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Yam dormancy: potential mechanisms for its manipulation

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Abstract *Tuber dormancy is of major importance in yam production, but the lack of a method to consistently break dormancy restricts the rate at which new clones can be multiplied for release to farmers. Much of the work on yam tuber dormancy was small scale, using only one or two clones and a few tubers. Often, the effects of a treatment on dormancy were seen as a side issue, and results were essentially anecdotal. Many chemicals were used in attempts to manipulate dormancy and although some success was achieved using gibberellic acid, this large amount of work yielded few future leads. Similarly, physical methods might be able to break yam dormancy but these studies have been unsystematic and inconsistent. Appropriate research directions are needed if yam breeding is to make progress and keep pace with food demands.*

Keywords: yams, *Dioscorea* spp., dormancy, manipulation, chemical and physical techniques.

Introduction

Yams (*Dioscorea* spp.) have received less research attention than is appropriate for a staple food in much of West Africa. Failure to achieve much progress in crop improvement programmes, related to the slow turnover in generations of yams, contributed to this lack of attention.

Yams are propagated vegetatively using small tubers (seed tubers) or tuber pieces as setts. Long-term vegetative propagation has reduced the number of flowers produced and viable seeds set to such an extent that, in some landraces, flowering is not observed. This creates severe problems for breeders trying to produce new varieties with high yield and disease resistance. Dormancy of yam tubers also creates a major problem. The current inability to break tuber dormancy prevents breeding programmes from advancing by more than one generation each year, so it takes many years to multiply any new material for commercial release. In contrast, crops such as cowpea or wheat can be advanced through two or more generations each year. This partly explains why there is yet to be an official release of new yam varieties by national programmes in Africa (Asiedu *et al.* 1998).

Most yam species are grown for their bulky tubers. Usually these are annually renewed, although in some species the tuber is perennial, being added to each year and becoming increasingly lignified (Coursey 1967). The tubers form large food reserves and as they grow deep in the soil, wild yams can survive the dry season and periodic bush fires. Survival then is

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aided by dormancy when a tuber will not sprout even in ideal sprouting conditions. Dormancy is not unusual in plants but in yam tubers it is unusual in its duration, from 28 to 180 days depending on the species, and on average 75–100 days. *D. cayenensis*, a species of the West African forest zone where the dry season is very short, has almost continuous vegetative growth. *D. elephantiphes*, at the other extreme, spends most of the year dormant as it is a native of semi-desert regions. *D. alata* and *D. rotundata*, the principal species cropped, are between these extremes, with considerable differences between varieties. The measurement of dormancy is complicated by the lack of knowledge of when it is initiated. The time from harvest is unreliable, as the harvesting date varies from farmer to farmer, and it has no physiological significance.

Tuber dormancy is important in cultivation, since it enables yams to be grown in areas without cool storage. When the yam tuber is dormant, it is very resistant to pathogen attack, and if undamaged it will survive through the dry season. Dormancy also ensures a continued food supply. Once dormancy has ended, the tubers become more susceptible to pathogen attack (Passam and Noon 1977), and nutrients in the tuber are mobilized for vine growth, reducing quality as a food source. It also has labour implications as farmers have to remove the sprouts regularly to minimize the loss of quality.

The ability to break yam dormancy consistently and to provide uniform sprouting times would enable farmers to grow two crops of early maturing varieties a year in environments with long growing seasons. More uniform sprouting would also allow more efficient weed control using herbicides, a considerable benefit given the necessity of regular weeding and the rising cost of labour. Storage space could be used more efficiently if sprouting could be induced at the most convenient time. The International Institute of Tropical Agriculture (IITA 1997) is studying selection for good sprouting ability and establishment in the field. This paper reviews techniques with which yam dormancy might be manipulated.

Sprouting in yam tubers

The formation of sprout initials on a tuber is the first external sign of dormancy break. The sprout initials may either be from pre-formed buds present at harvest or from differentiation of cells close to the tuber surface. The pre-formed sprout initials are part of the primary nodal complex (PNC) from which roots and shoots emerge, and this is the point at which the vine of the parent plant was attached. The tuber itself is a hypocotyl structure rather than a stem or root structure. Yam tubers exhibit apical dominance, so once a shoot has developed at the head of the tuber, others are slow to form. However, if the PNC is removed or damaged during harvest, buds will form anywhere on the tuber surface, but primarily towards the head. This characteristic led to the development of the minisett technique (Okoli 1978). Onwueme (1973) examined the external progression of events during dormancy break and the cellular changes at a microscopic level in *D. rotundata* and *D. alata*. He found that the differentiation of sprouts commences before there are visible changes on the tuber surface and that sprouts originate from meristematic cells lying close to the surface. This makes the sprouting region prone to pathogen attack and physical damage.

Dormancy

Although the dormancy of yam tubers is not fully understood, the changes in respiration rate and chemical composition during and immediately after dormancy have been studied. After harvest, respiration rates are high throughout the tuber, especially at the tail, since it is the most recently formed tissue. The respiration rate falls rapidly (Table 1), and immediately before the dormancy break the head region has the highest rate; during dormancy dry matter is lost due to respiratory activity and respiration rates decrease with temperature (Passam *et al.* 1978; Passam and Noon 1977). However, temperatures below 13°C result in chilling injury (Coursey 1967). Moisture loss also occurs during dormancy, perhaps around 10% (Ravindran and Wanasundera 1992). These authors also showed that in 150 days' storage at 24–28°C and 70–90% relative humidity, crude protein and starch levels fell, as did the vitamin C content.

Table 1. Overall yam tuber respiration rates and weight loss

Temperature	Time period	Respiration rate (ml CO_2/kg/h)	%Weight loss/day	%Weight loss due to respiration
25°C	After harvest	15	0.22 ± 0.02	27
	Dormant	3	0.15 ± 0.03	7
	Sprouting	34	0.21 ± 0.02	35
35°C	After harvest	29	0.36 ± 0.02	30
	Dormant	8	0.28 ± 0.06	10
	Sprouting	20	0.34 ± 0.07	20

From Passam *et al.* (1978).

The length of dormancy in a particular species seems to be genetically controlled. Nwoke and Okonkwo (1981) found that in *D. alata*, *D. rotundata* and *D. dumetorum* the dormant period was about 100 days under a wide variety of storage conditions and planting dates, suggesting endogenous control. The time from planting in one season to sprouting in the next was relatively constant even when harvesting dates varied (Okoli 1980). Sprouting took place only after a set period of time and it was not affected by planting, even if this was in ideal conditions immediately after harvest (Onwueme 1975). Tubers planted early remained dormant in the ground. Setts planted in dry sawdust sprouted as rapidly as those in moist sawdust for both *D. alata* and *D. rotundata*; once the tuber has begun to sprout respiration rates increase and the quality of the tuber deteriorates rapidly (Onwueme 1976).

Dormancy mechanisms

Although a great deal is known about the consequences of yam tuber dormancy, in terms of respiration and storage, understanding of the dormancy mechanism is by no means complete. Changes in the balance of growth substances occur during storage, and they are susceptible to external factors, but they have not been correlated to physiological behaviour (Osagie 1992).

The first insight into the mechanism arose from the observation (Hashimoto *et al.* 1972) that phenolic growth inhibitors, named batatasins, induced dormancy in stem bulbils of *D. opposita*. However, since this is a temperate species and dormancy is maintained over cold winters, the results could not be directly related to tropical species. Batatasins occur in tropical species where dormancy occurs in the dry season (Ireland *et al.* 1981) and control dormancy in *D. alata* by modifying membrane properties (Ireland and Passam 1984). Batatasin levels gradually decline during yam dormancy and they affect the physiological behaviour of other species, such as inhibiting coleoptile growth in *Avena* spp. (Hasegawa and Hashimoto 1973). However, a similar correlation between batatasin levels and the control of dormancy was not shown for *D. esculenta*, suggesting other mechanisms may also be involved. During the vegetative growth of *D. alata* plants, batatasins start to accumulate 175 days after planting (100 days after tuberization) and reach a peak level 75 days later (Ireland and Passam 1984); this increase was linked to the onset of tuberization. The distribution of batatasins was variable, the levels being highest at the proximal (head) end and lowest at the distal (tail) end. The periderm of the tuber had the highest levels of batatasins, while the centre had negligible levels. The role of batatasins in maintaining dormancy is clear from their concentration in the areas where meristems will form first.

Tuber dormancy in other crops

Of the world's tuber crops, the dormancy of the Irish potato (*Solanum tuberosum*) is the most studied, due to its commercial importance. A review of potato tuber dormancy (Wiltshire and Cobb 1996) demonstrates the similarities between yam and potato tubers during dormancy. Respiration continues, resulting in weight loss and cooler temperatures reduce this loss. Potato tubers can withstand much lower temperatures than yams, around 4°C, since they originate from a cooler climate. The breakage of potato tuber dormancy follows an increase in electrolyte leakage indicating a decline in membrane integrity (De Weerd *et al.* 1995). This link was confirmed by maximal sprouting ability occurring at, or soon after, the increase in electrolyte leakage. However, there is a major difference between potato and yam tubers which obstructs further comparison, particularly for manipulation of dormancy. Buds are already present on potato tubers when they are harvested, but in yams, bud differentiation is a sign of dormancy break. Thus in considering methods to break yam tuber dormancy, direct comparison with potato may be misleading.

Manipulation of tuber dormancy in Irish potatoes

The manipulation of Irish potato tuber dormancy is important in maintaining a continuous supply of tubers for processing. Dormancy normally lasts for 7–105 days, but this innate dormancy is not long enough to maintain supply. Cold storage is therefore often used to enforce dormancy, but it may result in undesirable chemical changes in the tuber. Light and humidity have little effect on dormancy. Changes in the oxygen and carbon dioxide concentrations of the storage atmosphere have an effect, although results have been contradictory. Electric shock treatment elicits dormancy break in potato tubers, possibly due to its effects

on membrane integrity (Kocaçaliskan *et al.* 1989). Research therefore focused on chemical methods to suppress sprouting. Three compounds which inhibit mitosis have long been used, Chlorpropham (isopropyl N-(3-chorophenyl) carbamate), Propham (isopropyl N-phenyl carbamate) and Tecnazene (1,2,4,5-tetrachloro-3-nitrobenzene). Concern over the safety of the first two led to a further search for less toxic sprout suppressants, notably maleic hydrazide, methylnapthalenes, Carvone and PSS25. These compounds have varied and less understood modes of action.

Although sprout suppression is not as advanced, some progress has been made on ways to break potato tuber dormancy. Bromoethane stimulates dormancy break (Coleman 1983, 1986) but due to environmental concern it is not widely used. Manipulation of the gaseous environment by increasing O_2 and CO_2 levels breaks dormancy, although the mechanism is not understood (Reust and Gugerli 1984). Gibberellic acid can break potato tuber dormancy (El-Asdoudi and Ouf 1994).

Manipulation of yam tuber dormancy

Much of the initial work on manipulation of yam dormancy was on extending the period of dormancy to maintain a stable food supply and ensure even sprouting of the tubers once planted. Since the appearance of shoots is the first visual sign of dormancy break, many farmers simply remove premature shoots, which results in increased emergence in the first 35 days after planting, increased leaf area index in the first 125 days and increased yield (Nwankiti 1988). This may be because the metabolites mobilized as the sprouts form remain available for the shoots when they are left to grow.

Chemical techniques

A wide range of chemicals was tested, including plant growth regulators (PGR) and chemicals used in potato dormancy manipulation. The most promising is gibberellic acid (GA_3). Despite early work which showed that it had no effect (IITA 1979; Passam 1977), GA_3 can extend dormany (Nnodu and Alozie 1992; Okagami and Tanno 1993; Wickham *et al.* 1984a,b,c). However, *Dioscorea bulbifera* does not respond, suggesting a different mechanism (Wickham *et al.* 1984a). Although the method of application has varied, the effects are relatively consistent. Initial studies involved soaking tubers for 22 h (Wickham *et al.* 1984a,b), but when the economics of tuber soaking were studied it was shown that 6 h was the optimum period (Nnodu and Alozie 1992). The effects of GA_3 were greatest when soaking was carried out immediately after harvest (Wickham *et al.* 1984b). Foliar application of GA_3 had a similar effect in *D. esculenta* but not in *D. alata*, suggesting variation in translocation between species (Wickham *et al.* 1984c).

GA_3 may act through a moderating effect on the batatasins (Okagami and Tanno 1977), through inhibited batatasin breakdown or increased batatasin synthesis. However, GA_3 increases batatasin levels in *D. batatas* bulbils (Hasegawa and Hashimoto 1974), and since GA_3 re-induces dormancy in sprouted tubers (Wickham *et al.* 1984b), its effect on synthesis may be important (Osagie 1992).

Two studies have shown that at very low concentrations GA_3 stimulates dormancy break (IITA 1979; Okagami and Tanno 1977). This apparent contradiction may reflect the complexity of the dormancy control mechanism. Osagie (1992) suggested that there is a balance of sprout-inhibiting and sprout-promoting proteins in the tuber, which is affected by their turnover rates. GA_3 at varying concentrations has different effects on the two pathways (Okagami 1978). 2-Chloroethyl trimethyl ammonium chloride causes dormancy break in *Dioscorea* spp. bulbils (Okagami and Tanno 1977), probably due to the inhibition of gibberellic acid synthesis.

Other work with PGRs and sprout suppressant chemicals has yielded inconclusive and often contradictory results. The response to each chemical depends on the concentration, timing of application, nature of tuber, variety and area of application (Degras 1993). The ineffectiveness of auxins in altering dormancy length may be due to their rapid metabolism (Wickham *et al.* 1984a). Maleic hydrazide is the most promising of the chemicals (Ireland and Passam 1984), but the effects have been variable. One study showed extension of dormancy in tuber pieces, but not in whole tubers (Wickham *et al.* 1984b). Campbell *et al.* (1962a) showed extension of dormancy or no effect when foliage of *D. alata* was treated with maleic hydrazide, but treatment of *D. rotundata* foliage did not affect dormancy (Adesuyi 1973; IITA 1973). However, when the tuber is treated dormancy is extended. Passam (1977) suggested that the main reason for the ineffectiveness of PGRs and sprout suppressants in prolonging yam tuber dormancy was the fact that yams have no well-formed sprout loci at harvest, so there is nowhere for the inhibitors to act. As sprouts differentiate at dormancy break, suppressants applied at this stage, Chlorpropham (Olorunda *et al.* 1974; Rivera *et al.* 1974a) and methyl-α-naphthalene acetic acid (Campbell *et al.* 1962b), are successful.

Research into chemical curtailment of dormancy has been less successful. Glutathione levels in potato tubers increased sixfold following treatment with ethylene chlorohydrin (EC, chloroethanol) (Guthrie 1940) and the potato tubers broke dormancy; glutathione itself will break dormancy. EC shortens *D. alata* tuber dormancy from 120 days to 21 days (Campbell *et al.* 1962a). The action of glutathione may be due to the presence of a sulphur–sulphur double bond; cysteine and thiourea, which also contain this double bond, have also been shown to break dormancy (Guthrie 1940; Passam 1977). Other compounds related to ethylene stimulate dormancy break: Ethrel (IITA 1973, 1979; Passam 1977) and Rindite (Okagami 1978). This supports a theory by Osagie (1992) that ethylene is involved in tuber dormancy break. Traditional practices to encourage sprouting use the leaves of *Croton aromaticus* and *Averrhoa bilbinbi*, which are also used to ripen bananas, suggesting that ethylene is involved.

Physical techniques

The lack of progress in finding chemical methods to manipulate yam tuber dormancy led to research on physical methods. Again this was mainly on the effect of storage conditions to prolong the supply of fresh yams, rather than to manipulate dormancy. This resulted in a broad understanding of the exogenous factors that affect the length of tuber dormancy. A traditional practice of curing yams in covered pits at 26°C and 90% RH for 11 days resulted in less weight loss and rotting and it increased but delayed sprouting (Nnodu 1987). Tubers

of *D. rotundata* cv. Iyawo stored in unmulched pits had better germination than those stored in a yam barn, and gave better yields than those stored in a mulched pit (Waitt 1960), perhaps because of more stable temperatures and higher humidity in the unmulched pit.

As with Irish potato, storage at reduced temperatures prolongs dormancy, although temperatures below 13°C result in chilling injury (Adesuyi 1973). Storage at 16–18°C and 80% RH prolonged dormancy by 200 days in *D. alata* cv. Florido (Rivera *et al.* 1974a), and dormancy in *D. alata* cv. Oriental was increased by over 150 days following storage at 20°C (Rao and George 1990). Mozie (1987) showed that storage at 15°C maintained 100% dormancy over a 'prolonged' period. Cool storage can also be used to enforce dormancy after breakage of the innate dormancy period. Tubers stored at 16°C and 70% RH remained dormant for between 120 and 150 days longer than a control at 21–32°C, 60–95% RH; however, they sprouted rapidly when moved to the control conditions as buds had formed at the end of the period of innate dormancy and they rapidly elongated (Mozie 1987). At 16–18°C sprouting occurred earlier at 70% RH than at 80% (Rivera *et al.* 1974a), but on the contrary Passam (1977) showed that high relative humidity promotes dormancy break, although his study was at higher temperatures, which may explain the different results.

Despite the success of cool storage in extending yam tuber dormancy, the large-scale cool storage of yams in West Africa, the main production area, is not feasible at present.

In work at IITA (1979, 1980), tubers were treated in an oven at 35°C for up to 20 days. In one year, treatment for more than 10 days accelerated sprouting by 20 days, giving uniform and vigorous sprouting, but repetition of the experiment in a second season gave inconclusive results. The work was not repeated again, and since only one clone was used despite the large variation between yam clones, few conclusions can be drawn.

Recent work suggests that storing yam tubers (*D. cayenensis*) at high temperatures may inhibit sprouting (Ajayi and Madueke 1990), but no explanation was given. It can be assumed that the increased temperatures increased the rate of respiration within the tubers, and other metabolic pathways, including those for sprout promotion and inhibition, may also have been affected. Since these pathways respond differently to GA_3, they may also respond differently to temperature.

Gamma irradiation has shown promise in attempts to manipulate yam tuber dormancy. A dose of 7.5 krad extended dormancy by 120 days in *D. alata* cv. Florido stored at 21–32°C, 60–95% RH (Rivera *et al.* 1974b). The reason for this is not clear, but it is interesting to note that the effect occurred even with tubers stored at ambient temperature. A similar dose maintained dormancy for 30 days when tubers were taken from 16°C, 80% RH to ambient conditions (Rivera *et al.* 1974a). Lower levels of gamma irradiation (0.5–1 krad) stimulated yam germination, vegetative growth and tuber yield (Martin *et al.* 1974), while higher levels retarded growth; it was not clear whether the tubers were treated at harvest or before planting.

Gamma irradiation has no detrimental effects on eating quality (Rivera *et al.* 1974a) so the technique might be attractive in areas such as Nigeria, where the quality of the cooked product is important. However, this technique may not be suitable for the storage of planting material, since genetic mutations might be induced.

Some work has been carried out on the effects of water. Since yam tubers readily sprout when stored in the open, water availability is not a major factor. However, Gupta *et al.* (1979)

found that regular sprinkling of yam tubers with water facilitated leaching of the inhibitor and promoted sprouting. Low oxygen levels (0.3–5.0% in nitrogen) promote sprouting in immature *Dioscorea* bulbils (Okagami 1979) and in *Begonia* bulbils (Okagami 1972), where increased polyphenol oxidase activity and induced dormancy resulted from GA_3 treatment, suggesting polyphenol oxidase participates in inhibition of sprouting by GA_3. It was also observed that the level of polyphenol oxidase activity decreased under limited oxygen. Since GA_3 treatment resulted in increased polyphenol oxidase activity along with extended dormancy, the role of polyphenol oxidase in dormancy induction appears definite (Okagami 1979). It has therefore been postulated that sprouting is a result of the suppression of polyphenol oxidase activity.

Okagami and Tanno (1977) showed the negligible affinity of polyphenol oxidases to oxygen and hence their susceptibility to inhibition at low oxygen levels or under anoxia. This suggests that the sprout-inhibiting mechanisms within the yam bulbil are susceptible to interference during anoxia or at low oxygen levels. Sprout-inducing mechanisms have a higher affinity for oxygen so they can still operate at low oxygen levels. Ajayi and Madueke (1990) found that reduced ventilation delayed sprouting: since a reduction in ventilation is likely to decrease oxygen levels, this appears to contradict the studies on anoxia. However, low ventilation is unlikely to reduce oxygen levels to 5%, so it may be that reduced oxygen levels slow down the metabolism of the yam tuber and thus prolong dormancy.

Keeping tubers in complete darkness delayed sprouting, while tubers stored under a daily cycle of light and dark sprouted more rapidly (Mozie 1975). The reason for this is unclear, since yam tubers do not have a visible means of detecting light levels, and since they remain underground in the wild, detection of light seems unnecessary. Since the tubers were stored outside under normal light conditions, the variation may be due to other factors, as maintaining permanent darkness around tubers implies some barrier between them and the outside world. Such a barrier would have reduced variations in humidity and temperature that may have had a more significant effect than the lack of light.

Conclusions

The manipulation of yam dormancy remains an intransigent research issue that has been considerably handicapped by lack of consistent and systematic research. Research on chemical interventions has been, by and large, unfruitful and it is unclear what should be investigated next. In contrast, the potential of physical means such as heat, light and water to break dormancy have shown sufficient indication to merit further research attention and initial results from work at IITA are reported in an associated paper (Barker *et al.* 1999).

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