Tuber Physiology in Yams *(Dioscorea* Spp) and its Agricultural Implications*

I.C. Onwueme
Department of Plant Science
University' of Ife, Nigeria

Abstract

The various physiological characteristics of the yam tuber are examined in detail under four general headings: tuber dormancy and sprouting, tuber formation and growth, tuber yield characteristics, and tuber storage.

The ways in which each characteristic determines or influences yam production practices are discussed.

Introduction

The yams (*Dioscorea* spp.) have several botanical peculiarities of their own. One of these peculiarities is that the tubers which they produce originate neither from the stem; instead they arise from the hypocotyl region of the plant (Martin and Ortiz, 1963; Lawton & Lawton, 1969). It is not surprising therefore that the tuber itself exhibits several unique morphological and physiological characteristics. Many of these characristics profoundly influence the productivity of the crop on the field, and determine how best the crop can be managed for optimum yields.

Tuber dormancy and sprouting. The yam tuber goes into a period of dormancy shortly after it is harvested or the growing season ends. The level of dormancy is high immediately after harvest, and the dormancy is characterized by the inability of the tuber to sprout readily when planted. As the level of dormancy decreases during storage, the period from planting to sprouting decreases. The end of the dormancy period is observed when the tuber sprouts spontaneously in storage. The duration of the dormancy period is about 2 - 3 months, but it varies with species. *D. cayenensis,* for example, has a shorter dormancy period than *D. rotundata.* The causes and mechanism of dormancy in the yam tuber are not clearly understood, but Campbell *et al* (1962b) have suggested that a high level of dormancy is associated with low levels of glutathione in the tuber.

Dormancy in yams can be broken artificially by treatments with 2-chloroethanol (Campbell *et al* 1962a) or gamma radiation (Gregory, 1968; Martin *et al* 1974). It has also been possible to prolong the dormancy of yam tubers and prevent their spontaneous sprouting by tuber applications of a methyl ester of alpha naphthalene-acetic acid (Campbell *et al*, 1962c) or gamma radiation (Adesuyi, 1973, 1976).

One major agricultural consequence arising from the dormancy of the yam tuber is that the time from planting to field emergence is usually exceedingly long. For tubers that are used as planting material shortly after they have been harvested (i.e. when their dormancy level is very high), field emergence may not occur for a very long time. With storage facilities being very poor, many traditional yam farmers resort to planting their yams shortly after harvest. In West Africa, for example, yams which have been harvested

in August or September may be used for planting again in October. Such plantings invariably fail to emerge until about February, a period of about 4 months. This unnecessarily adds to the total duration of field occupancy (period from planting to harvesting) of the yam crop.

The excessive length of the period from planting to emergence, which is a consequence of dormancy, has repercussions in herbicide weed control in yams. Pre-emergence herbicides applied at planting time usually have lost their effectiveness by the time of, or shortly after emergence. This necessitates additional weedings, or the use of other herbicides after the crop has emerged. One partial solution to this problem has been to apply the pre-emergence herbicide not at planting time, but at some time later, close to the anticipated time of emergence. Such an application must however cope with weeds which have already come up at the time of herbicide application, and one common practice is to combine a contact herbicide with the pre-emergence herbicide.

The dormancy of the yam tuber also imposes restrictions on out of season (or year-round) production of the crop. Ideally, the second or off-season crop should be able to utilize the tubers from the regular-season crop as planting material. However, this is not feasible because the dormancy factor prevents the regular-season crop from sprouting readily. The use of chemical treatments has only been partially successful in causing such tubers to sprout readily. The practice in off-season yam production would therefore be the use of tubers from the previous off-season crop. Such tubers would have been in storage long enough for their dormancy level to have been reduced, and for them to sprout readily after planting.

The dormancy of the yam tuber is, of course, a desirable feature in yam storage. It prevents sprouting, which is a major source of loss of tuber dry matter in stored yams. This will be discussed in detail later.

Sprouting in the yam tuber occurs as a result of activity of a layer of meristematic cells located just beneath the tuber skin. The process of sprouting has been described by Onwueme (1973). Two striking features of yam tuber sprouting need special mention. The first, referred to here as *de novo* budding, is that buds are initially absent from the harvested yam tuber (as opposed to the corm) and that buds are formed anew just before sprouting is observed. The second feature is that the yam tuber exhibits proximal dominance with respect to sprouting. The various aspects of this proximal dominance can perhaps be elaborated as follows:

a) The sprout usually arises from the head-ward (proximal) end of the tuber or sett (Onwueme, 1973; Passam, 1977). If the corm has remained attached to the tuber, the sprout arises from the corm.

b) For budless setts derived from the head, middle and tail of the tuber, bud formation (and subsequent sprouting) occurs most readily in the head setts. At the end of the dormancy period one or more sprout buds arise at the head region of the intact tuber. For this reason, head setts from such tubers emerge even more rapidly than middles and tails which are budless.

c) Once the first sprout (or group of sprouts) has been formed, the formation of subsequent sprouts is suppressed. This is true whether the sprout arose from the corm or from the head of the tuber proper. If, however, the initial sprout is removed, other sprouts will be produced in a short time (Onwueme, 1973).

The phenomena of *de novo* budding and proximal dominance encountered in yam sprouting together explain why setts containing the head region (i.e. heads or wholes) are more preferred as planting material than middles and tails. Such setts sprout most readily after planting.

When tubers that have been stored for some time are sub-divided for planting, the heads invariably have buds on them. The tails and middles, on the other hand, do not have buds since proximal dominance in the intact tuber has all along prevented buds from arising in these regions. Tails and middles must therefore differentiate sprout buds after planting. One consequence of this is that even if obtained from non-dormant tubers, the tail and middle setts cannot emerge earlier than about 5 weeks after planting. In addition, their emergence lags behind that of heads derived from the same tuber, so that on a field basis, overall emergence is spread out over a long time. As a result, the plants on the field are at various stages of development at any given time during the cropping season. This is certainly an undesirable feature which can best be eliminated by using only heads or wholes as planting material. Onwueme (1977a) has suggested that the difference in emergence time between early and late emergence is greatest when tubers of a high dormancy level are used.

The agricultural practice (pre-sprouting) of preparing the setts several weeks before field planting holds some promise for eliminating the adverse consequences of *de novo* budding and proximal dominance. During the period between sett preparation and field planting, *de novo* bud formation on the tails and middle can proceed since the proximal dominance exerted by the head region has been removed. At planting time, therefore, the tails and middles as well as the heads, have sprout buds on them. Emergence after planting is not only rapid in all cases, but it is also synchronous for all the categories of setts.

Tuber formation and growth. One of the most peculiar features of yams is the mode of formation of their tubers. The yam tuber is certainly not of root origin, and earlier workers (Burkhill 1960; Njoku, 1963) advanced evidence to suggest that it was a stem structure. More recent evidence (Martin & Ortiz, 1963; Lawton & Lawton 1969) however indicates that the yam tuber originates from the hypocotyl region.

The onset of tubering is promoted by short-day conditions (Njoku, 1963) and delayed by moisture stress (Onwueme, 1975a). It also appears to be dependent on the physiological age of the sett that was used for planting, since the time from emergence to tubering is shorter for setts derived from long-stored tubers than for setts derived from tubers stored for a short time (Onwueme, 1975b). Indeed, if the tubers used for planting have been stored for too long, tuber formation may begin so early that shoot growth is limited and eventual tuber size is small. More recently, it has been reported that plants growing from larger setts begin to form tuber earlier than those growing from small setts (Onwueme, 1978).

It appears that the onset of tubering is accompanied by the production of some tubering stimulus, probably hormonal in nature. One piece of evidence in support of such a stimulus can be found in the tubering behavior of vine cuttings of yam. If the cutting has been obtained from a young plant that is not yet tubering, the cutting grows, develops extensive root and shoot systems, and eventually produces tuber. In contrast, a cutting derived from a plant that is already tubering will begin to produce tuber almost immediately after it is established, and without extensive shoot growth. The final tuber size in such a case is extremely small since the total leaf area remains extremely small. In commercial or experimental propagation of yams by vine cuttings, it is therefore recommended that the cuttings should be taken from young, non-tubering plants (IITA, 1975; Nwosu, 1975). It is only such cuttings that will produce the required shoot growth, which will make for a reasonable tuber yield and/or supply subsequent vine cuttings for further propagation.

Some recent evidences (Gumbs & Ferguson, 1976) suggest that exposure of the

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underground portions of the yam plant to light results in decreased tuber yield per plant but increased number of tubers per plant.

Once tubering has been initiated, the tuber is first seen as an amorphous mass of cells. It soon becomes polar and (usually) positively geotropic in its growth. The meristem which produces the cells of the tuber remains at the distal apex of the growing tuber, and continues to divide and produce new cells until the tuber is nearly mature for harvest. This pattern of growth of the yam tuber is peculiar in the sense that the tuber is not an enlargement of some previously laid-down structure. In many other tuber crops, initial penetration of the soil is accomplished by some relatively-thin precursor organs (e.g. the thin root in cassava and sweet potato, or the stolon in the *Solanum* potato). In yam, however, it is the relatively blunt distal apex of the tuber itself that has the task of pushing through the soil. It is probably for this reason that yam, more than most other tuber crops, requires a loose layer of soil for easy penetration of the tuber. Such a loose layer is provided by mounds in traditional agriculture, and ridges in more modern systems. It is also this feature of penetrating with a blunt end that makes heaving a common problem in yam production, particularly for yams grown on the flat.

Most kinds of yam will usually produce only one or two tubers per plant. This implies that improvements in cultural practices and the general welfare of the plants will result in larger tubers rather than more tubers. Larger tubers are of course more difficult to harvest especially since, exhibiting positive geotropism, they tend to penetrate deeper into the soil. Efforts to improve yield have therefore tended to make harvesting (whether mechanical or manual) more difficult. In areas such as West Africa where there is a strong market preference for large tubers, this feature of producing few tubers per plant has been an advantage, since the average size of each tuber is relatively large.

The phenomenon of re-tubering is encountered when yam is double harvested. After the tuber of the first harvest has been removed, some new tuber material is formed in its place and this is harvested again at the end of the season. The second-harvest tuber which is produced as a result of re-tubering has several peculiarities (Onwueme, 1977a). It consists roughly of two regions: a tough fibrous, lignified region; and a fleshier distal portion. The lignified region results from partial fusion of the tuber head with the corm, and this region possesses several distinguishable buds. This latter feature makes the second-harvest tuber ideal for planting, and this is one of the main reasons why double-harvesting is practiced at all. The fleshier portion is usually composed of several rounded projecting knobs of tubers which are good for eating. The entire second-harvest tuber is amorphous in shape.

It is an interesting physiological problem to determine why the second-harvest tuber should differ so much from the first harvest tuber or the single harvested tuber. For example, does the removal of the first harvest tuber result in some hormonal readjustments which make the second-harvest tuber so different? Why are buds (eyes) present on the second-harvest tuber, while they are absent on the other kinds of tuber; or are these buds attributable to the corm? These and other questions have yet to be answered.

It has been shown that the practice of double-harvesting does not result in a greater seasons yield than single harvesting (Onwueme, 1977a and b). Indeed, if the first harvest of double harvesting occurred at certain times, the total seasons yield from double-harvesting could be significantly lower than that from single harvesting. This is rather surprising since it had been thought that removal of tuber material during the first harvest would result in more rapid accumulation of photosynthate in the new tuber. What

happens may be that removal of the first tuber deprives the plant of its normal sink, so that photosynthate may accumulate in the leaves and depress photosynthesis there. Alternatively, there may be a time lag between the removal of the first tuber and initiation of growth of the new tuber.

Tuber yield characteristics. One of the important determinants of yield in yam is the sett weight used for planting. Large setts produce a greater tuber yield per plant. This is probably because large setts sprout more readily, emerge more quickly, and produce a more vigorous plant with more extensive leaf area. The greater vigor of the plant growing from large setts is probably related to the greater quantity of food material available to support its growth. Large setts are also probably able to transfer a greater quantity of material from the sett to the growing tuber (Onwueme 1975a), thereby contributing to their greater yield. The advantage of large setts over small ones is further enhanced when yield per hectare is considered. This is because the percentage emergence (and therefore the number of harvestable stands per hectare) is usually greater for large-sett plots. The higher percentage of large setts is in turn attributable to two factors. First is the greater number of sprouts produced by large setts (Onwueme, 1973), so that if the main sprout is damaged, there exist alternative sprouts to accomplish emergence from that sett. Second is the greater rapidity and greater vigor of emergence from large setts.

As mentioned, large setts produce a greater number of sprouts per sett than do small setts. Apparently, the first sprout arising from a small sett is able to exert its dominance over the entire mass of the sett. The intensity of dominance probably decreases with distance from the sprout itself so that for a large sett, regions that are relatively remote from the initial sprout are able to develop alternative sprouts. Normally, multiple sprouts arising from the same sett usually become disconnected when the intervening sett tissue decays. The various sprouts grow to maturity as independent plants on the same stand, each producing its own tuber. It is for this reason that large setts usually produce a greater number of tubers per stand than small setts (Onwueme, 1972). Because very large setts produce a greater number of tubers per sett, their greater tuber yield per planted sett may not necessarily be translated into a greater mean weight per tuber. Medium sized setts may yield less than large setts but may not differ much in the mean weight per tuber produced.

One further difference between large and small setts is in their multiplication ratios (i.e., weight of tuber yield produced by a sett: weight of sett planted). In general, the smaller the sett, the greater the multiplication ratio (Onwueme, 1978). The reasons for this relationship are not quite clear, but several possibilities exist. It is possible that the large shoot system produced by large setts causes mutual shading of leaves, so that the net photosynthate produced per unit of leaf area in unit time is considerably less. The smaller plant growing from the small sett would exhibit less mutual shading of leaves. A second possibility is that as large quantities of photosynthate drain into the tuber, some degree of saturation is approached which reduces the rate of translocation and indirectly reduces the rate of leaf photosynthesis. In such a scheme, this back-up mechanism would operate only in plants with extensive leaf areas and an excess of photosyntate. For small-sett plants where leaf area is small and photosynthate is limiting, the tuber is never saturated, translocation occurs as rapidly as photosynthate can be supplied by the leaves, and the rate of leaf photosynthesis does not suffer diminution.

Recent evidence (Onwueme, 1978) has shown that the time of tubering is earlier for large setts than for small setts. This fact probably contributes to the yield advantage that large setts have over small setts, since the period of tuber bulking is greater for large

setts. However, the reasons for the earlier tubering of large setts are still not clear. Quite possibly, a definite excess of assimilate is necessary for tuber initiation to occur, and this excess is attained earlier in large-sett plants than in small sett-plants. In *D. batatas*, for example, an excess of photosynthate is required for bulbil formation to occur. It has been shown that excised stem portions must have the leaf blade attached or else must be supplied with sugar before bulbils can be formed (Ogawa, 1976).

One commonly observed feature in yam plots is the high degree of plant-to-plant variation in tuber yield. Even where soil type, sett type, sett weight, planting date and field operations have been uniform, the harvest still reveals wide variations even between contiguous plants. It has been extremely difficult to account for such variations, but they are probably due to differences in physiological behavior of the sett after planting as well as to differences in the degree of microbial rotting of the sett after planting. Even where all conditions are standardized, there will exist differences of several days in time of emergence. Even for plants that emerge at the same time, there will be further differences in time of tubering and therefore the period of tuber bulking. Differences also exist in the leaf areas of the various plants, which cause variations in the rate of tuber bulking. Variations in the degree of microbial rotting of the sett may even be a greater cause of yield variations in yams. When setts of the same weight are planted, rotting will occur at different degrees, so that the *de facto* (unrotted) sett weight will vary from stand to stand. A large sett which is extremely rotted will behave like a small sett in terms of shoot growth and tuber yield; whereas a contiguous large sett which is not rotted will behave like a large sett. Further variations are introduced by the location of the rot on the sett, and the timing of its onset. In short, the experience or exact behavior of each sett is unique to it. At one extreme, the setts of plants which emerge early, are unrotted, have a large leaf area, and form tuber early. At the other extreme are the late-emerging, extensively-rotted, sparsely-leaved, late-tubering ones. In between are stands which receive a boost in some aspects but are retarded in others; so that on a field basis all levels of yield performance result.

Tuber Storage. The main sources of storage losses in the stored yam tubers are rotting, respiration, dehydration and sprouting.

An intact yam tuber is normally surrounded by a layer of cork which protects the tuber from entry of rot-causing microorganisms. Any impairment of this corky layer, as by wounding during harvesting and handling, immediately creates weak spots through which pathogen attack can occur. If rotting must be minimized, it is important that the cork layer must remain intact, or that if wounding occurs, the wound should heal quickly.

While utmost care should be taken in the harvesting and handling of yams, some degree of wounding is unavoidable, and much reliance therefore has to be placed on the ability of the tuber to heal its wounds. Apparently, the healing of wounds on yam tubers occurs most rapidly at high temperature and high relative humidity, and this has formed the basis for suggestions (Gonzalez and Rivera, 1972; Adesuyi, 1973; Thompson et al., 1973) that freshly-harvested tubers should be cured under such conditions before they are stored. Passam, Read and Rickard (1976a & b) have described some of the physiological processes associated with wound healing in yam tubers. The sequence of events in cut or deeply wounded tubers comprises the migration of starch to the cut surface, formation of a suberized layer beneath the cut surface, and finally production of a periderm after about 5 days. It is however, emphasized that bruised or superficially-wounded (abraded) tubers did not go through this sequence of wound repair. Bruised tubers

experienced weight loss and high respiratory activity until they decayed, while superficial wounds dried up but did not heal further. This implies that superficial wounds and bruises are more likely to lead to rotting than sharply-defined deep wounds.

Storage of the tubers at reduced temperatures is one measure which reduces the rate of spread of rots in stored yam. Ideally, a storage temperature just above freezing point would be required to minimize the spread of rot. Unfortunately, however, yam tubers stored at temperatures below 10°C tend to become brown and unsuitable for consumption. Temperatures of 12-15°C are therefore normally recommended for cold storage of yam tubers. At these temperatures, the rate of rotting may not be as high as at ambient tropical temperatures, but it is still substantial.

Just as the corky layer surrounding the tuber prevent the ingress of pathogens, it also prevents moisture loss from the tuber flesh. Wounds create avenues through which moisture loss can occur, so that rapid wound healing can prevent excessive moisture loss from the tuber.

Respiration of the yam tuber results in dry matter loss during storage. This is because the starch stored in the tuber is utilized as substrate for the respiration. Ugochukwu, Anosike and Agogbua (1977) have reported an increase in various respiratory enzymes in yam tubers during storage, and have also suggested that the pentose phosphate pathway is important in the metabolism of the tubers. Storage at reduced temperatures is again one method of reducing the rate of respiration of stored yam tubers. As with rotting, the rate of respiration is reduced but still substantial at the recommended storage temperatures of 12-15°C.

Sprouting in stored yam tubers is another source of storage losses. There is a net movement of dry matter from the edible tuber into the inedible sprout. Sprouting occurs at the end of the dormancy period of the tuber. The characteristics of tuber sprouting and tuber dormancy have already been discussed. In storage, the objective is to prolong dormancy (and prevent sprouting) for as long as possible. Applications of the methyl ester of alpha napthalene-acetic acid (Campbell *et al* 1962c) or 12.5 krad of gamma radiation (Adesuyi, 1976) have been recommended for prolonging yam tuber dormancy during storage. Storage at low temperature and low relative humidity reportedly prolongs dormancy and delays sprouting (Passam. 1977).

In summary the capacity for rapid wound healing, and the provision of low temperature are two important considerations in yam tuber storage. Rapid wound healing not only wards off pathogens, but also prevents excessive dehydration. Storage at reduced temperatures reduces the rate of rotting, reduces respiratory loss, and delays sprouting. That yams develop chilling injury at temperatures as high as 10°C is indeed unfortunate, since storage at temperatures just above 0°C could have reduced the rates of respiration, rotting and sprouting still further. Olorunda and Macklon (1976) have characterized some features associated with this chilling injury. These features include changes in the ion absorption and salt retention capabilities of tuber discs, as well as changes in respiration rate. Such features could be used in a breeding program to select cultivars whose tubers can tolerate storage at temperatures closer to 0°C. Such tubers should, of course, also possess the capability for rapid wound healing.

References

ADESUYI, S. A. 1973. Advances in yam storage research in Nigeria. 3rd Int. Symp. Trop. Root Crops, Ibadan, Nigeria.

ADESUYI, S. A. 1976. The use of gamma radiation for control of sprouting in yams (*Dioscorea rotundata*) during storage. Nig. J. Plant Protection 2: 34-39.

BURKHILL, I. J. 1960. Organography and evolution of Dioscoreaceae, the family of yams. J. Linn Soc. (Bot.) 56: 319-412.

CAMPBELL, J.S., CHUKUEKE, V.O., *et. al.* 1962a. Some physiological investigations into the White Lisbon yam *(Dioscorea alata* L.) 1. The breakage of the rest period in tubers by chemical means. Emp. J. Exp. Agric. 30:108-114.

CAMPBELL, J.S., CHUKUEKE, V.O., *et. al.* 1962b. Some physiological investigations into the White Lisbon yam *(Dioscorea alata* L') 2. Growth period and out of season production. Emp. J. Exp. Agric. 30:232-238.

CAMPBELL, J.S., CHUKUEKE, V.O., *et. al.* 1962c. Some physiological experiments with White Lisbon yam *(Dioscorea alata* L.) in Trinidad. 3. Effect of chemicals on storage. Emp. J. Exp. Agric. 30:335-344.

GONZALEZ, M. A. and RIVERA, A. C. DE 1972. Storage of fresh yam (*Dioscorea alata* L.) under controlled conditions. J. Agric. Univ. Puerto Rico. 56: 46-56.

GREGORY, L. E. 1968. In J. Agric. Univ. Puerto Rico. 52: 155-163.

GUMBS, F. A. and FERGUSON, T. U. 1976. Effect on tuber yield of the exposure of yam tubers to light. Agron. J. 68: 831-832.

I.I.T.A. (International Institute of Tropical Agriculture, Ibadan, Nigeria) 1975. I.I.T.A. Letter No. 6.

LAWTON, J. R. and LAWTON, J. R. S. 1969. The development of the tuber in seedlings of five species of *Dioscorea* from Nigeria. Bot. J. Linn. Soc. 62: 223.

MARTIN. F. W., KOO, F. K. S. and CUEVAS, J. 1974. Stimulation of yam (*Dioscorea*) tuber growth by gamma irradiation J. Am. Soc. Hort. Sci. 99: 282-284.

MARTIN, F. W., and ORTIZ, S. 1963. Origin and anatomy of tubers of *Dioscorea floribunda* and *D. spiculiflora*. Bot. Gaz. 124: 416-421.

NJOKU, E. 1963. The propagation of yams (*Dioscorea* spp.) by vine cuttings. J.W. Afr. Sci. Ass. 8: 29-32.

NWOSU, N. A. 1975. Recent developments in vegetative propagation of edible yam (*Dioscorea* species). Proc. Agric. Soc., Nigeria 12:15.

OGAWA, Y. 1976. Formation of the bulbil in *Dioscorea batatas* 1. Physiological role of the leaf blade. Bull. Fac. Agric., Mie University No. 51: 9-14.

OLORUNDA, A. O. and MACKLON, A. E. S. 1976. Effects of storage at chilling temperature on ion absorption, salt retention capacity, and respiratory pattern yam tubers. J. Sci. Food & Agric. 27: 405-412.

ONWUEME, I. C. 1972. Influence of the weight of the planted tuber on the vegetative performance of white yam (*Dioscorea rotundata* Poir) plants. Niger. Agric. J. 9: 170-173.

ONWUEME, I. C. 1973. The sprouting process yam (*Dioscorea* spp.) tuber pieces. J. Agric. Sci., Camb. 81: 375-379.

ONWUEME, I. C. 1975a. Tuber formation in yam (*Dioscorea* spp.): Effect of moisture stress; contribution of the parent sett. J. Agric. Sci. Camb. 85: 267-269.

ONWUEME, I. C. 1975b. Influence of storage time on earliness of sprouting and tubering

in *Dioscorea rotundata* yams. J. Agric. Sci. Camb. 84: 503-505.

ONWUEME, I. C. 1977a. Field comparison of West African planting and harvesting practices in yam (*Dioscorea rotundata*): pre-sprouting, dry season planting, and double-harvesting. *J.* Agric. Sci., Camb. 88: 311-318.

ONWUEME, I. C. 1977b. Effect of varying the time of the first harvest, and of late planting, on double-harvest yield of yam (*Dioscorea rotundata*) in field plots. J. Agric. Sci., Camb. 88: 737-741.

ONWUEME, I. C. 1978. Sett weight effects on time of tuber formation and on tuber yield characteristics in water yam (*Dioscorea alata* L.). J. Agric. Sci., Camb. 91: 317-319.

PASSAM, H. C. 1977. Sprouting and apical dominance of yam tubers. Tropical Science 19: 29-39.

PASSAM, H, C., READ, S. J. and RICKARD, J. E. 1976a. Wound repair in yam tubers: physiological processes during repair. New Phytologist 77: 325-331.

PASSAM, H. C., READ, S. J. and RICKARD, J. E. 1976b. Wound repair in yam tubers: the dependence of storage procedures on the nature of the wound and its repair. Tropical Science 18: 1-11.

THOMPSON, A. K., BEER, B. O., and PERKINS, C. 1973. Reduction of wastage in stored yams. 3rd Int. Symp. Trop. Root Crops, Ibadan, Nigeria.

UGOCHUKWU, E. N., ANOSIKE, E. O. and AGOGBUA, S. I. O. 1977. Changes in enzyme activity of white yam tubers after prolonged storage. Phytochemistry 16: 1159-1162.