TUBER DEVELOPMENT IN YAMS; PHYSIOLOGICAL AND AGRONOMIC IMPLICATIONS

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SUMMARY

The growth of tubers in *Dioscorea* spp. is described. Four phases of growth can be recognized with associated major physiological processes. The number of tubers initiated appear to affect yield with an optimum number about 7. The effects of some of the more important factors on tuber development and yield are reviewed and discussed. Sett size affects tuber yield by shortening time before the start of rapid tuber bulking, lengthening the period of tuber bulking and increasing leaf area. Plant density, staking and nitrogen seem to affect yield by increasing leaf area index and also the rate of tuber bulking. The effect of potassium has been explained as an effect on the duration of tuber bulking. Organic matter and soil physical factors may obviously affect yield, but there is need for research into the way in which these factors affect tuber development.

RESUME

La croissance des tubercules de *Dioscorea* spp. a été exposée. On peut noter quatre phases de croissance avec les étapes de développement fondamentales qui y sont associées. Le nombre de tubercules essayées semblent affecter le rendement avec un nombre maximum d'environ 7. L'effet des facteurs les plus importants sur le développement et le rendement de l'igname a été passé en revue. La dimension des boutures a une influence sur le rendement en raccourcissant le temps avant que ne débute le développement accéléré de la tubercule, en prolongeant la période de développement de la tubercule et an augmentant la zone foliaire. La densité, le tuteurage et l'azote semblent affecter le rendement en augmentant l'index de la zone foliaire de même que la grosseur de la tubercule. L'effet du potassium a été exposé en tant que facteur ayant une influence sur la durée de développement de la tubercule. La matière organique et les facteurs physiques du sol ont certainement une influence sur le rendement, mais il faudrait, par la recherche, déterminer comment ces facteurs affectant le développement de la tubercule.

RESUMEN

Se describe el desarrollo de tubérculos en *Dioscorea* spp. Se pueden reconocer cuatro fases de crecimiento asociadas a los principales procesos fisiológicos. El número de tubérculos formados parece afectar el rendimiento, obteniéndose un óptimo de éste con un número cercano a 7. Se revisan 6 discuten los afectos de algunos de los más importantes factores que afectan el desarrollo del tubérculo y el rendimiento. El tamaño afecta el rendimiento de tubérculos acortando el tiempo en el que se inicia un rápido engrosamiento de los mismos, alargando el tiempo durante el que ocurre tal engrosamiento e incrementando el área foliar. La densidad de plantas, el estacado y el nitrógeno parecen afectar el rendimiento incrementando el índice de área foliar y también el grado de engrosamiento del tubérculo. El tiempo en el que el tubérculo permanece engrosando se explica como un efecto de potasio. La materia orgánica y los factores físicos del suelo pueden, obviamente, afectar el rendimiento pero es necesario investigar en que forma afectan estos factores, el desarrollo del tubérculo.

INTRODUCTION

Yield in yams (*Dioscorea* spp.) means tuber yield. The proportion of the CO_2 that is fixed by photosynthesis that is translocated to and stored in the developing tubers is clearly an important determinant of yield. Tuber yield is rate of tuber bulking integrated over the duration of tuber bulking. The physiological processes involved in tuber development can provide an explanation of the ways in which agronomic factors affect yield.

The growth of the tuber can be correlated with the growth of other plant organs. When compared to temperate crops such as the potato and sugar beet, there is scant information on tuber development in yams. We review available data and discuss these.

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TUBER DEVELOPMENT

Development patterns

The tuber of yams has been botanically regarded as a stem tuber which develops by the plagiotrophic lobing of a degenerate rhizome[3,17]. The part of the tuber nearest to the vine is older (more physiologically mature) than the distal region.

Roots, stems and tubers all however seem to develop from a common tissue arising on the planting sett. This tissue seems to be structurally highly organized and was termed the 'primary nodal complex' by Ferguson[10].

There is a lack of information on the time of tuber initiation in various species and cultivars, and also on morphogenetic and physiological processes involved in tuber initiation. In *D. esculenta*, where stolon-like structures precede tuber development, the time of tuber initiation is likely to be at the formation of these structures which are formed at about 2 months after planting. However, in the White Lisbon Yam (*Dioscorea alata*) the time of tuber initiation has been suggested to be at, or soon after, bud formation (i.e. at the time of 'germination' and formation of the primary nodal complex)[11]. The first external signs of tuber development in the White Lisbon Yam occur about 3 months after planting[16,4,6,11]. The corresponding time for *D. trifida* is about 4½ months[9].

The growth of the tuber in yams follows a similar pattern to that outlined for the potato by Milthorpe and Moorby[20]. At first there is a period of slow, more or less exponential growth and this is followed by a period of rapid tuber bulking and finally a period of reduced rate of increase (sometimes a decrease) and maturation (Fig. 1). This generalized sigmoidal pattern has been observed on *D. alata*[16,18,4,6,11], *D. trifida*[9] and *D. esculenta*[7,8,9].

Tuberization on *D. alata*

In a detailed study on tuber development in White Lisbon Yam[11], I described four distinct phases of growth which represented periods of different physiological activities in the tuber. The first phase extended from emergence to 13 weeks, and consisted mostly of the development of the primary nodal complex. It is however difficult clearly to separate the tuber from the primary nodal complex in *D. alata* because the primary nodal complex and the tuber seem to grow as a single organ (Fig. 2). The primary nodal complex is therefore now regarded as an integral part of the tuber. The dry matter content of the tuber remained at about 13 percent during this period (Fig. 3).

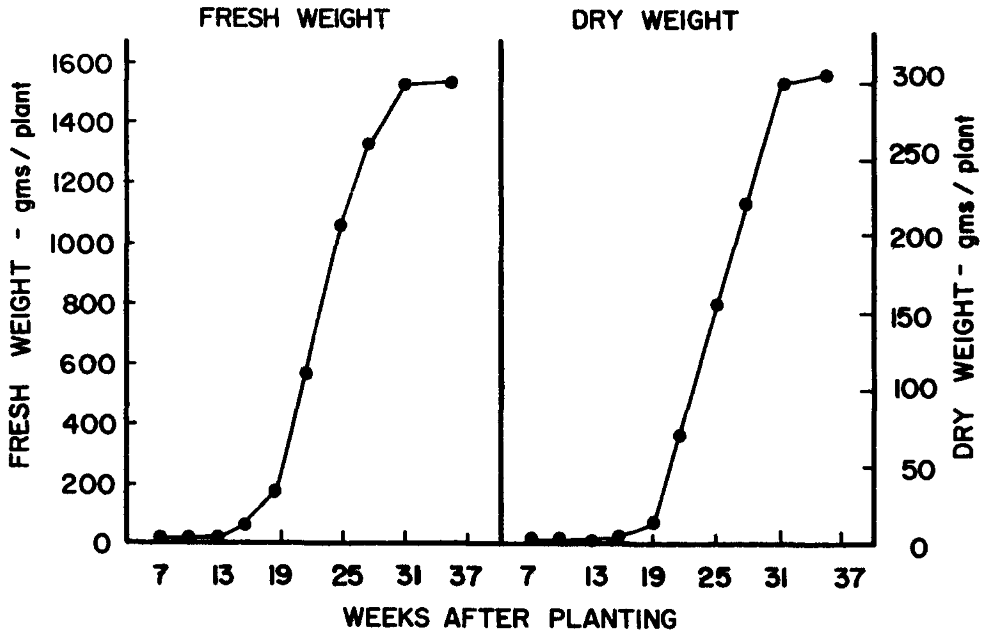

Fig I. Tuber development in White Lisbon Yam (D. alata) - fresh and dry weight changes .

The second phase extended from 13 to 19 weeks. Active tuber development beginning at 13 weeks was associated with a reduction in percent dry matter accumulation began during this period (Table 1), but the fresh weight increased relatively faster than dry weight. This period was interpreted as one of rapid cell division and some cell expansion in which many of the cells involved in subsequent tuber bulking were laid down. Hence, factors which affect the rate of cell division and expansion occurring during this phase will be important in the determination of final yield. Growth up to the end of the second phase could be considered exponential. The third phase extended from the 19th to the 32nd week and was a period of rapid accumulation of dry matter in tubers. The percent dry matter of tubers also increased during this phase and hence tuber dry matter showed a relatively greater increase than tuber fresh weight. Dry weight could be considered to increase more or less linearly with time during this phase. During the final phase from week 32 to week 36 dry matter accumulation slowed down and ceased altogether as maturity approached.

The above description of tuber growth represents the mean trend in the growth of a number of tubers. The changes in tuber number with time in White Lisbon Yam were also studied[11] (Fig. 4). Mean tuber number per plant was observed to increase steadily between 13 and 28 weeks but then to decrease. The decrease suggests that possibly a number of small tubers are resorbed during the final weeks of growth. Many of the tubers produced at maturity were in any case small and unmarketable. In the White Lisbon Yam the average number of tubers per plant of marketable size are probably developed early whereas tubers which are initiated and begin bulking later may be poor competitors for available assimilates and hence are likely to remain small.

Tuberization in *D. esculenta*

D. esculenta produces many more tubers than *D. alata*, and according to Enyi[7], tuber number seems to increase up to about six months after planting. Enyi also indicated that when many tubers are initiated the size of individual tubers is small and the proportion of initiated tubers that never reach harvestable size

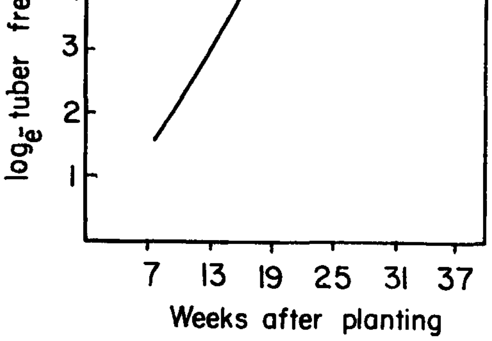

Fig. 2. Tuber development in white Lisbon Yam (D. alata) $\log_e$ tuber fresh weight

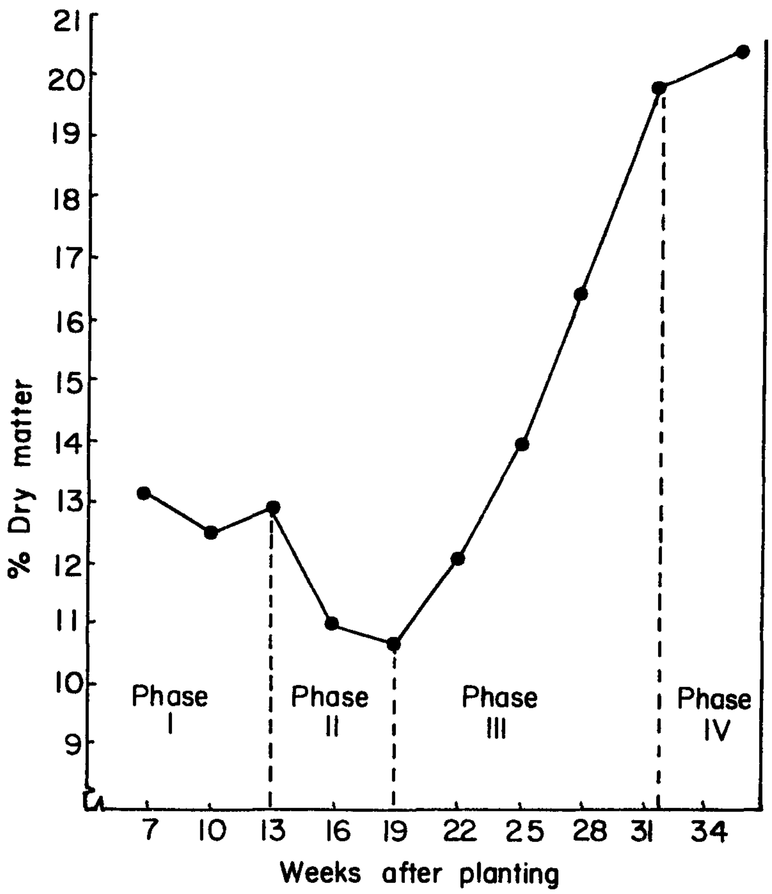

Fig. 3. Changes in percent dry mater of tuber in White Lisbon yam (D.alata)

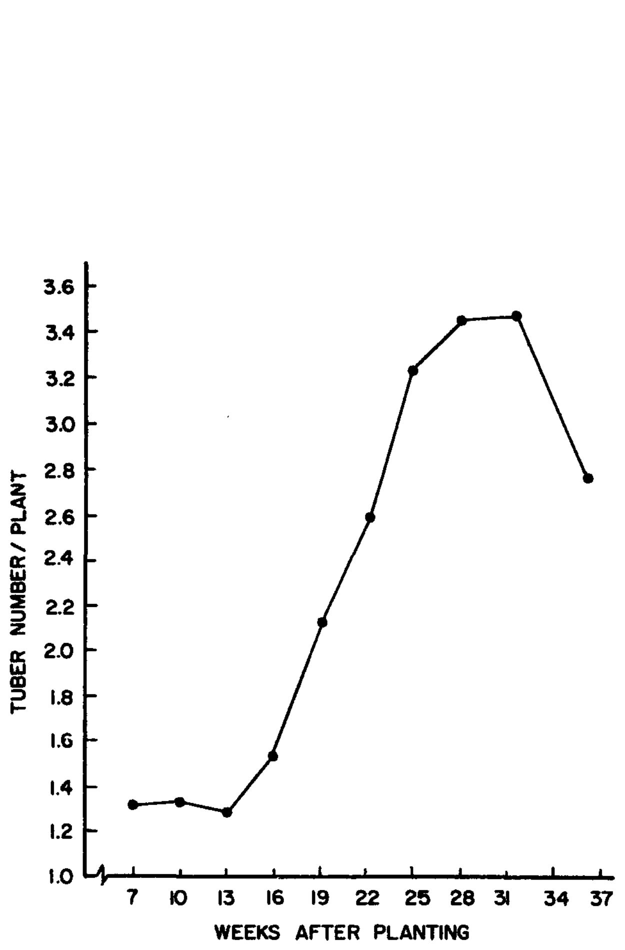

Fig 4. Changes in tuber number during growth of White Lisbon yam (D. alata)

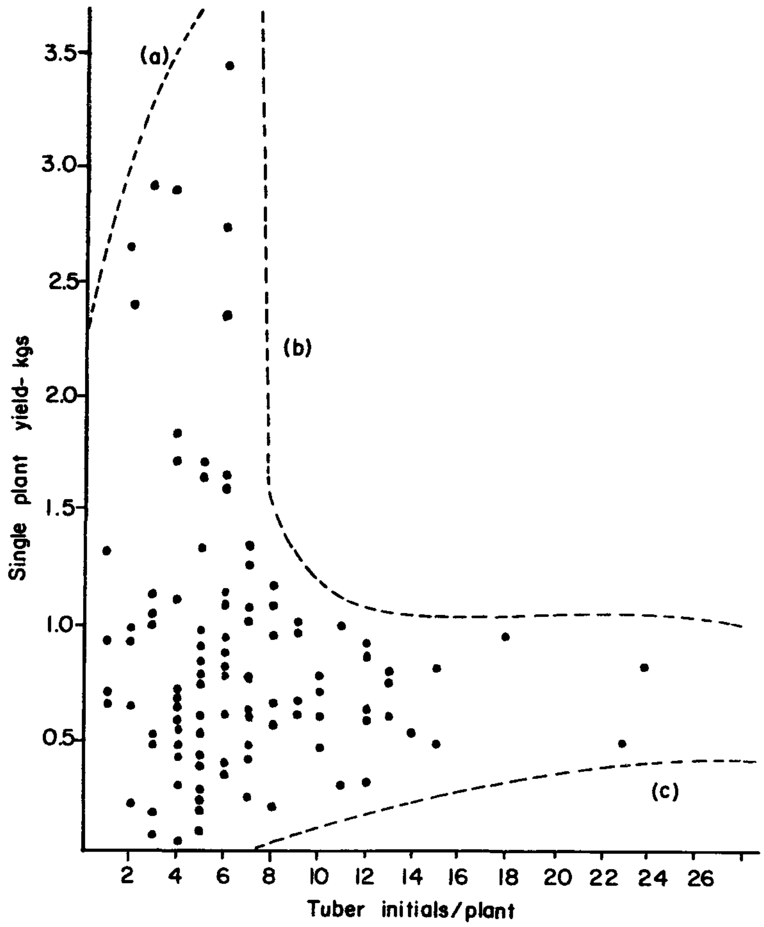

Fig.5. The effect of the number of tuber initials on yield per plant in white Lisbon Yam (D. alata).

is greater. Ferguson[9] had previously made a similar observation on *D. alata*. In this study the 'tubers' above 3 gm. are regarded as tuber initials. Yield per plant increased with tuber initials up to 7 per plant, but decreased markedly beyond this number (Fig. 5). It appears that factors which promote the initiation of an excessive number of tubers could therefore result in low yield in yams.

Aerial tubers are formed on the vines of some species of *Dioscorea*. Uduebo's data[23] indicate that the control of initiation of aerial tubers is under hormonal control. Sawada *et al.*[21] found that aerial tuber size increases with increase in sugar concentration in sterile culture but noted that sugar was not responsible for the induction of aerial tubers. In the White Lisbon Yam aerial tubers may be formed just after the period of maximum tuber bulking, and the build-up of assimilates (especially sugar) in the phloem (occurring perhaps as a result of restricted tuber growth) may be a factor involved in the formation of aerial tubers[11]. Aerial tubers in *D. alata* are also regarded as secondary sinks and seem to develop only after the primary sinks, the underground tubers, have passed their maximum period of tuber bulking.

FACTORS AFFECTING TUBER DEVELOPMENT AND YIELD

Tuberization

Many agronomic factors affect the yield of yams. There have been a few studies to determine the way in which these factors affect the growth and development of the plant. Haynes *et al.*[14] indicated the value of growth studies as an adjunct to agronomic experiments.

Chapman[6] found a strong correlation between leaf area and yield in White Lisbon Yam, and Ferguson[11], using the same cultivar related leaf area at 16 weeks with yield. Enyi[7,8] obtained a linear regression of yield on leaf area duration in *D. esculenta*. The relationship was better when yield was regressed on leaf area duration measured from after the time of tuber initiation than throughout the growth period[7]. The rate of tuber bulking increased with leaf area up to 490 dm^2 and decreased thereafter[7]. All these findings indicate the importance of assimilate supply in determining yield. One might therefore expect that agronomic factors which enhance leaf area would increase yield.

We do not have much evidence yet on the importance of the ability of the tuber to accept assimilates as a factor in yield determination. Factors which affect the time of tuber initiation and the time from then until rapid tuber bulking will affect the duration of tuber bulking and thus tuber yield. The time of tuber initiation was affected by K application and shown to affect yield in *D. esculenta*[8]. The time to rapid tuber bulking was shown to be shorter for plants grown from large setts of White Lisbon Yam, and also the size of the primary nodal complex at 8 weeks after planting (about 4–5 weeks old) was closely related to final yield[11]. It thus appears that yield in White Lisbon Yam could be determined early in the life of the crop.

Effect of some agronomic factors

Yield has been shown to increase with increasing sett size[1,2,7,11,19]. Plants from large setts of White Lisbon Yam were found to emerge earlier, produce larger primary nodal complexes, develop greater leaf area, begin rapid tuber bulking earlier and have a longer duration of tuber bulking than plants from small setts[11]. With *D. esculenta* Enyi[8] found that plants from large setts had greater leaf area duration and higher mean bulking rates than plants from small setts, but there was no difference in the duration of tuber bulking.

Yield of yams tends to increase with increasing plant density[1,2,5,8,13,14,15]. In *D. esculenta* increasing plant density resulted in higher leaf area index, greater leaf area duration and higher tuber bulking rates per unit area[8]. Yield per plant in *D. esculenta* and *D. alata* increased with decreasing density and has been related to the higher bulking rates per plant more than the duration of bulking[7,11].

Yield increases with nitrogen application and staking. The increase in yield can be accounted for as due to an increase in leaf area[6,8]. Treatments resulting in greater leaf area gave both a greater yield and higher tuber bulking rates.

Potassium has marked effect on the yield in *D. esculenta* and this seemed to result from a longer bulking duration because of earlier tuber initiation and also a small increase in leaf area[8].

Organic matter gave a marked positive yield response. In addition to supplying nutrients and improving the physical condition of the soil the organic matter may have added compounds which had a stimulatory effect on tuber growth. This merits further investigation.

Tuber growth may be greatly restricted in compact soils and this factor also merits consideration in future research.

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TABLE 1

Mean bulking rates of four phases of tuber growth in White Lisbon Yam (*D. alata*)

Gms/plant/wk.

Phase I 7-13 wks	Phase II 13-19 wks	Phase III 19-32 wks	Phase IV 32-36 wks
0.36	2.72	21.40	3.00

Source: Ferguson,1973