

THE USE OF PHYSIOLOGICAL STUDIES IN THE AGRONOMY OF ROOT CROPS

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In the past it has been customary to regard crop production largely as a technology. Efforts were concentrated on the actual details of field practice, such as seed and fertilizer rates, planting dates and crop protection technology in relation to yields. Furthermore, much of this practice was arbitrarily determined or adopted because of tradition. The problems that frequently arise by such an empirical approach may be illustrated by reference to nitrogen fertilizer application to sweet potatoes. The literature on this subject indicates conflicting results in the attempts at relating nitrogen application to yield (Stuckey 1914, Zimmerley 1929 and 1934, Leonard and Anderson 1947, Johnson and Ware 1948, Landrau and Samuels 1951 and Stino and Lashin 1963). As will be discussed later in this paper, detailed study of growth and development allows these conflicting results to be resolved (Walter 1966).

Thus agronomy is now seen as a complex of inter-relationships of a system made up of the plant, the soil and the atmosphere. For a proper understanding of this system it must be studied systematically, through the growth cycle of the plant. This approach is useful in identifying the basic physiological processes determining yield in crops and at the same time enables an integrated view to be taken of the growth of the plant which is on the one hand understandable to the physiologist and biochemist in their concern with the changes in rates of processes, patterns of metabolism and influence of growth regulators, and on the other hand this dynamic approach is meaningful to the soil scientist and the micrometeorologist in their study of environmental influences on crop growth. This dynamic approach does not neglect agronomic technology but allows its assessment on a more fundamental basis. Thus planting densities, potential for response to fertilizer and other agronomic parameters are studied as they relate to growth and development throughout the full growth cycle. Studies of this nature have been carried out on many temperate crops, but information on tropical crops is scarce.

In most of the studies discussed in this paper, growth analysis, that is the designation of dry matter changes of component plant parts in relation to leaf area, is used to describe the growth and development of the crops. In these growth analysis studies the crop system is considered in terms of the quantity of the photosynthetic system present and in terms of the efficiency of this system. The quantity of the photosynthetic system is here taken to be represented by the leaf area of the crop, measured as leaf area index, L , the area of leaf per unit area of ground, and the leaf area duration, D , that is the integration of L with time. The efficiency of the system is measured as the Net Assimilation Rate — E , that is the rate of dry matter production per unit area of leaf.

The relation between L and E have been discussed by Watson (1952). In this paper our concern is primarily with the influence of leaf area development on

yield. Our studies with tropical root crops have so far confirmed the view that L has the greater influence on yield and is of greater concern to the agronomist than E since it is more easily altered by field practice. The ready response of L to such factors as rainfall and nitrogen fertilizer are indications of the ease with which changes in L may be achieved. Changes in L are not easy to control and their effects on yield vary with the system of cultivation.

The basic growth patterns (as far as these are known) of yams (*Dioscorea alata*), sweet potatoes (*Ipomoea batatas*), tuberosum potatoes (*Solanum tuberosum*) in the lowland tropics, are described and this knowledge is discussed in relation to formulation of agronomic practice. Reference is also made to tannia, (*Xanthosoma sagittifolium*.)

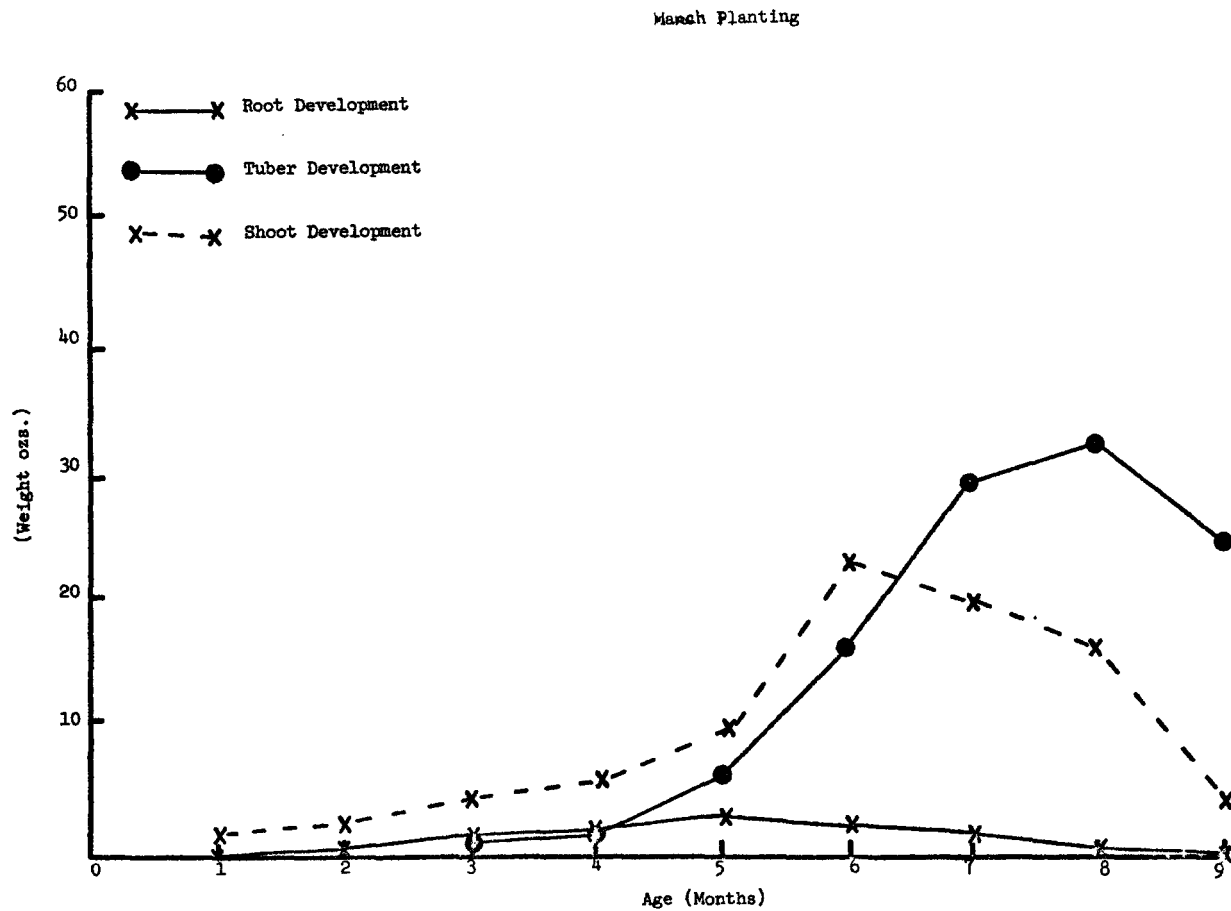
GROWTH AND DEVELOPMENT PATTERNS SELECTED ROOT CROPS AND SOME AGRONOMIC IMPLICATIONS

Yams

Of the many yams grown for food in the tropics studies of this crop at the University of the West Indies have been limited to the "White Lisbon" cultivar of *Dioscorea alata*. The earliest account of growth and development studies with this crop was that of James (1953). In this study observations were restricted to root and tuber development and little data was collected on leaf and stem development. It was observed that initial root development was superficial, being confined to the upper 4 ins. of the soil. It was also shown that fibrous root development reached a peak in the fourth month after planting, and that senescence of these roots had commenced by the fifth month. These observations pointed to the possibility of damage due to mechanical weeding during early growth of the crop, and to a reduced potential for absorption of nutrients after the fifth month of growth.

Yam tubers show a regular sequence of dormancy and growth. The tubers remain dormant for 3-4 months, depending on the cultivar, and growth lasts for 8 or more months. The sequence of growth and dormancy leads to periods of availability and shortage. In a series of investigations on the mechanism of dormancy, Campbell et al. (1962) showed that sprouting of yams was related to the level of glutathione present in the tuber. It was further shown that the glutathione level could be increased by treatment of yam tubers with 2-chlor-ethanol. This treatment permitted sprouting of yams to commence and enabled yams to be planted as early as March. It then became possible for the trends in growth to be followed for successive monthly plantings starting in March and ending in June. Such a study was reported by these workers but no dry matter measurements or leaf areas were determined and only fresh weight measurements were recorded for roots, shoots and tubers. The growth and development patterns for this crop at the different planting dates were based on these fresh weight measurements (Fig 1). These curves showed little difference in character with month of planting, and indicated that the production of yams could be staggered if the crop was planted on different dates. The peak development of roots observed by James (1953) was confirmed, and it was noted that shoots attained maximum development six months after planting thereafter showing a decline. Rapid tuber development commenced about five months after planting in all cases except for those planted at normal date (mid-May), in which case rapid development started in

Fig. 1 Fresh Weight grams for Yams (roots, shoots and tubers)
planted in early March - Taken from Teri a 1958.



the fourth month (Fig 2). Maximum fresh weight increase was attained by the eighth month in every case. By the ninth month the crop had matured. In the same series costing trials on the out of season production of yams was attempted (Ho-A-Shu 1958) by breaking dormancy with 2-chlor-ethanol treatment and growing the crop with irrigation. Recently commercial scale out of season production has been carried out with a good measure of success (Haynes and Thomas 1967).

Using the data collected by Teriba (1958), Campbell *et al.* (1962) suggested that nitrogen fertilizer could be more effective if applied 3 months after planting. This was subsequently confirmed by Chapman (1965 a) who showed that nitrogen applied three months after planting gave a greater increase in D and in yield than in those cases where application occurred at planting. It was suggested that since planting was carried out immediately before the onset of heavy rain there was a strong likelihood of losses of nitrogen due to leaching and in any case there may be a sufficiency of nitrogen in the soil due to dry season mineralisation (Birch 1960). On the other hand a delay in application of nitrogen beyond five months is unlikely to lead to its efficient utilization by the plant since roots begin to decline about this time.

In Trinidad yam vines are grown on supports. This is indicative of the response to better foliage display in this crop. The increase in yield due to staking of yams is well known (Burkhill 1920, Wood 1933, Campbell and Gooding 1962, and Gray 1962). It is, however, only recently that a study of the leaf area and yield relationships of yams grown with stakes have been described here (Chapman 1965 a) (Fig 3). This description is however general and the differences between staking and nitrogen treatments are not shown. In this study (Chapman 1965a) it was observed that plants grown on long stakes gave higher yields than those grown on short stakes. Differences in leaf duration were noted between yams grown on 3 ft. and on 6 ft. stakes, but these differences were not statistically significant. A further investigation of level of nitrogen and staking confirmed the effect of increased yield due to staking and suggested that stakes enhanced the effect of nitrogen application.

It is however felt that a comprehensive study of growth and development of yams is still needed, such studies are in progress in Guadeloupe (*c.f.* Degras, this Symposium) and in Barbados (Gooding and Hoad 1966). It is hoped that from these studies a better understanding of the leaf area/yield relationships will emerge.

Sweet Potatoes

In attempts to characterise leaf area development in sweet potatoes the dependence of leaf area on environmental and management conditions becomes clear. Such factors as nitrogen fertilizer level, provision of supports (staking) and spacing, alter the leaf area development curve and influence yield. The available evidence suggests that there is an optimum curve of leaf area development with which maximum yield is related. This hypothesis does not deny the influence of leaf display on yield nor that E may vary with cultivar or fertilizer level. It is contended, however, that the difference in yield due to leaf display and E are small, relative to the effects on yield due to leaf area development. It is also contended that fertilizer treatment and other agronomic practice are only capable of influencing yield within the limits determined by the leaf area curve. Based on these assumptions our recent work has been concerned with varying L and relating yield to these variations. This type of analysis has been made easy.

Fig. 2 Fresh Weight grams for Yams (roots, shoots and tubers)
planted at normal date (Mid-May) - Taken from Teriba 1958.

Normal Planting (Mid-May)

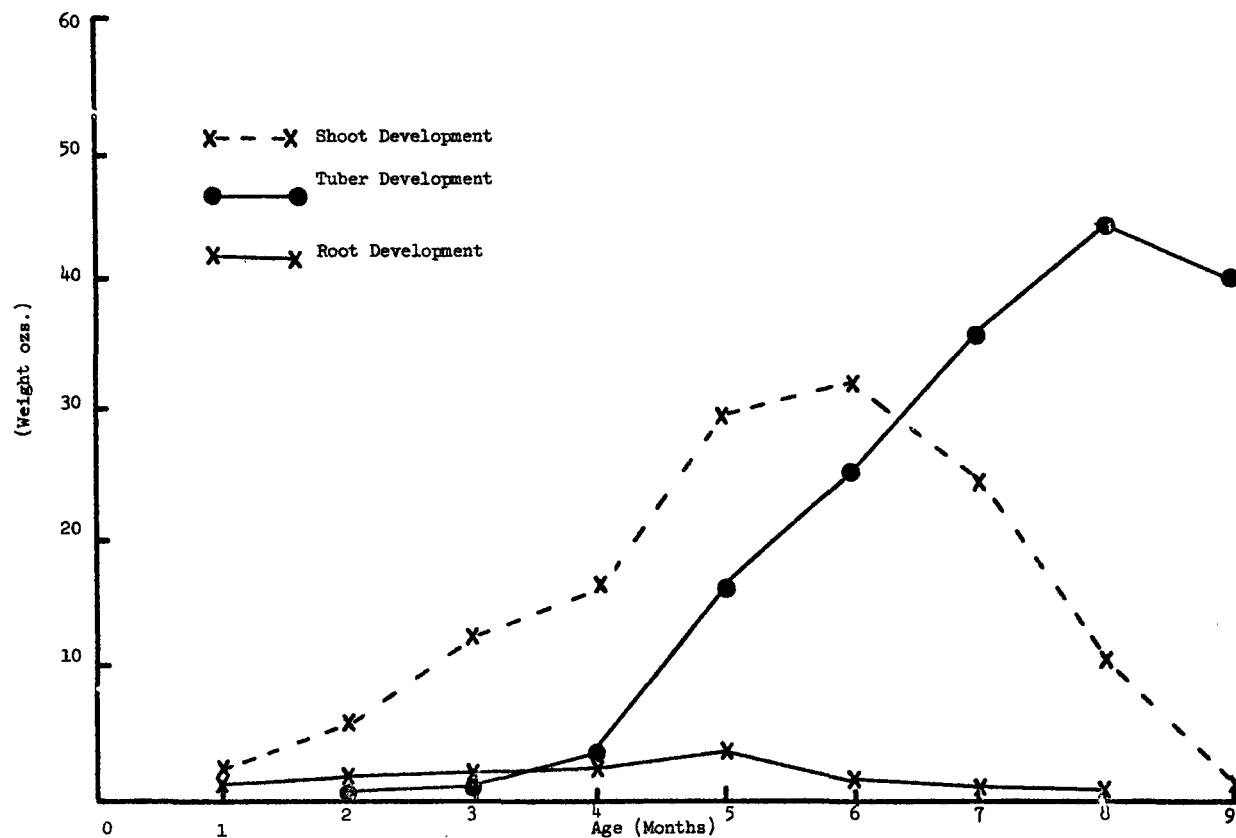


Fig. 3 Leaf area and tuber development in yams - a generalised version. Taken from Chapman 1965 a.

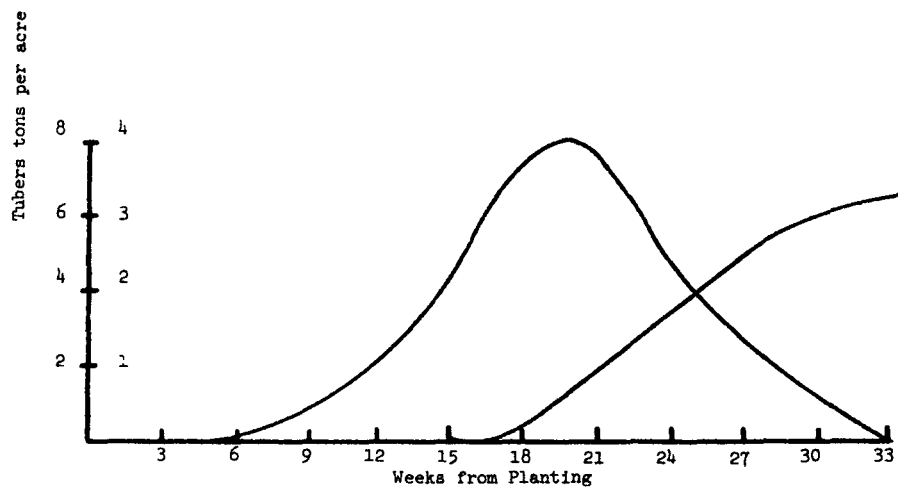


Fig. 4 Leaf area development for C 9 and Q49 at zero level of nitrogen.

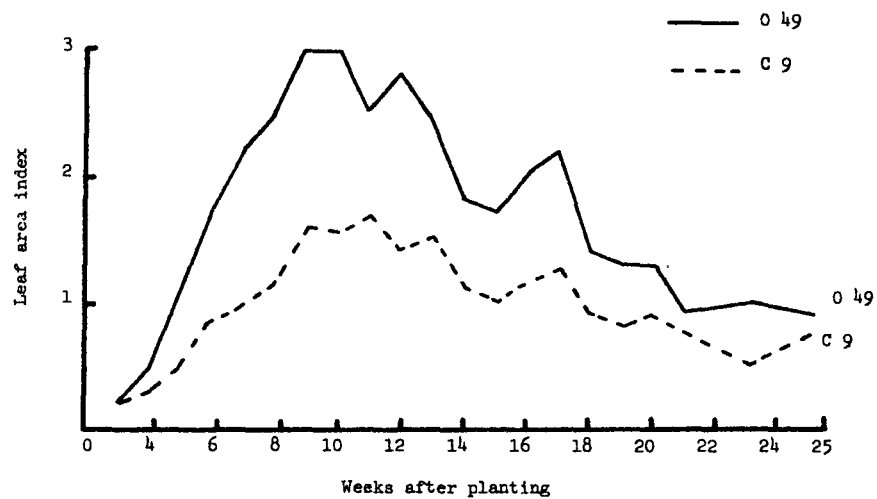
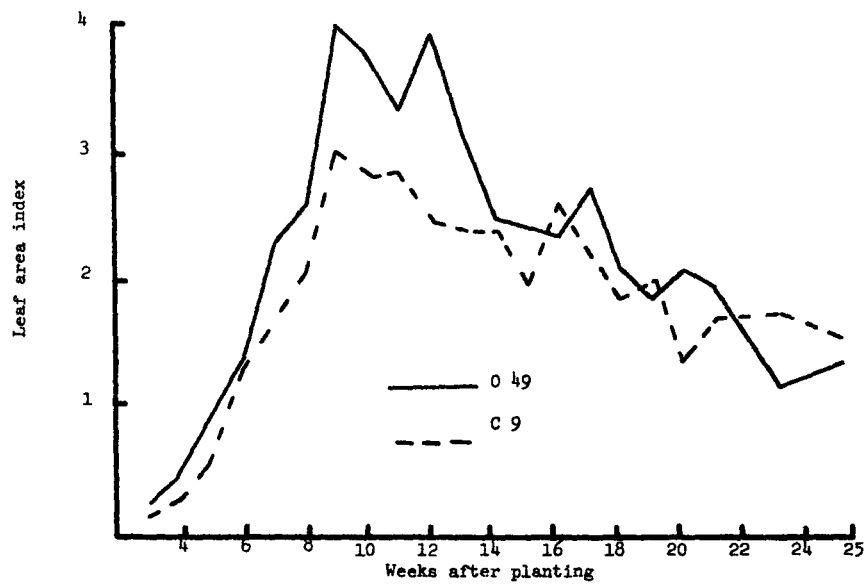


Fig. 5 Leaf area development for C 9 and O 49 at 120 lbs nitrogen per acre.



by the availability of a range of cultivars with differing values of *L*. It was therefore possible to select on the one hand a cultivar with relatively low *L* but possessing high tuber yield such as C9, and on the other a cultivar with high values for *L* and high commercial yield 049. By varying the levels of nitrogen fertilizer an increasing range of leaf area values for both cultivars was achieved and the resulting dry matter accumulation from these leaf area values assessed (Walter 1966). The responses to 0 and 120 lbs. of nitrogen per acre are shown for 049 and C9 in Figures 4 and 5.

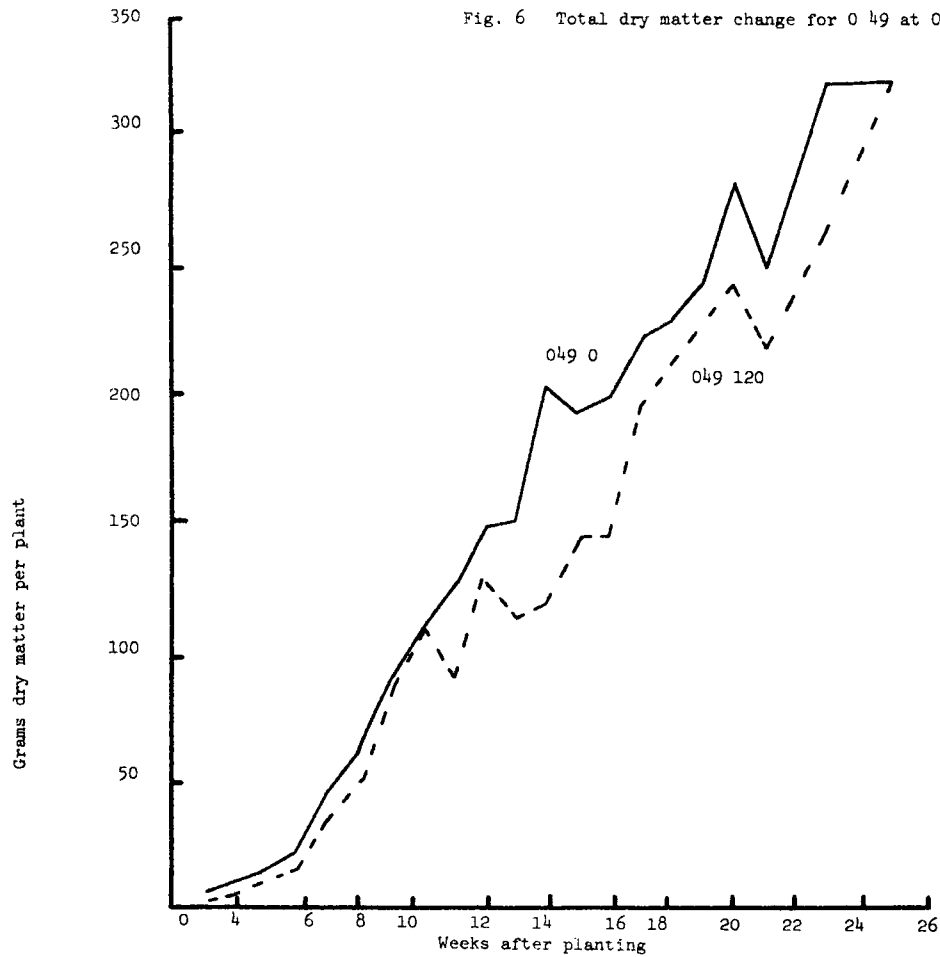
It is interesting to note the similarity between the leaf area index curve for C9 at 120 lbs. nitrogen per acre and that of 049 without nitrogen. This is in contrast to the curve for C9 without nitrogen which produces low *L* and low yield and the curve for 049 and 120 lbs. nitrogen per acre which produces excessive *L* and a low yield when harvested at the normal time for the commercial crop at 4 months. The response of 049 with high nitrogen deserves further comment.

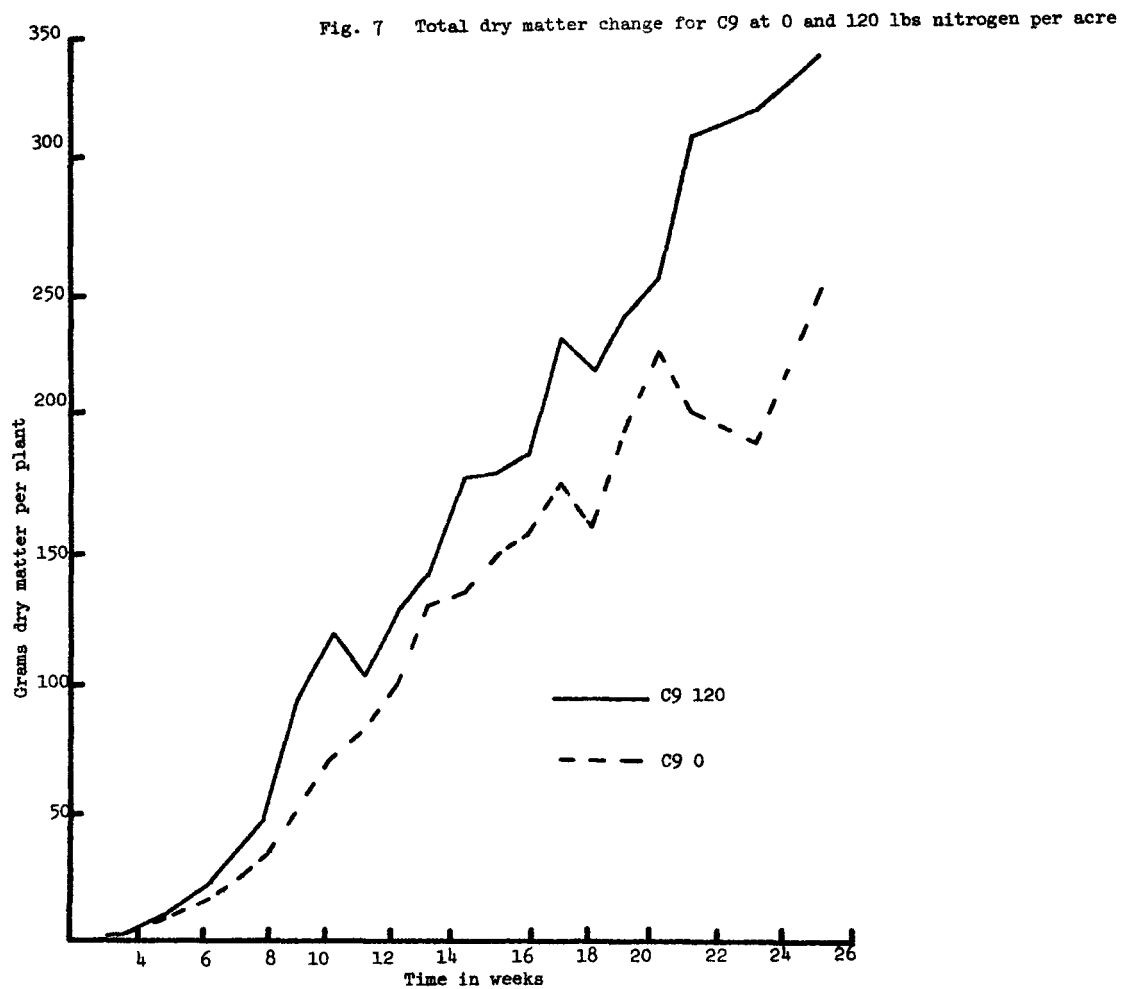
The curves for tuber dry weight with 049 (Fig 6) and (Fig 7) C9 at 0 and 120 lbs. nitrogen show contrasting effects of nitrogen for the two cultivars. In the case of 049 the higher level of nitrogen depresses tuber production in early growth. The subsequent rate of tuber development becomes rapid after the leaf area shows a decline. It is suggested that *L* in the first 12-14 weeks is excessive but during 16th-20th weeks when it is presumably nearer to the projected optimum, the rate of tuber bulking is rapid. The effect of this late and sustained development of dry matter gives rise to the possibility of higher ultimate yields from the high nitrogen treatment of 049, provided harvest is delayed beyond the arbitrarily selected 4-month growing period for this crop.

In an earlier paper (Spence and Haynes 1966) these results are discussed in connection with the breeding of high and low nitrogen response varieties. Tsunoda (1965) has also designated low response and high response (to nitrogen) varieties of sweet potato, the former having a high leaf area under low nitrogen levels and the latter having a low leaf area under low levels of nitrogen. In the low response varieties the application of nitrogen raises the leaf area above the optimum level with resulting mutual shading of leaves and reduced photosynthetic efficiency.

Tsunoda does not point to the compensating effect in the later stages of growth, of low nitrogen response varieties with high nitrogen treatment when *L* has fallen below maximum, but this may be due to restrictions imposed on the length of the growing season by climatic conditions in Japan. Trials in which the efficiency of display of canopy is improved (Chapman and Cowling 1965) indicate that the projected optimum *L* varies with display. The plant appears capable of maintaining *L* at a higher level without loss of efficiency in tuber production. This effect has been demonstrated (Chapman and Cowling 1965) using the cultivar A138 which normally produces high *L* and low yield. However, when the canopy is displayed on supports there is a marked increase in *L* and in yield. By addition of nitrogen to the supported plots further increase in *L* and in yield were obtained. It seems clear from this study that the idea of an optimum *L* must be related to the system of cultivation.

Variation in plant spacing provides another means of influencing leaf area. In a projected trial it is intended to vary the spacing at which cultivars with high





and low leaf areas are grown, and to assess the leaf area/yield relations which result from these manipulations. It is likely that cultivars with high L grown at close spacing would produce excessive leaf area and a lower yield. On the other hand, the cultivars with low leaf area may be grown at a closer spacing and might still be expected to produce a higher yield.

It is suggested that the leaf area development of sweet potato cultivars is influenced by nitrogen, foliage display and spacing and that there is an optimum L for a particular foliage display system. It is further suggested that cultivars may have equal maximum yield potential but that different systems of growth may be required to express this potential. In this connection the economic feasibility of the system must be considered. For instance, in a labour intensive system cultivars with large leaf area may be grown on supports, whereas in a labour extensive system a low leaf area cultivar grown at close spacing may be a more appropriate choice. Similarly, in areas remote from the manufacture of chemical fertilizer, use may be made of cultivars capable of producing a large leaf area when grown in the absence of nitrogen fertilizer. On the other hand where fertilizers are readily available and their cost is low, cultivars with low leaf area may be used and nitrogen fertilizer applied.

Tuberosum Potatoes at Low Elevation in the Tropics

The growth of Irish potatoes at low elevation in the tropics is characterised by a short growing period and high rates of tuber production, about 11 tons of tubers in about 13 weeks (Chapman 1965 b) (Fig 8). On the basis of yields of this order in so short a period of growth, the tuberosum potato would seem to be efficient compared to other tropical root crops. A yield of 11 tons per acre of sweet potatoes with the cultivars now in use in Trinidad might take from 20-24 weeks and about 36 weeks for yams or tannias so that, thinking in terms of production per acre, per annum this would seem to give a tremendous advantage to the tuberosum potato, provided varieties can be found which will give similar yields in the warmer season.

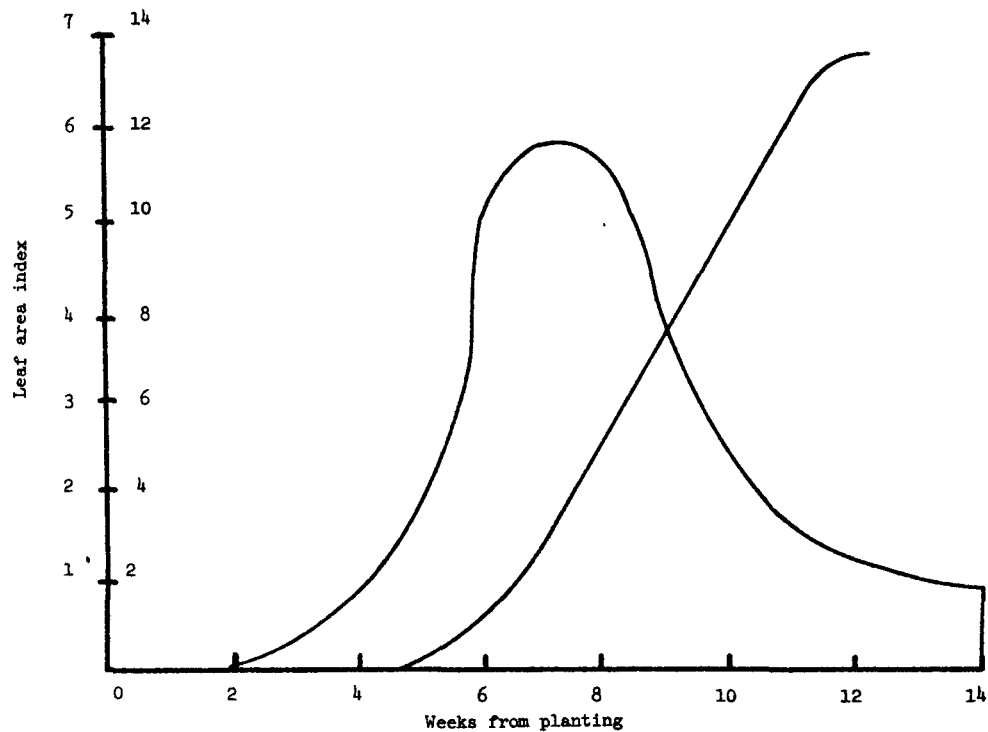
Due to the short crop period, attention is focussed on the patterns of leaf area development in this crop and on possible means of extending leaf area duration. Chapman (1965 b) also showed that nitrogen increased peak value of L and maintained L at a higher level until maturity. Although these peak values of L coincide with the period of maximum tuber development they are maintained for only a short period of this phase of tuber development. These data are in accord with the view that important increase in yield of this crop could accrue to treatments which served to maintain L at a high level (Brenner and Taha 1966). The application of nitrogen at planting is by itself inadequate and it has been suggested (Haynes 1966) that top dressing with nitrogen at seven weeks or spraying urea on the foliage is worth investigation.

Tannias

This crop is capable of progressive growth for long periods and is usually terminated because of shortage of soil moisture or because it is commercially advantageous to reap the cormels.

The natural disposition of the foliage of this crop to sunlight is such that there is apparently little competition within the plant for radiant energy. There

Fig. 8 Leaf area and tuber development in tuberosum potatoes after Chapman 1965 b.



would appear to be considerable scope for increasing leaf area through the use of nitrogen fertilizer and through closer spacing. The ease with which leaf area can be determined (Chapman 1964) recommends this crop as a convenient subject for study in field experiments, where changes in leaf area development are brought about by agronomic practice.

CONCLUSION

In the present paper the value of growth analysis is emphasized though recognition is also given to the fact that a knowledge of the morphology of the plant may influence agronomic practice. For example the superficial nature of yam roots was discussed in relation to mechanical weeding. Also, the necessity to seek an understanding of biochemical processes within the plant, in addition to the approach of growth analysis is indicated by the work described on breaking of dormancy in yams.

The limitations of the traditional approach to agronomic practice where treatment differences are assessed after a given period of time is illustrated by the conflicting reports on the response of sweet potatoes to nitrogen fertilizer. The value of a knowledge of the growth and development of the crop in understanding the effect of nitrogen fertilizer when applied at differential rates becomes evident in studies like that of Walter (1966) which has helped to clarify the nitrogen response (or lack of response) in this crop.

Using evidence from the work on sweet potatoes, the hypothesis is put that optimum yield is related to a given leaf area curve. The effectiveness of a given leaf area is related to its display and so optimum leaf area curves must be related to specific systems of culture. This leads to the contention that agronomic practice should vary with the level of technological input which is itself influenced by the economics of production.

While further evidence is needed for yams it seems likely that the same general principles will apply. In the case of tannias the system is simpler since the laminae have a simple display and the morphology of the plant will not allow the altering of this display by agronomic means.

The emphasis placed on L in this paper is in no way intended to minimise the importance of differences in E. Many of the factors affecting E will be discussed in other papers in this Symposium (Humphries, Wilson). Also it is not intended to minimise the importance of growth regulating substances such as a tuber initiating substance in the tuberosum potato (*c.f.* Milthorpe, this Symposium) or the effect of potassium fertilizer in many root crops. But in the present state of knowledge of tropical root crops it would seem that agronomic practices will have the greatest effect on influencing yields through their influence on L.

It is clear that plant breeders who provide the characteristics of the plants to be grown should bear the several circumstances of agronomic practice in mind when breeding new cultivars. If in this way material is produced with highly contrasting leaf areas (low or high) their yields may be maximised in both types by the varying practices which are possible at the different levels of production.

ACKNOWLEDGEMENTS

As is evident from this review, a number of research workers of the Imperial College of Tropical Agriculture and later the University of the West Indies, in Trinidad have contributed to our present state of knowledge of the physiological aspects of root crop agronomy, and the authors acknowledge their debt to all these researchers whose endeavours have made their present review possible.

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