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Successful manipulation of the growth cycle of yam (*Dioscorea* spp.) for year-round production for food security and climate change

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Yams are important items of diet throughout the Caribbean Region and, among them, the cultivars of the species, *Dioscorea alata* L. and *D. esculenta* (Lour.) Burkill are particularly important in the Eastern and Southern Caribbean, although the latter is so to a lesser extent. With a growing period of approximately nine months and a corresponding dormancy period, these cultivars are produced on an annual basis like clockwork, providing food yams for approximately three months of the year, the period of availability coinciding with the period of dormancy as the latter marks the natural period of storage of the tuber. Consequently, the breakage of dormancy marks the beginning of the end of natural storage as the emerging sprouts signal the onset of the next growing period. This coincides with the start of the rainy season and the yam is adapted to existing climatic conditions that provide the ideal environment for both plant establishment and tuber growth.

Cultivars of the two species bear no reproductive seed and therefore, are completely dependent on vegetative means for perpetuation. Any adverse development during storage or early growth that prevents sprouting or tuber initiation and growth, results in the permanent loss of the affected material and potentially threatens loss of the specific cultivar. Hence, climate change events such as shifts in the onset of the rainy season, extension of the dry period and incidences of severe weather associated with excessive flooding that can result in death of roots and developing tubers, pose real risks to the persistence of the cultivars of *D. alata* and *D. esculenta* that are produced in the Caribbean Region. In order to counteract these effects, what is needed is the manipulation of the growth cycle to allow for year-round production so that the changes that have been observed with respect to climatic and weather patterns will not result in a loss of planting material and, by extension, loss of germplasm.

It is well-established that the growth cycle is under hormonal control and that the key to year-round production is the breaking of the physiological lock on the growth cycle that is responsible for the seasonal production by which these species are characterized. There have been many attempts by researchers in the past to achieve this, but without success until relatively recently. Most attempts have explored the use of natural and synthetic plant growth regulators. Further, past attempts have focussed on the breakage of natural dormancy and induction of early sprouting, but instead, the success reported here, was achieved by delaying sprouting to beyond the period of natural dormancy in a novel approach that eliminates the use of growth regulators and other chemicals.

This paper reports how reduced temperature storage has been used successfully to break the physiologically controlled growth cycle in cultivars of *D. alata* and *D. esculenta*, producing yams all year long by delaying the breakage of dormancy, ensuring not only an extension of the availability of yam tubers for food but also availability of viable planting material throughout the year. It was found that tubers can be stored successfully for an entire cycle, so that tubers from the previous year can meet tubers of the current year's harvest providing a buffer against crop loss from any adverse biotic or climatic event. The effects on sprouting patterns are described. The use of reduced temperature storage for this purpose has not been reported and this account serves to fill an important gap in documented yam dormancy research.

Keywords: Yam, *Dioscorea* spp., growth cycle, year-round production, food security, climate change, reduced temperature storage

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The value of the yam tuber for food is inherent in ethnic and cultural practice as well as in its physiological dormancy that facilitates its natural storage period and the relatively long postharvest life for tubers of some species and cultivars (Coursey 1967; Degras 1993).

Yams are important items of diet throughout the Caribbean Region and, among them, the cultivars of *Dioscorea alata* L. and *D. esculenta* (Lour.) Burkill are particularly important in the Eastern and Southern Caribbean, although the latter is so to a lesser extent (Wickham 1981). With a growing period of approximately nine months and ten months, for *D. alata* and *D. esculenta*, respectively, and a corresponding dormancy period of about three months and two months, respectively, these cultivars are produced on annual basis like clockwork, providing food yams for approximately three months of the year, the period of availability coinciding with the period of dormancy as the latter marks the natural period of storage of the tuber. It was established long ago that tubers planted early remained dormant in the ground despite favourable growing conditions and that tubers sprouted after a pre-set period of time regardless of the planting environment (Onwueme 1975; 1976; Passam et al. 1982). Consequently, the breakage of dormancy marks the beginning of the end of natural storage as the emerging sprouts signal the onset of the next growing period. The onset of the growing period coincides with the start of the rainy season and the yam is adapted to existing climatic conditions that provide the ideal environment for both plant establishment and tuber growth at the required time. Accordingly, yams are characterized by a cyclic pattern of growth, making them seasonally available for food and making the prospect of year-round availability through extension of dormancy or year-round production, a much sort after goal.

Cultivars of the two species bear no reproductive seed and therefore, are completely dependent on vegetative means for the perpetuation of the species. Any adverse development during storage or early growth that prevents sprouting or tuber initiation and growth, results in the permanent loss of the affected material and threatens permanent loss of the specific cultivar as well. Hence, climate change poses a real risk to the persistence of the cultivars of *D. alata* and *D. esculenta* that are produced in the Caribbean Region.The threat of climate change has heightened the awareness of the potential for negative impact on the yam as a food crop, the four major ones being:

- Anthracnose (leaf spot disease) incidence early in the growth cycle killing plants before tuber initiation or before they form viable tubers. It is noteworthy that cultivars of *D. esculenta* are resistant to anthracnose.
- Proliferation of pests like nematodes and mealy bugs during prolonged storage as occurs when rains are late. Such pests destroy the tuber germination meristem, the area where adventitious shoots and roots are produced *de novo*.
- Extremes of soil water availability that can lead to complete crop loss as in the case of permanent wilting of newly-established plants or death of roots and newly-formed tubers by flooding, destroying not only yield, but the possibility of future crops.
- Shifts in the dry and wet seasons (that have been observed already with very negative consequences), resulting in such hazards as pest and disease proliferation, bush fires, loss of planting setts/poor plant establishment related to unavailability of water at critical times in the growth cycle.

In order to mitigate potential negative climatic changes, achieving sustainable production must be the goal. What is needed is the manipulation of the growth cycle to allow for year-round production so that the changes that have been observed with respect to climatic and weather patterns will not result in a loss of planting material and, by extension, loss of the genetic material, because, at any given time, plants and tubers will be available at the various stages of development eliminating the risk of total loss.

However, the production of these yams is never assured and is threatened by factors including, for susceptible species like *D. alata*, the incidence of the leaf spot disease, anthracnose, caused by *Colletotrichum geosporoides*. Anthracnose is unique in that its strong tendency to mutation to produce new strains makes treatment and management of the disease difficult. For the same reason, yam breeding programmes for the development of anthracnose-tolerant species also yield short-term success as tolerant types succumb to new strains. *D. esculenta* is resistant to anthracnose (Wickham 1981).

Typically, *D. alata* cultivars are adapted to the environmental conditions of the area where they are found with the adaptation often associated with the availability of ground water resulting from precipitation. The conditions that are ideal for yam growth are also favourable for the proliferation of the anthracnose organism. Further, yam tuber formation does not begin until three to four months after planting/ breakage of dormancy. The end result of all this is the constant threat of loss of yam germplasm as a result of this disease. Achieving year-round production will also reduce this threat.

It has been known for decades, that reduced temperature storage above chilling temperatures can delay the breakage of dormancy in yams to varying extents, depending on the period of storage and the temperature used (Coursey 1968). Also, the use of the naturally-occurring growth regulator, gibberellic acid, has been demonstrated to have great efficacy in delaying the breakage of dormancy, or rather, in extending the length of the dormant period in yams after harvest (Okagami and Nagao 1971; Wickham 1981; Wickham et al. 1984). However, both methods have not been used commercially to any extent, the latter because of tradition and the lack of dissemination of information for adoption of the technology, and the former, because of the cost of energy for reduced temperature storage maintenance on an extremely valuable, but low-priced crop.

Given the relatively long growth period, of approximately nine months, and its seasonal availability as a result of its dormancy, the natural reasoning is to go for an extended period of dormancy to allow for year-round production, and thus, year-round availability through manipulation of the period of dormancy, and through it, the period of growth. It is well-established that the growth cycle is under hormonal control and that the key to year-round production is the breaking of the physiological lock on the growth cycle that is responsible for the seasonal production by which these species are characterized. There have been many attempts by researchers in the past to achieve this (Wickham 1981; Wickham et al. 1984; Ireland and Passam 1985; Barker et al. 1999; Craufurd et al. 2001; Ile et al. 2006) but without the expected effect on the growth cycle. Even when natural compounds were used such as reported by Tortoe et al. (2015) using plant extracts from cocoa pod (*Theobroma cacao*) potash, neem (*Azachirata indica*) seeds, neem leaves, sweet potato (Ipomoea batatas) leaves to inhibit bud and sprout formation, emphasis was on prolonging dormancy and not on manipulation of the growth cycle.

Given the effect of gibberellic acid, its use to bring about year-round production in yams was explored and found to be not feasible. It was found that while exogenous applications of GA3 resulted in extension of the dormant period and that repeated applications resulted in further extensions, the treatment resulted in eventual direct sprouting-tuber to developing-tuber transfer of assimilates through the primary nodal complex (Ferguson 1972; Wilson et al. 1998) without the institution of obvious shoot growth (Wickham 1981; Wickham et al. 1984), and with no effect on the growth cycle. The unique association between the harvest date and the time of sprouting was also reported later by several researchers including Swannell et al. (2003) and Ile et al. (2006) who found that the date of harvest had no effect on the time to 50% sprouting and Ile (2004) had earlier hypothesized that yam tubers are only receptive to plant growth regulators applied near their natural sprouting time, i.e., the observed effect was on the rate of shoot development and not on tuber dormancy.

With the goal of achieving sustainable year-round production of yams still elusive, more recent studies have demonstrated the induction of sprouting in dormant yam tubers with the use of gibberellin inhibitors (Shiwachi et al. 2003), and use of propriety products, CF1 and CF2, to break the dormancy of 10 g slices of freshly harvested tubers (*D. alata*) reducing the pressure on the use of ware tubers as propagules (Acedo and Arradaza 2013). The efficacy of Fluridone, an inhibitor of abscisic acid (ABA) synthesis, in inducing sprouting in dormant yam (*D. alata*) tubers, as well as immature tubers shortly after tuber initiation has also been reported (Somina and Hamadina 2018).

On the other hand, while the efficacy of reduced temperature storage for extension of the shelf life and availability of yams for food is well known (Barker et al. 1999), although not a common practice, its use to extend tuber storage life under controlled conditions, generally, has not been explored beyond production for off-season availability (Gonzalez and Collazo de Rivera 1972; Rao and Calixte 1990). This is probably because of the relatively high cost of reduced temperature maintenance. Research investigations with respect to manipulations of dormancy and sprouting, using higher temperatures, have also been conducted and reviewed (Barker et al. 1999; Craufurd et al. 2001), but without yielding results significant to year-round production.

The objective of this investigation was to determine the effects of reduced temperature storage on the dormancy, subsequent sprouting and the growth cycle of cultivars of *D. alata* and *D. esculenta* and to observe the effects of storage of *D. alata* tubers from one growth cycle to the next, i.e., for up to one year and beyond.

Materials and methods

Observations of the effects of reduced temperature storage at 15°C on dormancy, sprouting and subsequent growth of yam (*D. alata* and *D. esculenta*) tubers were made over a period of eight years, from 2011 to 2019.

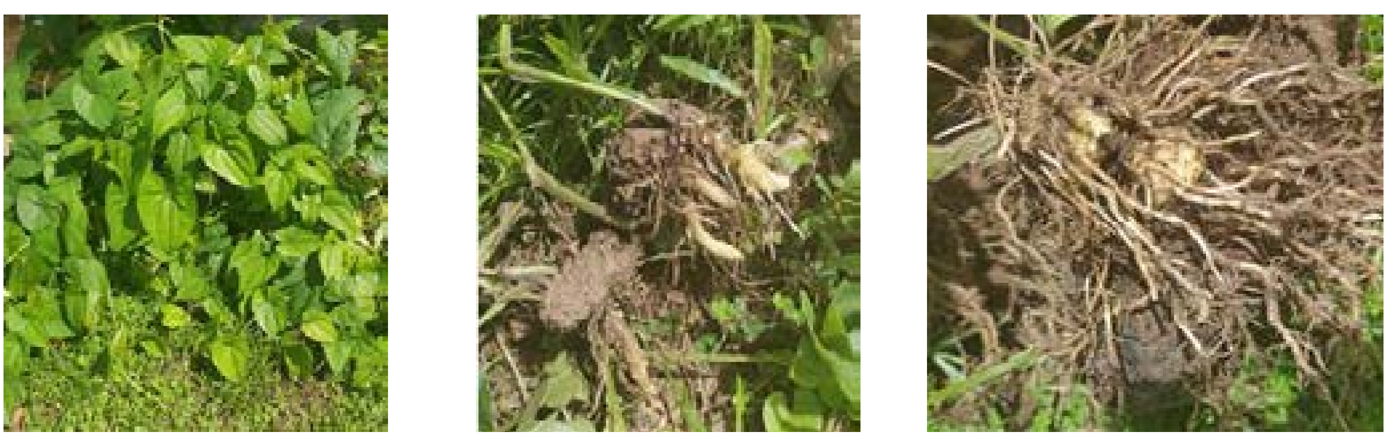
On an annual basis, freshly-harvested dormant tubers were placed in storage at 15°C and 90% relative humidity (supplemented with wetting of the floor of the storage room and light cardboard covers to keep moisture loss from the tubers at a minimum). Tubers were stored for the duration of natural dormancy and for up to 12 months and beyond. Yams from the same harvest, stored under normal tropical ambient conditions, were used as the control. After natural dormancy was broken in the control tubers, stored tubers were removed at intervals and placed under tropical ambient conditions for continued observations. Tubers were examined for the production of sprouts during and after removal from storage. Following removal from storage to tropical ambient conditions, tubers were left to sprout, unplanted, either in a ventilated storage room, or in a moist natural environment to observe the time to tuber initiation and early tuber development. Selected tubers were prepared as planting setts or were planted in containers for observation on the length of the growth cycle, or were planted in beds in the field and observed for growth patterns, length of the growing period, onset of senescence/dormancy, length of dormancy and subsequent sprouting of daughter tubers. Irrigation was supplied as necessary for plants that were in the active growth phase during the normal dry season, i.e. plants that were demonstrating out-of-season production.

Plants established from stored tubers were left unharvested and allowed to sprout, grow, senesce, go through a subsequent dormant period and sprout again to confirm the growth cycle in the prevailing natural environment. Water was supplied to ensure the survival of plants that were growing off-season.

Results and discussion

As expected, tubers were stored successfully at 15°C (16 ± 1°C) with no symptoms of chilling injury which occurs in yam tubers between 10-12°C (Coursey 1968), and no sprouting occurred in tubers while held at that temperature.

Plate l. Entwined vines of sprouting tubers of *Dioscorea alata* and *D. esculenta* (A) left in a moist environment without burial after removal from reduced temperature storage, show developing tubers (B, C) five months after commencement of sprouting.



A B C

Plate 2. A. Plant of *Dioscorea alata* with extensive vine growth, in tuber bulking phase, September 14, 2018. B. Same plant, showing symptoms of anthracnose infection, in senescence phase, November 07, 2018. This represents a four-month advancement in the normal growth cycle that will allow tubers to sprout in approximately three months providing a crop to be established in mid-February instead of late May. C. Plant of *Dioscorea alata*, established early July, with vigorous vine growth four months after sprouting and in tuber initiation phase, November 07, 2018. This represents a six-week delay in natural crop establishment.

A B C

Plate 3. A. *Dioscorea esculenta* cv. Chinese in advanced stage of sprouting mid-April 2017. Sprouting commenced early March 2017, two months before normal breakage of dormancy. B. *Dioscorea alata* cv. Sweet in early stage of sprouting mid-April 2017. Sprouting commenced early April 2017, five weeks before normal breakage of dormancy.

A B

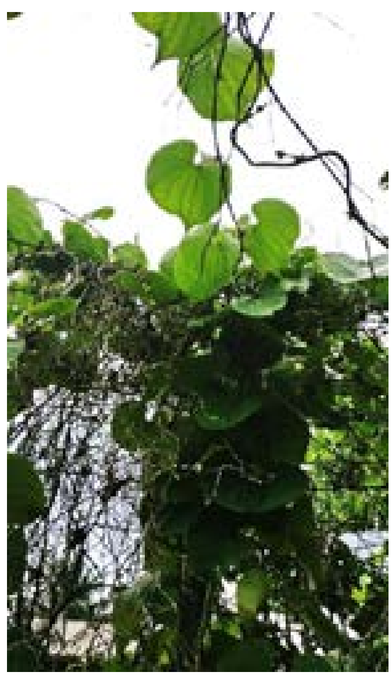
Plate 4. January 22, 2018, vines of *Dioscorea esculenta* cv. Chinese showing plants existing at completely different phases at the same time: A. Heavy vine growth, tuber bulking phase. B. Early stages of sprouting.

A

B

Plate 5. April 19, 2018, vines of *Dioscorea esculenta* cv. Chinese at three different growth stages at the same time. Second generation tubers from tubers allowed to sprout by returning to ambient conditions after storage at l5°C, were left unharvested to observe the natural growth cycle: A. Plant establishment stage, five weeks after sprouting. B. Advanced stage of growth, heavy vine growth seven months after sprouting. C. Senescent vines, nine months after sprouting with senescent vines indicating onset of tuber dormancy.

A



B

C

It was found that yams could be stored at 15°C, for a period equivalent to the length of natural dormancy, and then returned to ambient conditions at monthly intervals to be released from the induced/extended dormancy in such a way that sprouting tubers could be available every month of the year. Plants established from such tubers underwent a normal growth period, followed by vine senescence, before becoming dormant and sprouting after approximately three and two months respectively for tubers of *D.alata* and *D. esculenta*. In other words, tubers experienced a growth cycle of normal length after sprouting occurred. Thus, this approach resulted in year-round production of tubers.

Observations on the length of the growth cycle of plants from stored tubers of *D. alata* and *D. esculenta*

Sprouting occurred in tubers returned to tropical ambient conditions over a period of four to eight weeks and tuber initiation occurred three to four months after the onset of sprouting, providing plants that senesced, similarly, over a period of time. This pattern facilitated year-round production and by careful selection and selective establishment, the sprouting tubers were used to create plots that yielded tubers throughout the year (Plates 1,2,3,4, and 5).

Effect of reduced temperature storage for one year after harvest on tuber dormancy

It was found that tubers could be stored successfully at 15°C for one year, with freshly harvested dormant tubers meeting tubers stored from the previous crop. Yams were found to sprout normally after removal to ambient conditions following storage at 15°C for one year after harvest. This meant that yams from a previous year's harvest could be sprouted alongside yams from the current year's harvest (Plate 6A). Off-season production from smaller setts yielded smaller tubers with otherwise normal postharvest physiology (Plate 6B).

Effect of prolonged storage on sprouting pattern and proximal end dominance

While normal proximal end dominance was displayed by sprouting tubers after removal to tropical ambient conditions, there was evidence of increasing loss of proximal end dominance, the longer after harvest the tuber was kept. This was progressively more pronounced with prolonged storage in excess of one year, giving rise to a condition in which numerous sprouts arose over the surface of the tuber when dormancy was broken after removal from reduced temperature storage to tropical ambient conditions.

After storage for one year, removal of tubers to ambient conditions resulted in the development of sprouts within four weeks. Tubers kept at ambient conditions without planting, continued to develop sprouts on the tuber surface (Plate 7A). Tubers kept at ambient but under moist conditions developed sprouts all over the tuber surface, demonstrating loss of proximal end dominance, and had excessive root growth and sprout elongation (Plate 7B). When tubers were kept for several weeks under these conditions, without planting, daughter tubers developed as stored material was transferred to the areas of new tuber initiation (Plate 7C). This development was probably as a result of depletion of growth regulators, possibly auxins, that control the location of sprouts after breakage of dormancy and is responsible for the strong proximal end dominance displayed in yam tubers.

The sprouting pattern was characterized by continued sprout development after plant establishment and the emergence of early sprouts. This gave rise to clumps of vines arising from a single planting sett or tuber, as several yam plants developed in close proximity to each other. Each plant produced at least one tuber. The number and shape of the tubers produced were characteristic of the cultivar. However, the tubers were miniature replicates because of the level of competition resulting from multiple vine development from each planting sett (Plate 7D).

From a practical standpoint, this occurrence proved to be very positive as it gave rise to large numbers of shoots and associated tubers, resulting in yield of large numbers of small, generally unmarketable tubers (Plate 7D) that served as planting setts and that went on to perform normally with a growth cycle of normal length. Thus, not only did this storage procedure produce tubers that sprouted at varying times in the year, based on the length of storage at reduced temperature, but it also produced tubers that served as a source of intact planting material, eliminating the need to dissect the tuber into setts, thus reducing the risk of loss of planting material due to microbial infection.

Plate 6. A. Tubers of *Dioscorea alata* cv. Sweet harvested in February 2012 and stored for one year, alongside freshly harvested tubers from crop of February 2013. B. Small tubers from off-season production in 2013 alongside tubers from normal 2013 crop.

A

B

Plate 7: Tubers of *Dioscorea alata*: A. Tuber with loss of proximal end dominance after prolonged storage at reduced temperature. B. Tuber kept moist at tropical ambient conditions, to observe the effect on sprouting pattern after prolonged storage at reduced temperature. Proximal end dominance is eliminated as seen from multiple shoot development all over the tuber surface. C. Tuber kept for several weeks under moist conditions, without planting, showing development of daughter tubers as stored material was transferred from the sprouting stored tuber to the areas of new tuber initiation. D. The approximately 30 tubers shown here, represent the yield from a single planted tuber (planting sett), demonstrating the result of multiple shoot formation, with each shoot producing at least one tuber. Normally, this cultivar produces one or two tubers per planting sett.

A

B

C

D

Plate 8. Strong proximal end dominance displayed in sprouting, miniature tuber of *Dioscorea alata*, one of many tubers resulting from multiple shoot growth from a single planting sett in which proximal end dominance had been lost as a result of prolonged storage under reduced temperature conditions.

It was found that this effect on pattern of sprouting did not extend beyond the current batch of propagules, and yam tubers returned to normal patterns of sprouting and proximal end dominance by the following harvest season. Normal cultivar differences with respect to time to sprouting and rate of sprout development were evident, for example, cv. Lucie was early while cv. Sweet was late. The development of sprouting in the second-generation tubers was characterized by strong proximal end dominance and the yams were re-established in the field in May, the traditional planting month for *D. alata* yams in this area. Therefore, while long-term storage resulted in abnormal sprouting patterns with excessive shoot and tuber development, tubers from plants that arose from such multiple shoots, exhibited normal physiology and strong proximal end dominance (Plate 8).

Conclusion

Propagated only by vegetative means, with a distinct period of vegetative growth followed by a distinct period of dormancy, environmental changes that affect development of the vines and or tuber pose great risk to the sustainability of the production of some species of yam. It has been demonstrated here that yams can be grown year-round as a result of delaying tuber sprouting beyond the period of natural dormancy by the use of reduced temperature (15^{o}C) storage. Tubers can be returned to tropical ambient conditions at controlled intervals for sprouting and plant establishment in order to provide material for year-round production.

Also, these investigations demonstrated that tubers of selected cultivars of *D. alata* can be kept under reduced temperature storage conditions for in excess of twelve months i.e. overlapping of harvests. Planting of this material gave rise to several sprouts per tuber or planting sett and yielded many corresponding small daughter tubers. The tubers from this establishment were dormant at harvest as is common for yams, were morphologically normal, and demonstrated a period of dormancy consistent with the cultivar and sprouted with strong proximal end dominance as is characteristic of *D. alata* yams. Thus, the loss of proximal end dominance is not permanent, lasting only for the current cycle as long as there is no further manipulation of the storage environment.

The implications of this finding is that yam tubers, normally propagated by vegetative means and subject to the risk of loss of the germplasm as a result of various agronomic, biotic and adverse environmental conditions, can be stored from harvest to harvest, with retained sprouting vigour but with reduced proximal end dominance, providing not only preservation of planting material, but also large numbers of viable propagules, eliminating or greatly reducing that risk.

What has been reported here offers real hope for the future with respect to the possible impact of climate change on yam production. Already demonstrated are the sustained shifts in the growing season, so that at any given time it will be possible to have established plants, at all phases of growth, along with dormant tubers (planting material) of the yam species, *Dioscorea alata* and *Dioscorea esculenta*. Thus, achievable, sustainable year-round production has been demonstrated for these two species.

Dedication

This paper is dedicated to the memory of Professor Lawrence A. Wilson who, in 1976, introduced me to the incredible wonder of the physiology of Dioscorea species.

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