancy ends when tubers germinate and the growing shoot(s) or vines emerge. The duration of this phase is typically between 30 and 50 d but can be protracted if conditions are unfavourable. At this stage the plant is not yet capable of photosynthesizing and has no cataphylls or leaves so the growing vine is completely dependent on the mobilization of stored reserves in the tuber (Orkwor and Ekanayake, 1998).

Phase 2: Canopy establishment and tuber initiation. Typically, this phase lasts between 20 and 70 d. The vines elongate, cataphylls and then true leaves are initiated and expand and the plant becomes autotrophic. By the end of this phase maximum leaf area is attained. Tuber initiation also starts during this phase, typically 60–100 d after sprouting in *D. esculenta* (Ferguson, 1977) and *D. alata* (Campbell *et al.*, 1962a; Chapman, 1965). The onset of tuber initiation correlates with the start of the linear phase of exponential shoot growth (Fig. 2).

Phase 3: Maximum canopy development and maximum tuber growth rate. This third phase is the most critical period for growth of the yam tuber; it is characterized by

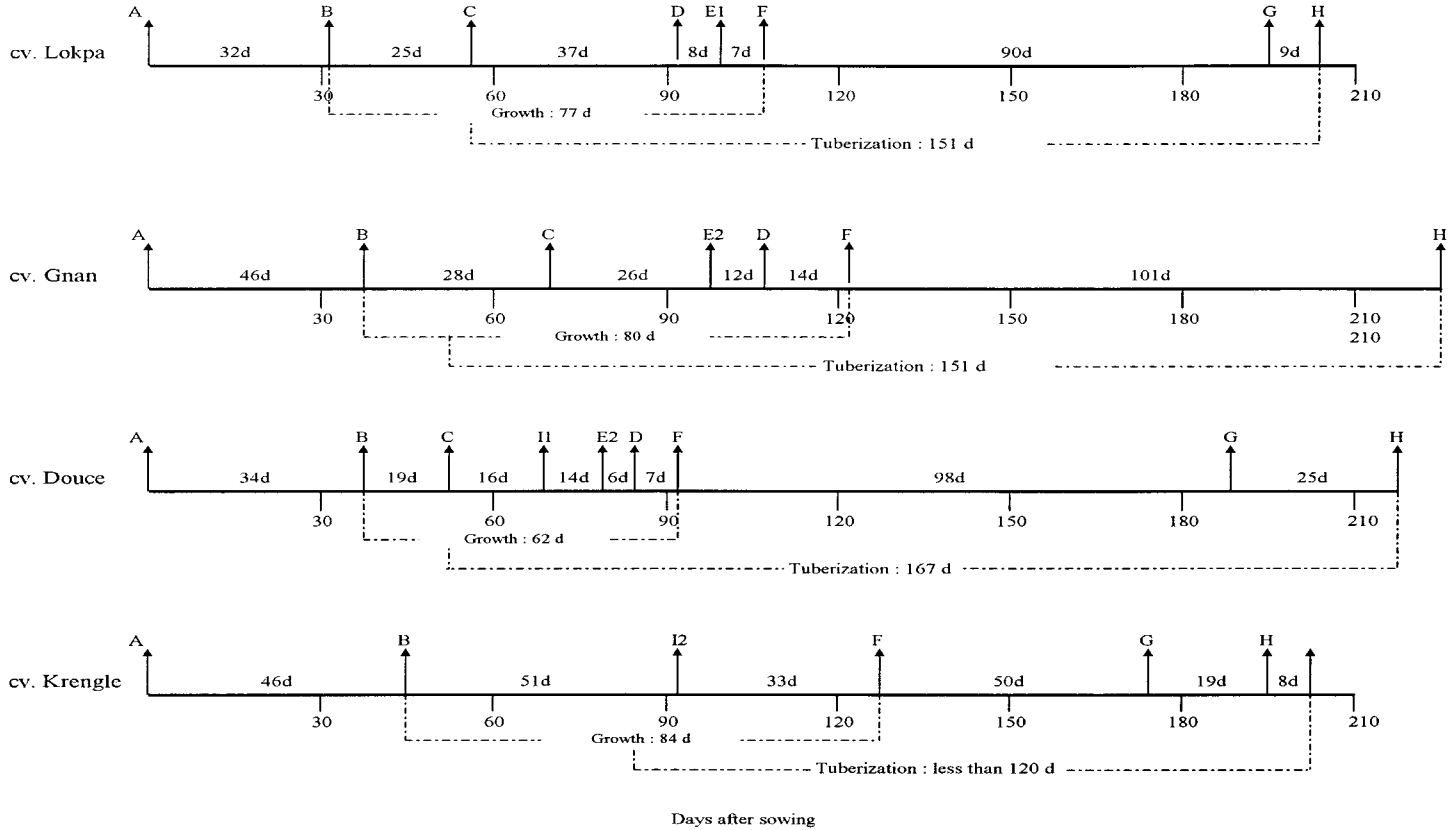

Figure 2. Growth cycles of four cultivars of *D. rotundata* grown from tuber pieces in the field in the forest zone of Côte d'Ivoire. The experiment was planted between 15–23 April 1977. From Trouslot (1982).

Key: A, Planting of tuber; B, Shoot emergence; C, Start of linear axial growth and tuberization; D, Cessation of linear axial growth; E1, Female flowering; E2, Male flowering; F, Cessation of aerial growth; G, Cessation of tuber elongation; H, Cessation of tuber thickening and senescence of leaves; I1, 0.1 to 1 cm tuber; I2, 1 to 2 cm tuber.

maximum canopy development and tuber growth rate. It has a typical duration of 60–90 d. During this period plant growth is highly plastic in response to both positive and negative elements such as management inputs, weeds, fertilizers and pests. Any biotic or abiotic stresses during this phase, therefore, can affect drastically the growth and development of plants, and correspondingly increase or reduce ultimate tuber yield.

Phase 4: Canopy senescence and tuber maturity. During the fourth phase of development leaves senesce and dry-matter accumulation declines. Tubers attain their maximum volume and weight. The combined duration of Phases 3 and 4 varies from about 80 to >150 d.

TUBER ORIGIN AND INITIATION

The most economically important part of the yam plant is the tuber. Most *Dioscorea* species produce two types of tubers; large underground tubers at the base of the stem and much smaller aerial tubers (bulbils) in the leaf axils. Some species or genotypes within species produce only the underground tubers. Both types of tuber are morphologically identical and in some countries have similar economic uses. Tubers vary greatly in size and shape depending on species, cultivar and environment (Coursey, 1967; Onwueme, 1978). Most tubers from cultivated yams are elongated cylinders rounded at both ends. The tubers of *D. alata* tend to branch more than do those of *D. rotundata* or *D. cayenensis*.

Origin and initiation

Yam tubers have been classified traditionally as stem tubers rather than root tubers (Burkhill, 1960; Njoku *et al*., 1984). They lack the typical characteristics of a modified stem, however: there are no visible pre-formed buds or eyes on or concealed within the tuber; no scale leaves on the tuber surface that reveal the position of stem nodes; and there is no equivalent of a terminal bud at the distal (tail) end or growing point of the tuber (Onwueme, 1973; Hahn *et al*., 1987). The tuber, therefore, may be neither a true stem nor a true root but one that originates from the hypocotyl, a small region of meristematic cells between the stem and the root (Lawton and Lawton, 1967).

The first microscopically discernible event in tuber formation is the onset of rapid cell multiplication in the meristematic tissues at the junction of the stem and root (Onwueme, 1978; Trouslot, 1982). This meristematic activity produces an amorphous mass of cells, possibly analogous to the primary nodal complex (PNC) (Ferguson, 1972) that becomes visible during tuber germination and the development of stem cuttings of yams (Wickham *et al*., 1981). The first macroscopically visible sign of tuber initiation is the bursting of the suberous layer (*éclatemant du suber*) of this amorphous mass. The mass of cells soon differentiates into a growing point, usually whitish in colour, which begins to elongate with a recognizable head (proximal) and tail (distal) end.

The tuber grows as a result of meristematic sub-apical activity within 15–20 mm of the distal apex. At the distal end, younger cells are geotropic and grow downwards, while the older cells at the proximal end harden and support the twining yam vine (Orkwor and Ekanayake, 1998). The small (1–3 cm) corm-like structure from where the roots, shoots and tuber arose may or may not remain attached to the tuber after harvest.

Timing and control of tuber initiation

The timing of tuber initiation and the duration of the period of tuber formation vary within and between species (Fig. 2), and are affected also by environmental factors. In *D. rotundata*, for example, initiation has been reported to occur from sprouting to 84 d after sprouting (Okezie *et al.*, 1981; Njoku *et al.*, 1984). In contrast, in *D. alata* and *D. trifida* tuber initiation occurs about 84 and 120 d respectively after sprouting (Campbell *et al.*, 1962a; Chapman, 1965; Ferguson, 1977). These are relatively superficial statistics, however, given that tuber initiation has not been adequately defined and that there have been few detailed, analytical studies on the timing of this important event.

Trouslot (1982) analysed the timing of tuber initiation in four cultivars of *D. rotundata* in relation to the growth of the shoot (Fig. 2). He defined tuber initiation as the stage at which the amorphous mass of cells first 'bursts' and went on to show very clearly that this event corresponded with the beginning of the linear phase of aerial axial growth. Furthermore, initiation occurred within cultivars when a predetermined number of main-stem nodes had been initiated, that is about 16 for cv. Lokpa, 17–19 for cv. Gnan and 30–32 for cv. Douce. In these three cultivars, therefore, tuber initiation started 19–28 d after emergence of the sprout. Similarly, Shiwachi *et al.* (1995) reported that tuber initiation in a range of clones of *D. alata* started 14–40 d after planting, by which time 3–11 leaves had appeared.

Storage duration. The duration of post-harvest tuber storage has an effect on the timing of tuber initiation in the next generation. Onwueme (1975b) observed that setts from tubers from which the sprouts and visible buds had been removed and setts from tubers stored for only a short period of time after harvest (33 d) sprouted later and grew for a longer period (165 d) after sprouting before they, in turn, initiated tubers. In contrast, setts from tubers that had been stored for up to 285 d sprouted more readily (in 10 d) and initiated a tuber more rapidly (90 d; Fig. 3). He based his analysis on the duration from the end of the storage period, not from the previous harvest. Thus the authors calculate that when durations to sprouting and second-generation tuber initiation are expressed relative to first generation harvest date (Fig. 3) it becomes clear that storage periods of 33–159 d had no effect on the duration to tuber initiation, which was 285 d. The time period from harvest to sprouting, however, was affected by storage period; the duration from sprouting to tuber initiation, therefore, varied from 167 d after 33 d storage to 94 d after 226 d storage.

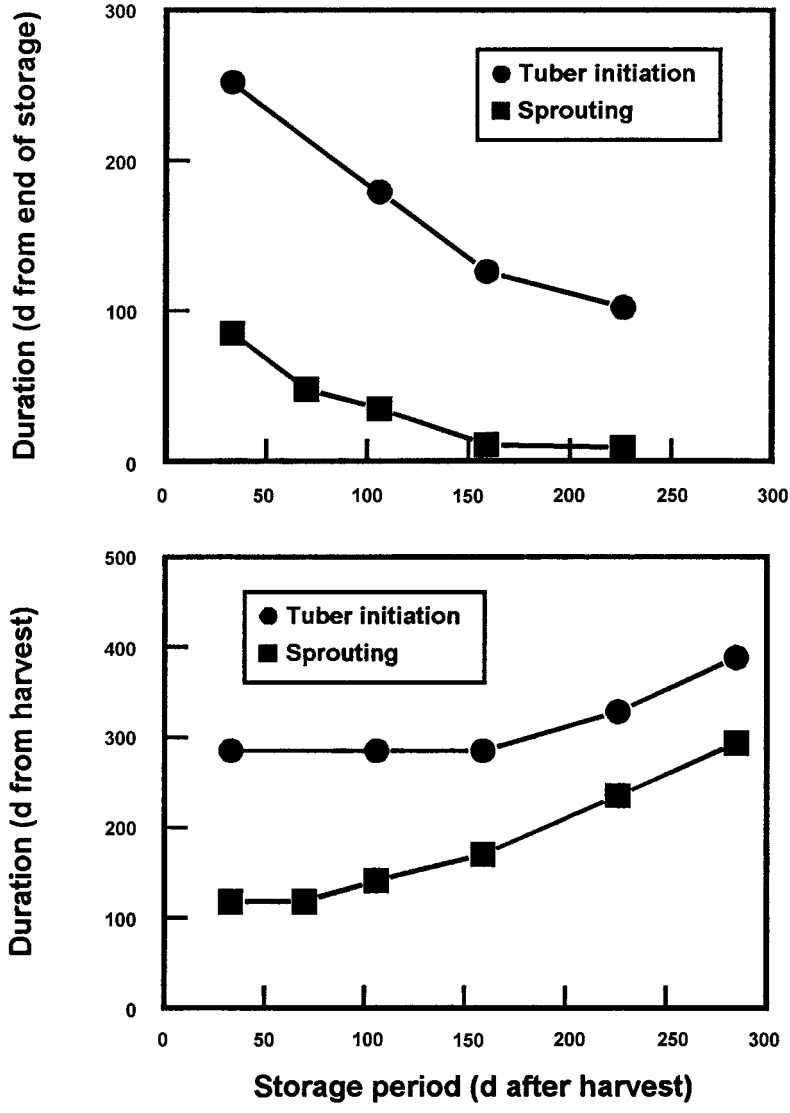

Figure 3. Effect of storage period on tuber sprouting and tuber initiation in *D. rotundata* cv. Okukunmo. Relation between sprouting and initiation expressed relative to end of the storage period and time of harvest. Redrawn from Onwueme (1975b).

These data serve to emphasize the importance of and the possible interrelations between the timing of phenological events in yams. Without doubt the relationships between the timing and duration of phases within the annual life-cycle are complex. More precise definitions of the key developmental or phenological events are needed, as are further studies on factors that affect the whole life-cycle rather than just specific phases.

Sett size. Tuber initiation is reported to occur sooner from larger setts than from smaller ones (Enyi, 1972), a response that may also be linked to the size and rate of development of the main shoot.

Daylength. In common with other sub-tropical and tropical root crops, tuber initiation is promoted by short-days (<12 h) and inhibited by long-days (>14 h) in several species of yam, including *D. rotundata*, *D. alata*, *D. opposita* and *D. bulbifera* (Miginiac, 1980; Okezie, 1987; Yoshida and Kanahama, 1999; Shiwachi *et al*., 2000). In *D. alata*, the response to photoperiod is greatest at the start of tuber initiation and during the early stages of tuber growth (Shiwachi *et al*., 2000). Jasmonic acid, which promotes tuberization (Koda and Kikuta, 1991; Koda *et al*., 1994), may be regulated by photoperiod. It is not known whether the response to photoperiod is a classical quantitative short-day response (Roberts and Summerfield, 1987) or whether there is a critical photoperiod that triggers tuber initiation. Furthermore, the typically critical interactions between photoperiod and temperature effects on plant phenology have yet to be explored and quantified.

Illuminance. Differences in natural illuminance seem to have no effect on underground (as opposed to aerial) tuber initiation in yams. For example, Onwueme (1978) observed tuber initiation in sprouted tubers that were left on an illuminated shelf.

Temperature. Surprisingly, the effects of temperature on tuber initiation *per se* have not been studied. There may also be indirect effects of temperature. For example, if tuber initiation is linked to a particular stage of development, such as main shoot node number, then cooler or warmer temperatures that delay or hasten shoot development may also affect the time of tuber initiation in a predictable manner.

Soil moisture. Onwueme (1975a) reported that soil moisture stress delays tuber initiation in *D. alata*. He subjected pre-sprouted setts to the following treatments: regular watering (control); water withheld from 15 to 35 d after sowing (DAS) (early stress); water withheld from 36 to 56 DAS (late stress); and water withheld every 14 d (intermittent stress). All the water-stress treatments delayed the duration to 50% sprouting: from 7 d (early stress) to 30 d (late stress) and an extreme of 70 d (intermittent stress). No data on shoot growth were presented but, again, factors that affect the growth and development of the shoot are likely to affect the timing of tuber initiation.

Tuber initiation in vitro

Tissue cultured yam plantlets will produce micro-tubers (5–20 mm diameter) *in vitro*, usually at the base of the stem node (Ng, 1988; Passam, 1995). The effects of factors that affect tuber initiation have been investigated.

Photoperiod and spectral quality. In *D. rotundata* the most favourable photoperiods for tuber initiation at 3 to 5% sucrose were 12 and 16 h d^{-1}, whereas at 8 to 10% sucrose initiation was greatest in continuous daylight (Ng, 1988). In studies on *D. alata*, Mantell and Hugo (1989) found a photoperiod of 8 h d^{-1} was more inductive than 12 or 16 h d^{-1}. Jean and Cappadocia (1992) reported no effect of either 8 or 16 h d^{-1}. The photoperiodic effect is known to be mediated through phytochrome, the state of which is controlled by red (R) and far-red (FR) light. John *et al*. (1993) gave *D. alata* plantlets grown *in vitro* in an 8 h d^{-1} photoperiod, end-of-day light treatments of R, FR or FR followed by a burst of R (FR/R). Red light had no effect on the proportion of plantlets with micro-tubers or on micro-tuber fresh weight. However, FR significantly reduced the proportion and fresh weight of micro-tubers and FR/R partially reversed these effects. These data suggest that phytochrome is involved in tuberization in yams.

Hormone treatments. *In vitro* systems provide a convenient medium for investigating the effects of hormone or other chemical treatments on tuber initiation. In *D. alata*, John *et al*. (1993) reported that ABA (1 μM) stimulated initiation whereas kinetin (2.5 μM) inhibited micro-tuber development. Also, in *D. alata* high concentrations of NAA (27 and 54 μM) favoured the production of large micro-tubers, as did ABA, but only under an 8 h photoperiod (Jean and Cappadocia, 1992).

TUBER DORMANCY AND SPROUTING

Dormancy, a physiological rest period without obvious external signs of physiological or biochemical activity, is an extremely important adaptive mechanism that allows propagules to survive a prolonged dry season. Tuber dormancy is widespread among *Dioscorea* species and the inherent dormancy period varies between and within yam species (Table 2). For example, among 286 *D. rotundata* accessions grown in the field and stored in a yam barn at IITA, the duration from harvesting to sprouting ranged from 60 to >110 d, with the greatest number of accessions sprouting between 70 and 80 d after harvest. *Dioscorea* species from the forest zone of West Africa, which has no discernible dry season, do not exhibit dormancy. In contrast, species such as *D. elephantiphes* from semi-desert regions have a very prolonged dormant period (Purseglove, 1972). Furthermore, *D. rotundata* and *D. alata* grown in the forest zone and the moist savannas are intermediate with considerable variability between cultivars. Clearly, the total duration of the dormant period is of great ecological significance and appears to be an adaptation to the environmental conditions that prevail in the region of origin (Alexander and Coursey, 1969; Passam, 1982; Orkwor and Ekanayake, 1998).

In most studies to date, the duration of tuber dormancy has been measured from harvest or some other arbitrary, ill-defined starting point (for example, leaf senescence) through to sprouting. Without a clear definition of when dormancy starts or ends, the analysis and interpretation of existing data is very difficult. In a

Table 2. Dormancy periods between- and within-yam species. Modified from Passam (1982).

Species	Location	Duration (d)	Reference
D. alata	Caribbean	98–112	Passam (1977, 1982)
	Caribbean	112	Campbell *et al.* (1962a)
	West Africa	98–126	Hayward and Walker (1961)
	West Africa	102–131	Nwoke and Okonkwo (1981)
	West Africa	105–112	Coursey (1967)
D. rotundata	West Africa	91	IITA (1976)
	West Africa	56–112	Agbo (1992) Quoted in Orkwor and Ekanayake (1998)
	West Africa	105–112	Coursey (1967)
	West Africa	63–112	Agbo (1992)
	West Africa	95–125	Nwoke and Okonkwo (1981)
D. cayenensis	West Africa	28–56	Hayward and Walker (1961)
	West Africa	70–126	Passam (1977, 1982)
D. esculenta	West Africa	84–126	Agbo (1992)
	Caribbean	28–56	Passam (1977, 1982)
	West Africa	112–119	Agbo (1992)
D. trifida	Caribbean	28	Passam (1977, 1982)
D. bulbifera	West Africa	135	Nwoke and Okonkwo (1981)
	West Africa	105–112	Agbo (1992)
D. dumetorum	West Africa	94–126	Nwoke and Okonkwo (1981)
	West Africa	105	Agbo (1992)

review of potato (*Solanum tuberosum*) dormancy and sprouting, Burton (1957) commented on similar problems and suggested that 'the dormant period should be regarded as beginning at the time of tuber initiation and ending with the resumption of active bud growth under favourable conditions of storage. The dormant period after harvest is an undefined portion of the true dormant period. In considering the effects of such factors as the climate from year to year, or the origin of tubers upon the dormant period, it is not possible to state the nature of the effect unless the date of tuber formation is known'. Similar considerations should apply also to yams.

An ability to manipulate the duration of tuber dormancy in yams would have obvious agricultural significance. On the one hand, an ability to break dormancy would be extremely useful to plant breeders (so that more than one generation could be grown each year) and potentially useful to farmers too by allowing out-of-season yam production. On the other hand, an ability to prolong dormancy during storage is very important for yam food quality. Once dormancy is broken, physiological and biochemical changes in the yam tuber progressively impair texture, taste and flavour.

Definition of dormancy

'Dormancy is the term used generically to encompass the processes that constitute a programmed inability for growth in various types of plant meristematic apices, often in spite of suitable environmental conditions' (Lang, 1996), and this is usually accompanied by a lack of visible growth. Dormancy can be

categorized further by the regulatory processes involved (Lang *et al.*, 1987): endo-dormancy (or rest) is controlled by endogenous conditions within the affected organ; para-dormancy (or correlative inhibition) is controlled by conditions outside the affected organ but within the parent plant; and eco-dormancy (or quiescence) is controlled by conditions in the external environment. These definitions apply equally to tuber meristems, seeds and aerial buds. Furthermore, dormancy can be due to different combinations of these types in varying degrees, and the regulatory type of dormancy may change with time.

Although the phenomenon of dormancy has been studied in yams, particularly aerial bulbil dormancy (Okagami and Tanno, 1977;1991; Okagami, 1986), the processes regulating dormancy, that is endo-, para- or eco-dormancy, and their relative importance, are poorly understood.

Formation of the primary nodal complex and the process of sprouting

The anatomy of dormant tubers and the process of tuber germination and sprouting have been described in detail by Onwueme (1973) and Wickham *et al.* (1981). In stark contrast to other vegetatively propagated species such as potato, yam tubers do not have any buds or 'eyes' visible on the surface at harvest. Later on, during storage, one or more buds may develop, usually at the proximal (head) end or from the corm if present. Also in contrast to potato, all parts of the tuber are capable of producing buds (and thus permitting mini-setts to be used for propagation) with no surface feature to forewarn of that eventuality.

The tuber has an outer layer of suberized cells internal to which is a layer of secondary cork cells and associated cambial layer (Fig. 4). The inner cortical region comprises parenchyma and storage-parenchyma cells. In *D. rotundata*, a meristematic layer of cells representing the primary thickening meristem is present; in *D. alata* there is an inner cortical region 4–5 cells thick consisting of small, poorly differentiated cells. Shoot genesis is initiated by cell division in the inner cortex (*D. alata*) or in the primary thickening meristem (*D. rotundata*). These divisions soon produce a mass of undifferentiated cells (the tuber germination meristem) which organize into a shoot apical meristem. The first foliar primordia and axillary buds are initiated shortly after organization of the shoot apical meristem and protect the shoot apex during growth through the cortex. Immediately following axillary bud formation, meristematic activity in the region of the first node of the developing bud forms the primary nodal complex (PNC)-initial.

The first exterior sign of meristematic activity in the tuber germination meristem is the appearance of a typically white, sometimes purple, puffy callus-like protuberance (the sprout locus) breaking through the skin of the tuber, followed by the appearance of one or more differentiated shoot buds on the sprouting locus. As meristematic activity continues, the PNC-initial forms the PNC, a mass of amorphous cells from which roots and subsequently the new tuber are initiated (Fig. 4). The bud continues to increase in size while the rest of the sprouting locus becomes brownish as it desiccates. The whole process of sprouting,

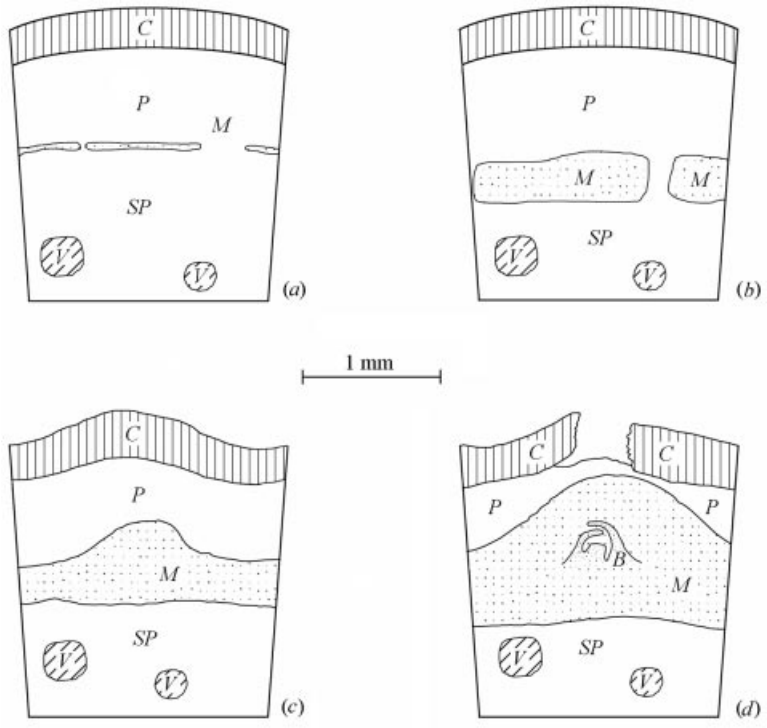

Figure 4. Progressive stages (*a-d*) in the formation of the sprout in *D. rotundata*. The duration from (a) to (d) takes 7–15 d. From Onwueme (1973).
Key: B, newly differentiated bud; C, cork layer; M, layer of meristematic cells; P, parenchyma cells with only a small amount of stored starch; SP, storage parenchyma with stored starch and constituting the bulk of the tuber; V, vascular bundles.

from cell division to emergence of the shoot occurs in about 7 to 15 d (Onwueme, 1973). Sprouting loci appear more readily on the upper and lower parts of horizontally-stored tubers than on the sides (Onwueme, 1973).

Yam tubers are capable of producing sprouting loci anywhere on their outer surface though sprouting is more often first observed at the proximal end (Table 3) both in intact tubers and in transversely bisected tubers (Passam, 1977). Sprouts at the proximal end also exert apical dominance over shoots on the rest of the tuber. Indeed, throughout individual tubers there seems to be a gradient of

Table 3. The number and morphological position of sprouts following the break of dormancy in intact yam (*D. rotundata*) tubers. From Passam (1977).

Days from breakage of dormancy	Total no. of sprouts	Percentage sprouts		
		Proximal	Middle	Distal
0	28	100	0	0
10	44	84	5	11
30	47	78	5	17

dominance that is independent of the developing sprouting locus or apical bud. This gradient may be related to the maturity of the meristematic tissues, the most mature tissues being at the proximal end.

Cell division in the cortex or primary thickening meristem also produces tuber roots, first visible as small protuberances all over the surface of the tuber. The degree to which these roots develop during storage varies, however, with relative humidity; high humidity favours their development (Passam, 1977; Wickham *et al*., 1981; Passam *et al*., 1982b). Furthermore, since they develop independently of the shoot the development of tuber roots does not necessarily indicate tuber germination. Tuber root germination, therefore, should not be used to indicate the breaking of dormancy.

Based on the anatomical features reviewed earlier, the authors suggest that the end of dormancy occurs when the tuber germination meristem is formed and produces the shoot apical bud (Fig. 4d). The first external sign of germination is the appearance of a sprouting locus which is most likely to be regulated by endo-dormancy factors. Further development and growth of the shoot apex, however, is more likely to be regulated by environmental factors such as temperature, illuminance, photoperiod and water which, although they may impose eco-dormancy, should not be confused with endo-dormancy as may well have been the case repeatedly in past studies.

Physiological and biochemical changes during dormancy and sprouting

Although the dormancy mechanism of yam tubers is not fully understood, various changes in respiration rate and chemical composition during the dormant period and during sprouting have been described.

The dormant period is associated generally with a minimum of endogenous metabolic activity, resulting in very little loss of storage reserves. Respiration rates are high at harvest, but fall rapidly during curing and remain slow during dormancy (Olorunda *et al*., 1974; Passam, 1977; Passam and Noon, 1977; Passam *et al*., 1978; Wickham *et al*., 1981. Table 4). Respiration rates are higher in the distal end of the tuber than the proximal end since the former is the most recently formed tissue. Upon the breaking of dormancy, respiration rates increase

Table 4. Effect of temperature on the respiration rate (ml CO_2 (kg fresh weight)$^{-1}$ h^{-1}) of whole tubers of *D. rotundata* and proximal (head) and distal (tail) segments at three stages of development. From Passam *et al*. (1978).

	35 °C	25 °C		
Stage	Whole tuber	Whole tuber	Proximal end	Distal end
After harvest	29	15	19	4
During dormancy	8	3	4	7
During sprouting	20	34	44	14

Table 5. Effect of storage temperature on water and dry matter loss, and sprouting in tubers of *D. alata*. From Olorunda *et al.* (1974).

Temperature (°C)	Weight loss (% initial weight)		Sprouting‡
	Water	Dry matter	
10†	32.4	65.0	0
15	9.4	7.3	0
20	18.4	11.4	+ + +
25	16.1	4.0	+

† Chilling damage.
‡ 0 = no sprouting, + few sprouts, + + + profuse sprouting.

substantially particularly at the proximal end where sprouting occurs first. Warmer temperatures during dormancy or during storage increase respiration rates, and dry-matter losses are greater (Table 5). Dry-matter losses during dormancy are typically of the order of 5 to 10% (Ravindran and Wanasundera, 1992; Hariprakash and Nambisan, 1996) although they can be substantially greater if the tuber is damaged.

Changes in starch content and in concentrations of reducing and non-reducing sugars during dormancy and sprouting have been recorded in *D. alata*, *D. rotundata* and *D. esculenta* (Ravindran and Wanasundera, 1992; Hariprakash and Nambisan, 1996). In the study of the latter two authors, starch contents were reduced by up to 35% in all three species and more than 50% of the starch reduction took place during the dormant period. Fructose was detected 20 d after storage suggesting the catalysis of sucrose, whereas maltose was detected only after sprout formation, indicating the activity of amylase in starch breakdown during these later stages. Mozie (1987a), however, did not detect fructose in *D. rotundata* until dormancy broke.

The activities of the enzymes amylase, phosphorylase and G-6-PD are low during dormancy but increase at sprouting (Ikediobi and Oti, 1983). The increase in G-6-PD enzyme activity was very marked. This enzyme is important in the pentose-phosphate pathway and the breaking of dormancy in seeds (Roberts, 1973; Roberts and Smith, 1977). Polyphenol oxidase acitivity, on the other hand, steadily declines during storage (Ikediobe and Oti, 1983). Shortly before dormancy breaks, glutathione concentrations increase from 0.6 to 1.0 mg g^{-1} tuber (Campbell *et al.*, 1962*a;* Wellington and Ahmad, 1993), and the concentration of glutathione has been suggested as a measurable indicator of the end of dormancy.

Factors affecting the duration of the dormant period and sprouting

The duration of the dormant period varies widely (Table 2) and is generally held to be under strong genetic control and to be location-specific, reflecting the adaptive nature of dormancy in *Dioscorea*. For example, Passam *et al.* (1982b)

quote the case of tubers, harvested in Nigeria and shipped to the Caribbean, sprouting at the time of the start of the rains in Nigeria.

In nearly all published papers on factors that affect the duration of the dormant period, it is the duration to sprouting that has been recorded rather than an earlier stage of dormancy break. Usually too, sprouting is poorly defined. Therefore, results described may in fact include effects on dormancy as well as on shoot growth and development. Furthermore, studies do not always indicate if the corm was still attached to the tuber or whether there were any buds on the corm prior to storage of the tuber. In short, they hinder rather than help advances in genuine understanding.

Storage treatments and planting date. Several studies support the view that duration to sprouting is under endogenous control. In the Caribbean, Passam *et al*. (1982b) planted *D. alata* in June and harvested it at the end of November. The harvested tubers were stored and then re-planted on four different dates. Sprouting (shoot emergence) was recorded. The durations to 50 and 100% sprouting (Table 6) show clearly that planting date, and hence differences in factors associated with storage and planting (such as moisture, light and temperature), had no effect on duration to sprouting. Onwueme (1977) harvested *D. rotundata* tubers at shoot maturity (October) and then subjected them to different storage and sprouting treatments (Table 7). Although the different treatments affected the duration from planting to sprouting by nearly 100 d, all tubers nonetheless sprouted at a

Table 6. Dates of sprouting in tubers of *D. alata* harvested in late November and planted at different times after harvest. From Passam *et al*. (1982a).

	Date of sprouting		
Date of planting	10%	50%	100%
6 December	1 May	No data	No data
2 January	27 March	17 April	15 May
16 January	13 March	3 April	1 May
6 March	27 March	3 April	1 May

Table 7. Duration from harvesting on 15 October to 50% sprouting of tubers of *D. rotundata* subjected to different sprouting environments. Modified from Onwueme (1977).

		Duration to sprouting (d) from:	
Treatment	Date of 50% sprout emergence	Planting	Harvesting
Pre-sprouted outdoors – November	16 April	61	178
Pre-sprouted indoors – November	12 April	57	174
November planting	28 March	145	159
Pre-sprouted indoors – December	7 April	52	162
February planting	14 April	59	176

similar time relative to harvest, that is between 159 and 178 d later. The same conclusion can be drawn from the work of Nwoke and Okonkwo (1981) with *D. rotundata*, *D. alata*, *D. dumentorum* and *D. bulbifera*. Similarly, in Guadaloupe Lacointe and Zinsou (1987) planted *D. alata* on six different dates between September 1982 and April 1983 and found that, with the exception of the December planting, the tubers all sprouted between late March and early April irrespective of planting date. Their results support the view that the duration of the dormant period is under strong endogenous control and is not affected by either growth or storage environment.

The time of harvesting. Dormancy is widely assumed to start at or shortly after tuber maturity and most studies begin measuring 'dormancy time' from harvest. Reports by Okoli (1980) and Wickham *et al*. (1984b), however, show that in fact tubers are dormant from well before harvest.

Okoli (1980) harvested the tubers of four *D. rotundata* cultivars every seven days between 98 and 252 d after planting and recorded the time of sprouting in a common storage environment. Tubers harvested after 98 d sprouted about 175 d after harvesting, whereas those harvested after 252 d sprouted within 14 d of harvest (Fig. 5). There was a negative linear relation between the time of harvesting and sprouting, such that the duration from planting to sprouting was more or less constant. In this experiment, therefore: (i) tubers were clearly dormant from at least 98 d after planting; (ii) tuber maturity and size had no effect on the duration of the dormant period; and (iii) the duration of the dormant period was 'fixed' and was not affected by any differences between the storage and growing environment.

Wickham *et al*. (1984b) conducted a similar experiment in the Caribbean with *D. alata* and *D. esculenta*. They harvested tubers up to 98 d before shoot maturity and stored them at ambient temperatures (26 to 32 °C) until sprouting occurred. *D. alata* tubers harvested 98 d before shoot maturity sprouted after 140 d whereas those harvested at maturity sprouted after 90 d (Fig. 6). Relative to shoot maturity, however, the earliest harvested tubers sprouted first, up to 50 d before those harvested at maturity. Similar results were found for *D. esculenta*. These data also show that tubers were dormant well before maturity although, in contrast to *D. rotundata* (Okoli, 1980), the dormant period was longer in the earliest harvested and, presumably, more immature tubers.

Unfortunately, neither of these reports give sufficient information on the environments experienced by tubers either in the ground or in storage. Therefore, the possibility that differences (or lack of differences) in the duration of the dormant period are due to factors such as temperature cannot be ruled out.

Temperature during storage. Temperature has a significant effect on dormancy and the duration to sprouting. Coursey and Nwankwo (1968) reported that the mean temperature in traditional storage barns in Ghana is about 30 °C and that internal tuber temperatures are about 27 to 31 °C. The optimum temperature for

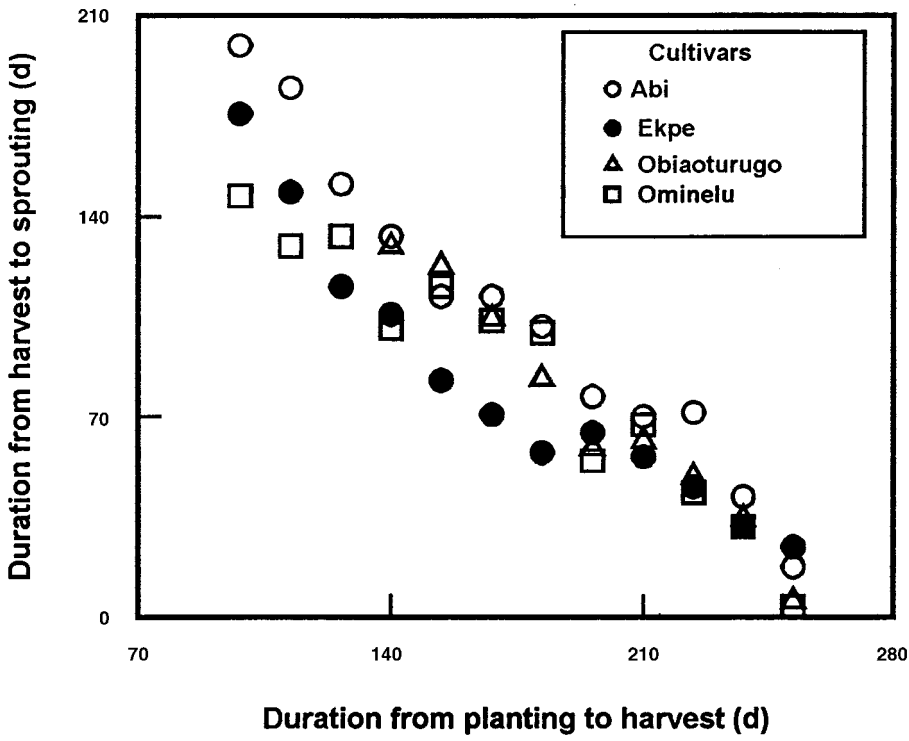

Figure 5. Relation between the duration from planting to harvest and the duration from planting to sprouting in three cvs of *D. rotundata* and one cv. of *D. alata* grown at Umudike in Nigeria. Redrawn from Okoli (1980).

sprouting in *D. rotundata* and *D. alata* is said to be between 25 and 30 °C; temperatures above (supra-optimal) and below (sub-optimal) this range delay sprouting (Onwueme, 1978). Okagami (1986) studied tuber and bulbil sprouting in several species of *Dioscorea* grown along a transect covering cool temperate to sub-tropical environments. He found that the proportion of tubers or bulbils sprouting was greatest in tropical species at the warmest temperature, that is 38 °C. Sprouting in species from warm temperate environments had an optimum of 15 to 25 °C. Quantitative data to support this statement is scarce, however, and most studies that have used different temperatures have done so to delay sprouting and hence prolong storage and maintain food quality.

Passam (1977) examined the effects of temperature at saturating relative humidity (RH) on *D. alata*. He observed sprouting to occur after 20 d at 25 and 30 °C, and 30 to 40 d at 17 °C (Table 8). Many other studies have also shown that cool temperatures between 16 and 20 °C delay sprouting (Gonzalez and Collazo de Rivera, 1972; Passam, 1977; Rivera *et al.*, 1974a; Rao and George, 1990). Mozie (1987a) showed that tubers stored at 16 °C remained dormant for between 120 and 150 d longer than those stored at 21 to 32 °C. Cooler temperatures of 10 to 12 °C cause chilling damage (Coursey, 1968). Data presented in Mozie (1987a)

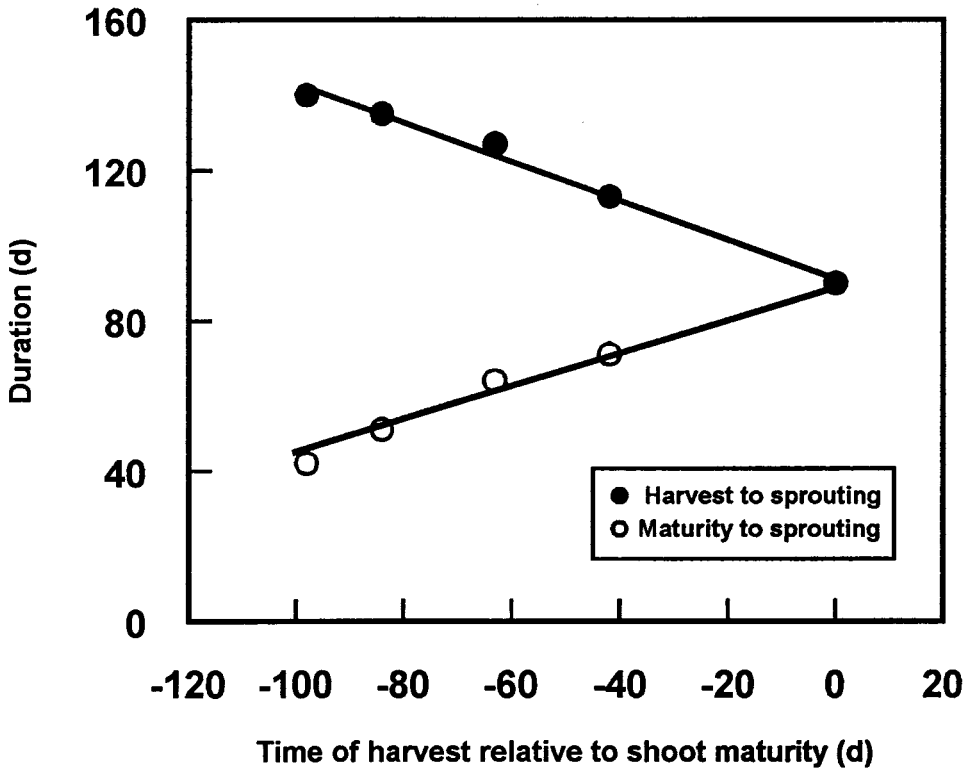

Figure 6. Duration from maturity to sprouting and from harvest to sprouting in tubers of *D. alata* harvested at different times relative to maturity. Redrawn from Wickham *et al.* (1984b).

Table 8. Effect of temperature and RH on duration (d) to sprouting in tubers of *D. rotundata*. From Passam (1977).

	Relative humidity (%)	
Temperature (°C)	100	60–70
17	30–40	No data
25	20	40
35	20	40

also show that sprouting started slightly earlier at 25 than at 20 °C, and that the rate of sprouting was also slightly faster at the warmer temperature (Fig. 7).

The most detailed study of the effects of temperature on the duration of the dormant period and on subsequent sprout growth is that undertaken by Preston and Haun (1963) on *D. spiculiflora*, a species from southern Mexico. They conducted several experiments using different temperature treatments (20–44 °C) and observed the times to 50% of tubers having epidermal cracks (the first visible sign of the end of dormancy), first sprouts appearing and sprouts of 2.5 cm length.

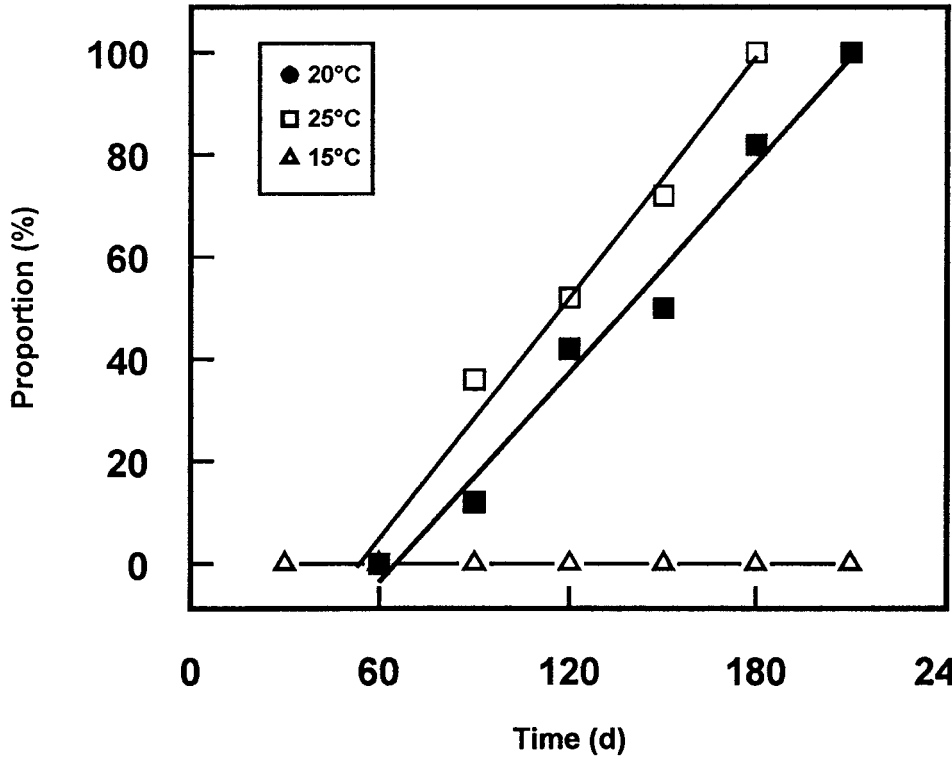

Figure 7. The effect of storage temperature on the proportion of tubers sprouting in *D. rotundata*. Redrawn from Mozie (1987a).

In their first experiment, segments taken from dormant tubers (in May) were subjected to four temperature regimes between 23.9 and 32.3 °C, all at high humidity. Resultant data show a clear and linear response of the appearance of epidermal cracks (end of dormancy) and sprouts 2.5 cm long, to mean temperature (Fig. 8). Also, the time required to observe these experimental criteria was shorter at 32.3 than at 23.9 °C. The response to temperature of sprout appearance and growth, at least between 26° and 32 °C, was similar and parallel to that of the end of dormancy. Accordingly, the duration from the end of dormancy to the first appearance of sprouts and from then to sprouts of 2.5 cm length was constant at 13–14 and 9–10 d, respectively. At 24 °C, however, the duration from the end of dormancy to sprout appearance and growth was increased. These data suggest (i) that the optimum temperature for epidermal cracking or dormancy breaking was at least 32 °C and (ii) that the optimum temperature for sprout growth was between 26 and at least 32 °C. Temperatures below 26 °C inhibited sprout growth.

In a second experiment, segments taken from actively growing tubers (in August) were subjected to temperatures of 21 to 44 °C and epidermal cracking and 2.5 cm sprouts were recorded. After 79 d some sprouting was observed at 27 °C and 50% in those stored at 32 °C whereas, at 21 and 38 °C, no sprouting was

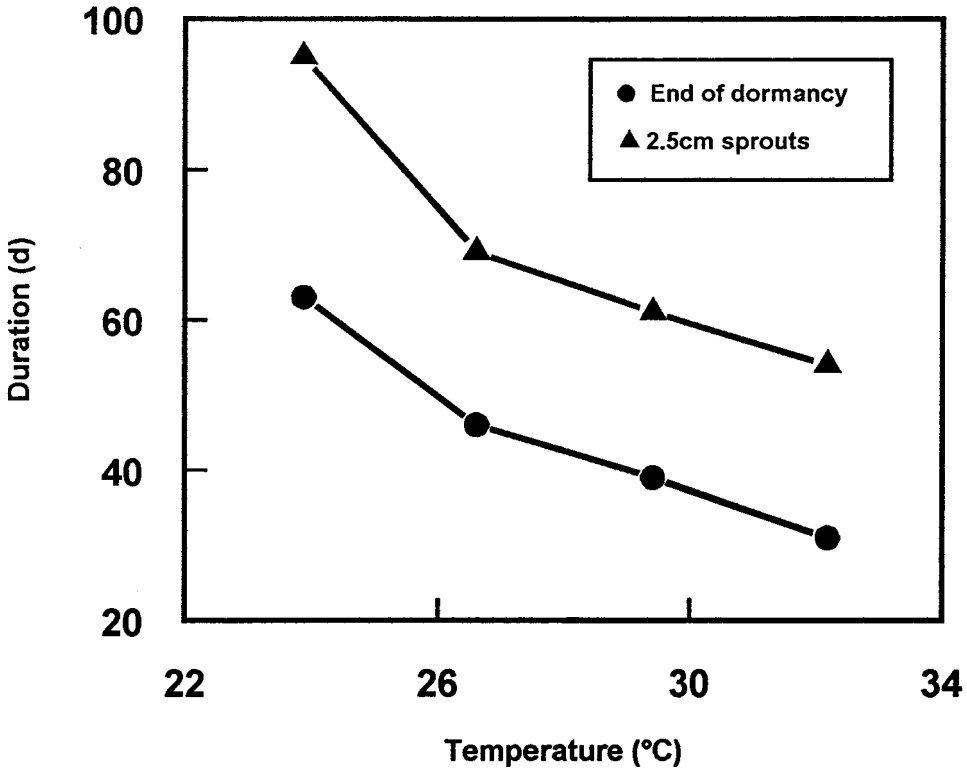

Figure 8. The effect of temperature on the duration to the end of dormancy (epidermal cracks visible) and the existence of sprouts 2.5 cm long in tuber pieces of *D. spiculiflora*. Temperature treatments started in May, towards the end of the dormant period. Redrawn from Preston and Haun (1963).

observed within the 115-d period of the first stage of the experiment. Therefore, in tubers harvested from actively growing plants and for tubers at the end of the dormant period (Experiment 1) the optimum temperature for sprouting was similar at about 32 °C.

Tubers from the second experiment that had not sprouted by 115 d after harvest were then subjected to a constant temperature of 32.3 °C and epidermal cracking and 2.5 cm sprouts were recorded (Fig. 9). About 25 d after transfer dormancy broke in all but tubers previously stored at 21 °C where ending of dormancy was further delayed. Furthermore, previous storage temperature also had a significant and linear effect on sprout growth rate. Average sprout lengths of 2.5 cm were reached after 33 d at 43 °C and 66 d at 21 °C. The data suggest that conditioning or acclimatization had occurred. It is also possible, however, that this response to previous temperature is simply a manifestation of tuber tissue temperature that is likely to have been warmer at the warmer ambient storage temperatures.

In a third experiment, Preston and Haun (1963) compared the duration to 2.5 cm sprouts in tubers kept at 32 °C and high relative humidity (RH) with those

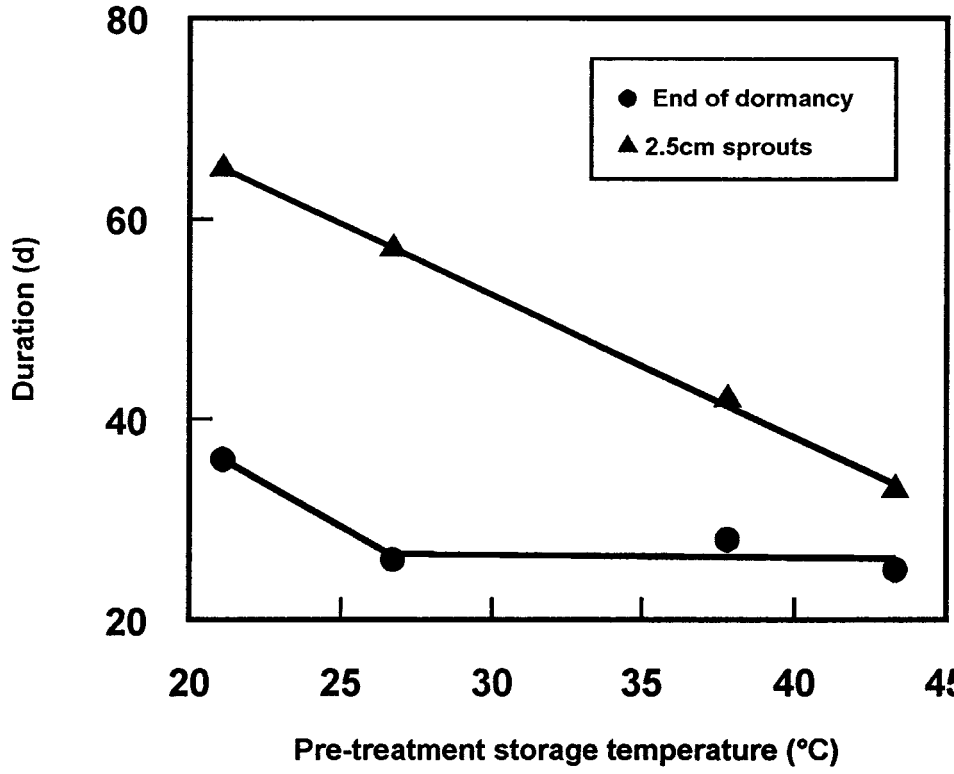

Figure 9. The effect of pre-treatment storage temperature on the duration of dormancy (epidermal cracks visible) and the presence of sprouts 2.5 cm long in tuber pieces of *D. spiculiflora*. Actively growing tubers were harvested in August and stored for 115 d at the temperatures shown and then transferred to a common temperature. Redrawn from Preston and Haun (1963).

subjected to 16 h of 40.6 °C and then maintained at 32 °C, both again at high RH. The duration to 2.5 cm sprouts was reduced from 63 to 47 d by the 16 h warmer temperature treatment. Experiments at IITA (Akoroda, 1995; Barker, 1998) have also examined the effect of short periods of warmer temperatures. Barker (1998) imposed temperatures of 35 °C for 5, 10 or 15 d on nine clones of *D. rotundata* and compared the duration to 2.5 cm sprouts with clones kept at about 25 °C. He found no significant effect. Experiments with a very short period of extremely high temperature (12 min at 120 °C) also had no effect on the same criterion (Barker, 1998).

Relative humidity and water-soaking treatments. Relative humidity can also have a significant effect on the duration to sprouting. For example, sprouting at 25–30 °C occurred 20 d earlier at 100% compared with 60–70% RH (Table 8). In contrast, Rivera *et al.* (1974a) observed that at 16–18 °C sprouting occurred earlier at 70% than at 80% RH. In *D. spiculifolia*, storing tuber segments at 32 °C and a low (described as dry) relative humidity delayed sprouting relative to tubers stored at the same temperature at high (described as moist) relative humidity (Preston and

Haun, 1963). Curing, that is the process of drying and hardening the surface skin of tubers prior to storage, does not have any affect on duration to sprouting (Akoroda, 1995).

Water-soaking treatments also affect the duration to sprouting. Degras (1982), for example, found that *D. alata* bulbils germinated in 7 d instead of 28 d following submersion in water for four hours. This hastening of development may have been due to the leaching of putative 'sprouting inhibitors' (Gupta *et al.*, 1979). Similarly, reducing oxygen concentration in the air to below ambient values also broke dormancy in bulbils of *D. opposita* (Okagami, 1979). Barker (1998), however, soaked five clones of *D. rotundata* in water for 24 or 48 h at ambient temperatures (about 25 °C) and found either no effect or an increase in the duration to sprouting of about 10 d. He also soaked two clones in a water bath at 50 °C for 1 h and this treatment too prolonged dormancy by 15–25 d, an effect he attributed to high temperature and damage to the outer layers of cork cells.

Temperature and relative humidity are the major determinants of evaporation rate and hence water-loss. Considerable care must be taken, therefore, with experiments (and their interpretation) which involve these weather variables. Most studies to date have not recorded water-loss nor given any indication of water content, data that might be critical for comparative as well as analytical and interpretive purposes.

Daylength, light quantity and quality. The authors know of no research on the effects of either daylength or of spectral quantity and quality on yam dormancy. Indeed, in contrast to potato, yams have no obvious organ ('eye') capable of sensing changes in daylength or light quantity and quality. Mozie (1975) reported that storing yam tubers in complete darkness delayed sprouting relative to storage under a natural photoperiod of 12–13 h d^{-1}. As Barker *et al.* (1999a) have pointed out, however, this finding may have been due to other factors confounded in the experiment such as temperature or relative humidity.

The effects of light quantity and quality on dormancy in potato have been studied and light quality is used commercially in the management of sprouting in seed-potato tubers (Wiltshire and Cobb, 1996). Wavelengths below 500 nm (blue) and above 650 nm (red and far-red) have the greatest inhibitory effects on sprouting. Phytochrome B also has an important role in tuberization in *S. tuberosum* ssp. *andigena* (Jackson and Prat, 1996). As discussed earlier, R:FR ratio effects have been reported on tuber initiation in yam (John *et al.*, 1993).

MANIPULATION OF TUBER DORMANCY

The mechanism of dormancy in yam tubers (and for that matter in other tuberous species too) is poorly understood and so the physiological dormancy period cannot be easily predicted or manipulated (Orkwor and Ekanayake, 1998). Many researchers have investigated the effect of different chemical (hormonal) and physical treatments on dormancy, principally to prolong storage-life. These

methods have been reviewed previously first by Degras (1993) and most recently by Barker *et al.* (1999a;b). Few researchers have investigated the mechanisms of dormancy *per se* that are involved.

Hormonal and chemical intervention

Various hormones and chemicals (selected on the basis that they block or promote the action of particular hormones) have been tested and, in some cases, used successfully to either prolong dormancy and storage-life (Table 9) or to break dormancy (Table 10) of tubers.

Table 9. Effects of various chemical compounds on the duration of the dormant period of yam tubers. Modified from Degras (1993).

Chemical compound	Yam species	Effect†	Reference
Abscisic acid (ABA)	*D. alata*	0	Wickham *et al.* (1984a)
	D. esculenta	0	Wickham *et al.* (1984a)
Gibberellic acid (GA)	*D. alata*	-ve	Wickham *et al.* (1984ab); Mantell *et al.* (1977); Girardin *et al.* (1998ab); Ireland and Passam (1984)
	D. rotundata	-ve	Wickham *et al.* (1984ab); Nnodu and Alozie (1992); Girardin *et al.* (1998ab)
	D. rotundata	0	Passam (1977)
	D. esculenta	-ve	Wickham *et al.* (1984ab); Ireland and Passam (1984)
	D. trifida	-ve	Wickham (1988)
	D. cayenensis	-ve	Girardin *et al.* (1998ab)
Clormequat chloride (CCC)	*D. alata*	0	Wickham *et al.* (1984a)
Indole acetic acid (IAA)	*D. alata*	-ve	Wickham *et al.* (1984a)
	D. esculenta	0	Wickham *et al.* (1984a)
	D. rotundata	0	Passam (1977)
2,4-D (100–1000 ppm)	*D. rotundata*	-ve	Mozie (1987b)
	D. alata	-ve	Wickham *et al.* (1984a)
	D. esculenta	-ve	Wickham *et al.* (1984a)
CPA	*D. rotundata*	-ve	Passam (1977)
Methyl-α-NAA	*D. rotundata*	-ve	Campbell *et al.* (1962a)
Maleic hydrazide	*D. rotundata*	-ve	Passam (1977)
	D. alata	0	Hayward and Walker (1961); Wickham *et al.* (1984a)
	D. alata	-ve	Wickham *et al.* (1984a); Ireland and Passam (1984)
	D. esculenta	-ve	Ireland & Passam (1984)
	D. esculenta	0	Hayward and Walker (1961)
Kinetin	*D. rotundata*	0	Passam (1977)
TCNB	*D. alata &*	0	Campbell *et al.* (1962a)
	D. rotundata	0	Passam (1977, 1982)
PCNB	*D. alata*	0	Campbell *et al.* (1962a); Passam (1977, 1982)
IIPC	*D. alata*	0	Campbell *et al.* (1962a); Passam (1977, 1982)
CIPA	*D. alata*	-ve	Rivera *et al.* (1974a)

† + ve = shortens period and promotes sprouting; 0 = no effect; -ve = prolongs dormancy and delays sprouting.

Table 10. Summary of experiments involving ethylene-based growth regulators and their effects on yam tuber sprouting. Modified from Degras (1993).

Chemical compound	Species	Organ	Effect†	Reference
Ethrel (α-2-phosphonic chloroethyl)	*D. alata*	Tuber	++ve	Martin and Cabanillas (1976)
	D. alata	Tuber at harvest	+ve	Martin and Cabanillas (1976)
	D. alata	Tuber segment	0	Wickham *et al.* (1984a)
	D. composita	Tuber	+++ve	Gupta *et al.* (1979)
	D. rotundata	Foliage	+++ve	IITA (1979)
	D. rotundata	Tuber	-ve	IITA (1973)
	D. rotundata	Tuber	+ve	Passam (1977)
	D. esculenta	Tuber segment	0	Wickham *et al.* (1984a)
Ethylene chlorohydrin (2-chloroethanol)	*D. alata*	Tuber	++ve	Campbell *et al.* (1962a)
	D. composita	Tuber	+ve	Gregory (1968)
	D. floribunda	Tuber	+ve	Gregory (1968)
	D. alata	Tuber	+ve	Mantell *et al.* (1977)
	D. alata	Tuber	0	Ireland and Passam (1984)
	D. esculenta	Tuber	+++ve	Ireland and Passam (1984)
	D. alata	Bulbil	+ve	Passam *et al.* (1982b)
	D. bulbifera	Bulbil	+ve	Passam *et al.* (1982b)
Ethylene chlorohydrin + thiourea	*D. alata*	Tuber	+ve	Cibes and Adsuar (1966)
Thiourea	*D. rotundata*	Tuber	+ve	Samarawira (1983)
Thiourea	*D. rotundata*	Tuber	0	Passam (1977)
Rindite (Ethyl chloride + ethylene dichloride + carbon tetrachloride)	*D. alata*	Tuber and tuber segments	+ve	Mathurin (1977) Quoted in Degras (1993)
	D. alata	Tuber and tuber segments	+ve, -ve	Mathurin (1977)
	D. cayenensis	Tuber and tuber segments	+ve, -ve	Mathurin (1977)
	D. trifida	Tuber and tuber segments	+ve, 0, -ve	Mathurin (1977)
	D. cayenensis	Tuber 7–157 d after harvest	+ve	Mathurin (1977)

† +ve = shortens period and promotes sprouting; 0 = no effect; -ve = prolongs dormancy and delays sprouting; the symbols +, ++ and +++ denote slight, moderate and strong response, respectively.

Chemicals that prolong dormancy. Dormancy of tubers can be extended by several chemicals, most notably gibberellic acid (GA) and the anti-auxins 2,4-D and CPA (Table 9). Indeed, soaking tubers in GA solutions is an effective, economical and practical means to extend the storage life in yams (Girardin *et al.*, 1998a;b;c). Gibberellic acid can also re-impose dormancy on sprouted tubers (Wickham *et al.*, 1984a) (Table 11). Maleic hydrazide also has extended dormancy in some studies. In contrast the major plant hormones, abscisic acid (ABA), auxin (indoleacetic acid, IAA) and kinetin, had no effect on dormancy in the experiments summarized in Table 9. Similarly, tetrachloronitrobenzene (TCNB), pentachloronitro-

Table 11. Duration to 20% sprouting (d) of tubers of *D. alata* treated with GA_3 (150 mg L^{-1}) at different times before, at and after maturity. From Wickham *et al.* (1984b).

	Days before maturity				Days after maturity			
Treatment	98	84	63	42	0	14	35	70
Water control	140	135	127	113	90	88	88	87
GA_3	270	190	172	160	175	172	164	125
s.e.		3.8				3.5		

benzene (PCNB) and isopropyphenyl carbamate (IIPC), all of which affect dormancy in potato, had no effect on dormancy of yams (Campbell *et al.*, 1962a;b; Passam, 1977, 1982). Bazabakana *et al.* (1999) reported that dormancy in microtubers (tubers produced in tissue culture) was extended by high concentrations of jasmonic acid (30 and 100 μM).

Chemicals that break dormancy. Of the wide range of chemical compounds tested to date, ethylene or ethylene precursors [full names ethrel, 2-chloroethanol, and ethylene chlorohydrin] are clearly the most effective at breaking dormancy in tubers and bulbils of many yam species (Table 10). For example, Campbell *et al.* (1962a) showed that soaking tuber pieces in an 8% solution of ethylene chorohydrin resulted in 47.5% of tubers sprouting, compared with 0% in the controls. These compounds are also effective in other species such as potato (Coleman *et al.*, 1992; Coleman and McInerney, 1997). Little or no work has been done, however, to develop a protocol suitable for manipulating dormancy on a larger scale (for example in a breeding programme) presumably because the focus of interest to date has been primarily in prolonging dormancy and storage life.

Physical intervention

Physical factors that affect tuber dormancy such as temperature, relative humidity and light have been discussed earlier. Other physical factors such as gamma radiation, oxygen and carbon dioxide concentrations have been discussed by Barker *et al.* (1999b) and so are reviewed here only briefly.

Gamma radiation. Sprouting of *D. rotundata* tubers can be delayed by non-lethal doses of gamma radiation. For example, Rivera *et al.* (1974b) exposed tubers of *D. alata* cv. Florido to various doses of gamma-radiation and discovered that exposure to 7.5 krad extended dormancy by 120 d. Similarly, in *D. rotundata* doses greater than 7.5 krad also extended dormancy by eight months (Adesuyi, 1982). In contrast, however, Gregory (1968) and Martin *et al.* (1974) found no effect of gamma radiation on dormancy, possibly because they used smaller radiation values. Indeed, values of gamma radiation from 0.5 to 1 krad stimulated yam germination, as well as vegetative growth and tuber yield, whereas values above 2.0 krad retarded growth (Martin *et al.*, 1974).

Oxygen and carbon dioxide concentrations. Reduced ventilation extended dormancy in yams, possibly because lower oxygen concentrations would decrease the metabolic rate of the yam tubers (Ajayi and Madueke, 1990). In *D. opposita* bulbils, however, a concentration of less than 10% O_2 in N_2 was effective in breaking dormancy (Okagami, 1979). Similar findings have been made with potato tubers where reduced oxygen concentration (Burton, 1989) and an atmosphere enriched in carbon dioxide (Reust and Gugerli, 1984) were effective in breaking dormancy.

Other physical methods. Barker (1998) tested various physical means of manipulating tuber dormancy in *D. rotundata*, including electric shock and microwave treatments. He concluded that none of 50 or 100 V of AC or DC nor microwave treatment (30 s at 350 W) had any significant effect on the duration of dormancy.

Endogenous control of dormancy

The state of 'dormancy' has been intensively studied in seeds and buds. Research on seeds in particular has revealed a number of possible control mechanisms (Bewley and Black, 1994). Dormancy has also been studied intensively in potato (Coleman, 1987), but it is critically important to remember that potato and yam tubers are botanically very different. In yam, some progress has been made in understanding the dormancy mechanism in bulbils, particularly in *D. opposita* (formerly *D. batatas*) where both photo-sprouting (in young bulbils) and thermo-sprouting (in dormant bulbils) mechanisms have been identified (Okagami, 1979).

In potato, exogenously applied ABA inhibits sprout growth and endogenous concentrations decline during storage and prior to sprouting (Suttle, 1995), though the breaking of dormancy was obviously not associated with any threshold concentration of ABA. Similarly, ABA controls the onset of, and maintains dormancy in seeds (Bewley and Black, 1994). Gibberellic acid, on the other hand, promotes dormancy breaking in both seeds and potato, as do cytokinins and ethylene in potato. The role of auxins (IAA) is not clear in either seeds or potatoes. Mechanisms that control dormancy in seeds have not been fully elucidated, though it is clear that the pentose-phosphate pathway, polyphenol oxidases and membrane permeability are important components (Bewley and Black, 1994).

Far less is known about the control of dormancy in yams, particularly in the tubers of the most economically important species. However, the gross effects of exogenous applications of the major hormones on sprouting are known (Table 9 and 10). These are summarized and compared with the response of potatoes in Table 12. It is immediately apparent that the responses of yams and potatoes to ABA and GA are very different; ABA has no effect and GA is an inhibitor of sprouting in yams. Ethylene, however, promotes sprouting in both species. Clearly, the dormancy mechanism in yam tubers is very different from that of potato and this is probably due to the absence of apical meristems in yam tubers.

Researchers on aerial bulbils of *D. opposita* (Hashimoto *et al*., 1972; Hasegawa

Table 12. Comparison of the effects of exogenous applications of hormones and growth regulators on sprouting in potato (after Suttle, 1996) and yams (various sources).

Hormone or growth regulator	Potato	Yam
ABA	Inhibitor	No effect
GA	Promoter	Inhibitor
Auxin/IAA	Unknown	No effect
Cytokinin/Kinetin	Promoter	Unknown
Ethylene	Promoter	Promoter

and Hashimoto, 1974a;b) have detected the endogenous phenolic plant growth inhibitors 'batatasins'. Concentrations of these inhibitors in *D. opposita* correlate well with the depth of dormancy (the higher the concentration of endogenous batatasins the longer the duration of the dormant period). Furthermore, cold-stratification, which in this temperate species is required to break dormancy, lowers the concentration of endogenous batatasins. The application of GA, which extends dormancy in bulbils and tubers, increases the endogenous concentration of batatasins. The exogenous application of batatasins can also extend dormancy (Ireland and Passam, 1984, 1985). Several forms of batatasin have been found in other yam species (Ireland *et al*., 1981). However, the relation between batatasin concentration and the control of dormancy has not been established for all the species of *Dioscorea* and it is not at all clear how batatasins maintain dormancy. Also, given the cold-stratification requirement in *D. opposita* and other bulbil-producing species, these studies may not be wholly relevant to tropical tuber species.

Ireland and Passam (1984) examined the concentration and distribution of phenolic plant growth inhibitors, including batatasins, within and between tissues and organs in *D. alata* and *D. esculenta*. Batatasins were present during plant growth in very small tubers of *D. alata* (described as pre-suberized), that is at 130 d after planting. Concentrations increased substantially thereafter to a maximum, about 100 d later, when tubers were said to be mature. This supports the view expressed previously that dormancy develops in very young tubers, perhaps even from the start of suberization. It must be noted that the data in Ireland and Passam (1984) are expressed as a proportion of the maximum tuber size at maturity. They also observed in both species that batatasin concentrations declined throughout the period of tuber dormancy, as occurred in *D. opposita* (Hasegawa and Hashimoto, 1973), and by the time sprouting started the growth-inhibition effect of the batatasins or other phenolic growth substances was minimal.

Ireland and Passam (1984) also examined the concentrations of growth inhibitors within dormant tubers of *D. alata* and *D. esculenta*. Throughout dormancy, greater concentrations were found in the proximal than in the distal end; the proximal end is where sprouting occurs first. They also found that growth

inhibitors were concentrated in the outer layer of the tubers, in the meristematic and periderm layers; no inhibitors were found in the cortex.

Wickham *et al.* (1984b) showed that the effectiveness of GA_3 declined during dormancy in *D. alata* (Table 11). Conversely, exogenously applied ethylene chlorohydrin became more effective during dormancy (Campbell *et al.*, 1962a). The concentrations of growth inhibitors and the duration to sprouting in *D. alata* and *D. esculenta* were increased by the exogenous application of GA_3 and lowered by treatment with ethylene chlorohydrin (Ireland and Passam, 1984). Endogenous glutathione concentrations also increased when dormancy broke, and were enhanced by the application of ethylene chlorohydrin (Campbell *et al.*, 1962a).

RETROSPECT AND PROSPECT

The control of tuber dormancy in white yam (*D. rotundata*) as well as water yam (*D. alata*) is poorly understood. Although many studies have examined single environmental factors (principally temperature) and *ad hoc* chemical treatments that might prolong tuber dormancy, there has been little focus on tuber dormancy *per se*. Indeed, despite the obvious importance of dormancy as an adaptive mechanism, there have been no systematic studies of tuber dormancy in relation to factorial combinations of those environmental and ecological conditions in which yam clones are grown. The authors conclude that precise definitions of key developmental events are needed along with an analytical framework that places dormancy in the context of overall adaptation of yams to their growing and storage environments. In particular, the following factors need to be considered:

- Yam cultivars are in fact clones grown mostly as annual crops in tropical and sub-tropical environments with well-defined dry seasons. Tuber dormancy is an adaptive mechanism that allows propagules to survive the dry season and so it is not surprising that the duration of the dormant period varies substantially between clones or cultivars. There is some anecdotal evidence to suggest that the duration of the dormant period is not only cultivar-specific but also linked to the duration of the dry season. An investigation of dormancy in relation to growing season and storage environments, and using clones of known provenance harvested from locations along a gradient from long to short rainy-seasons, would generate much needed basic data about adaptation.
- *When do yam tubers become dormant?* The data from several studies can be interpreted to suggest very strongly that dormancy starts at tuber initiation and not at tuber maturity (however this second event might be defined). This interpretation requires confirmation. If dormancy does indeed start at tuber initiation then most previous studies have unknowingly targeted only the post-harvest portion of the true dormant period and so the results contribute relatively little to an understanding of tuber dormancy. Furthermore, if dormancy starts at tuber initiation then, as Burton (1957) has pointed out for potatoes, seasonal variations in climatic factors and edaphic variables, and

hence in crop growth, may also affect the duration of the dormant period. The timing of tuber initiation is, therefore, also a key developmental event.

- *When does tuber dormancy end?* In practical macroscopic terms the end of tuber dormancy is marked by the appearance of apical buds or shoots from the surface of the tuber. However, the end of tuber dormancy is marked anatomically beforehand by the formation of the primary nodal complex (PNC) and apical meristem or bud, which events occur below the epidermal and cork cells. The authors believe that it is this developmental event, and not sprouting (however defined), which marks the end of tuber dormancy. A correlated biochemical, physiological or morphological marker is urgently needed as a reliable indicator of the end of tuber dormancy.
- This review suggests there is good evidence that the end of tuber dormancy is under the control of endogenous factors, that is, endo-dormancy. Several studies have monitored biochemical changes during storage and sprouting, but no strong candidates for biochemical markers have been identified. Most of those studies, however, have measured concentrations of compounds during the perceived dormant period and at sprouting, and they did not explicitly relate changes in concentration to the ending of dormancy as it is defined here. More informative and unambiguous measures of the physiological state of the tuber both during dormancy and at the end of dormancy are needed, including a quantitative measurement of the depth or intensity of dormancy.
- The period from the end of dormancy (that is the formation of the PNC or appearance of an apical bud) until the appearance of sprouts (that is the growth and development of the apical bud) must be accepted to be a separate developmental event to that of dormancy breaking. Thus, whilst the formation of the PNC and apical meristem is most probably under endogenous control, the subsequent growth and development of the apical bud is more likely to be influenced strongly by factors outside the tuber, that is by eco- and exo-dormancy factors. Because to date this period has not been separated from the true dormant period, it is inevitable that the factors that affect the growth and development of the apical bud have not been clearly defined.
- The key developmental events that affect tuber dormancy are tuber initiation, the end of dormancy as indicated by the formation of the PNC and subsequent appearance of the apical bud, and apical bud growth and development to form a sprout. Given that tuber initiation can occur within 28 d of sprouting or shoot emergence above the soil surface, step one of an analytical framework for research on dormancy needs to start at tuber initiation. It must take account of environmental conditions during the growing season as well as during storage, whether the latter be in barns or in soil.
- Although the dormancy mechanism is poorly understood, it is clear that ethylene compounds can promote sprouting in yam, though whether they promote the break of dormancy and apical bud growth is not known. Further detailed investigations of the impact of ethylene and ethylene-promoted triggers to break dormancy are a priority and should include work on the probable

interacting effects between ethylene and other yet-to-be-identified, synergistically bioactive molecules or factors.

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