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B. GENERAL AGRONOMY

LEAF AREA AND NET ASSIMILATION RATE AS DETERMINANTS OF CROP YIELD

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ABSTRACT

The relation of agronomic practice to crop yield is discussed in terms of photosynthetic efficiency of the crops (as measured by Leaf Area and Net Assimilation rates). The importance of a study of these factors in certain tropical crops is indicated.

INTRODUCTION

In the past when the influence of some agronomic practice (such as the response of the crop to fertilizer) has been studied, measurements of the yield of the crop or crop product have been taken after a predetermined interval of time. Useful as this practice has been in indicating the relative value of specific treatments, it has shed little light on the processes by which the increased yields have been achieved. So too with the breeding and selection of new varieties. By and large, selection of better varieties has been made on the basis of a final yield and attempts to designate components of yield have been on a morphological rather than on a physiological basis.

In the more recent approach the question of increasing the productivity of crops has become an integrated problem in plant physiology depending fundamentally on control of photosynthesis rather than as a collection of separate agronomic problems. This is the view taken by Niciporovio (Blackman and Watson, 1960) and when followed through this permits a bridging of the gap which exists between the work of physiologists using a single plant growing under controlled conditions and studies in the field.

The present outlook then is to break down the crop growth into component physiological systems and to study the effect of different treatments or of environmental changes on these components in relation to final yield. In addition the Plant Breeder must take account of the inheritance of these physiological processes which affect yield in synthesising new and heavier yielding varieties. In this approach the first broad designation of the crop plant system is made into (1) the quantity of the photosynthetic system present and (2) the efficiency of this system.

This designation allows separate study under these two broad headings of the factors affecting crop growth. The quantity of the photosynthetic system present is for many studies taken to be represented by the leaf area in a crop. This is recorded as the Leaf Area Index, L, and is defined as the area of leaf per unit area of ground. The persistence of the photosynthetic system during the growth period of the crop will also be of great importance. This is assessed by the integration of Leaf Area Index with time and is referred to as the Leaf Area Duration. The efficiency of the photosynthetic system is recorded by the Net Assimilation Rate, E, defined as the rate of dry matter production per unit area of leaf.

Certain points should be noted in connection with these parameters of growth.

(a) The above definitions assume that assimilation takes place mainly in the leaves. This is not always the case; for example, in cereals grain growth is contributed to substantially by assimilation in the ear.

(b) E does not measure photosynthetic efficiency but the excess of dry matter production by photosynthesis over dry matter utilization in respiration.

(c) This system is concerned with total (biological) yield on a dry weight basis and not yield of a marketable product. It is often necessary to include a consideration of the distribution of assimilates throughout the plant system if a clear picture is to emerge. This is particularly the case when only part of the plant serves as the economic product. Further marketable yield is usually assessed on a fresh weight basis and this may not be directly related to dry weight yield.

(d) No account is taken of quality in this system.

Clearly E and L are complex factors but further subdivision is inconvenient and their complexity is best considered in relation to factors affecting them.

Watson (1956) has discussed the relationship which may exist between L and E and indicates the factors which might alter the value of E. Increase in E and/or L should increase crop growth if they may vary independently. However it is found that in some crops as L increases the upper leaves of the canopy shade the lower leaves and this mutual shading effect may lead to less efficient photosynthesis thereby reducing E. Increase in L will not therefore lead to a continuous increase in dry matter production.

It is through the adoption of growth analysis that crop growth may be studied in the field in relation to the photosynthetic system. In growth analysis samples of the crop are harvested at frequent intervals and leaf areas and dry weights of separate plant parts are determined. This technique has been reviewed by D. J. Watson (1952) and is becoming well-known to all agronomists though its use is still more extensive in temperate than in tropical areas. Extensive studies have been carried out by Japanese workers on sweet potato and rice (Tauno and Fujise, 1965, Tsunoda, 1965), but this work has been done in temperate or subtropical areas. A great deal of work therefore neeeds to be done on these crops under tropical conditions, and in other tropical crops.

In the Faculty of Agriculture, University of the West Indies, the growth analysis technique is being used to study the growth and yield of rice, maize, tannia, yams, sweet potatoes, Solanum Potato, soybean and sesame, in terms of E and L, and these field studies will be followed by greenhouse studies on particular physiological processes in these plants where such studies are indicated.

The crop which is receiving much attention at the moment is sweet potato and some of the work on this crop has been reviewed recently (Spence and Haynes, 1966). In the present paper it is intended, by reference to the work at U.W.I., and some of the studies to progress elsewhere, to indicate how a detailed study of growth and development may influence (1) Agronomic practice and (2) Breeding and selection of new varieties.

AGRONOMIC PRACTICES

Three different aspects of agronomic practice which have been studied at U.W.I. will serve to illustrate the usefulness of growth studies in elucidating environmental influences on crop yield. These are (1) Response to nitrogen (2) Display of foliage (3) Type of planting material.

Response to nitrogen

This has been studied in sweet potato and to a lesser extent in Solanum potato. The work on Solanum potato is discussed in a separate paper at this Conference (Haynes, 1966).

Reports in the literature indicate conflicting results in response to nitrogen application in sweet potato fertilizer trials (Johnson and Ware, 1948); Landau and Samuels, 1951; Nettles, 1962; Acland, 1963). Growth analysis studies have now yielded information that should be useful in offering possible explanations for these diverse results.

Acland (1963) studied a range of U.W.I. (Faculty of Agriculture Food Crops Breeding Unit) selections and showed these to vary considerably in Leaf Area Indices, but found no direct correlation between Leaf Area Index and Yield. Some varieties possessed high Leaf Area Index and gave high yield (e.g. F_2), others had low Leaf Area Index and high yield (e.g. C_9) and still others had high Leaf Area Index and low yield (e.g. A_{138}).

Chapman and Cowling (1965) however investigated further the growth of cultivar A_{138} in order to determine whether the high Leaf Area Index was in any way responsible for the low yield.

The Leaf Area was modified by nitrogen application and the leaf display was altered by staking. This latter modification will be discussed more fully later. It need only be noted here that there was a slight reduction in yield (in fresh weight of tubers) in the nitrogen plots of the unstaked treatments but an increased yield due to nitrogen application in the staked plots.

Recent work has involved a comparison of the effects of nitrogen on two high yielding U.W.I. cultivars which are contrasting in Leaf Area, namely C_9 (a low leaf area) and 049 (a high Leaf area) cultivar (Walter, Haynes and Spence-unpublished data). A fairly heavy nitrogen application (120lbs. per acre) increased Leaf Area Indices in both cultivars.

In 049 (high leaf area cultivar) dry matter production was reduced by nitrogen until the very late stages of growth (about the 25th week from planting), whereas in C_9 dry matter production was increased by nitrogen. The Leaf Area Index curve for C_9 plus nitrogen corresponded closely to that of 049 without nitrogen, whereas that of C_9 without nitrogen was lower throughout growth and that of 049 plus nitrogen was greater. In each cultivar the Leaf Area Index was maintained at a higher level with the nitrogen application than without it.

It would seem that the high nitrogen application increased the leaf area in 049 to a level where the photosynthetic efficiency was reduced by mutual shading of leaves whereas in C_9 the increase in leaf area resulted in increased yield since the leaf area did not reach such a high level. However, in the later stages of growth when the Leaf Area Indices have reduced in all treatments the level at which leaf area was maintained appeared to be critical and dry matter production tended to rise in 049 with high nitrogen so that the earlier depression in yield was almost nullified. On the whole changes in tuber production (in terms of dry weight yield) with the different treatment was closely related to total dry matter production except that nitrogen application tended to delay the start of tuber bulking.

It is apparent from these results that nitrogen response can vary markedly with the cultivar and that the response in terms of final yield may be very different according to the time of harvest. It is not surprising therefore that the results of nitrogen fertilizer trials recorded in the literature have been so varied.

FIG. 1

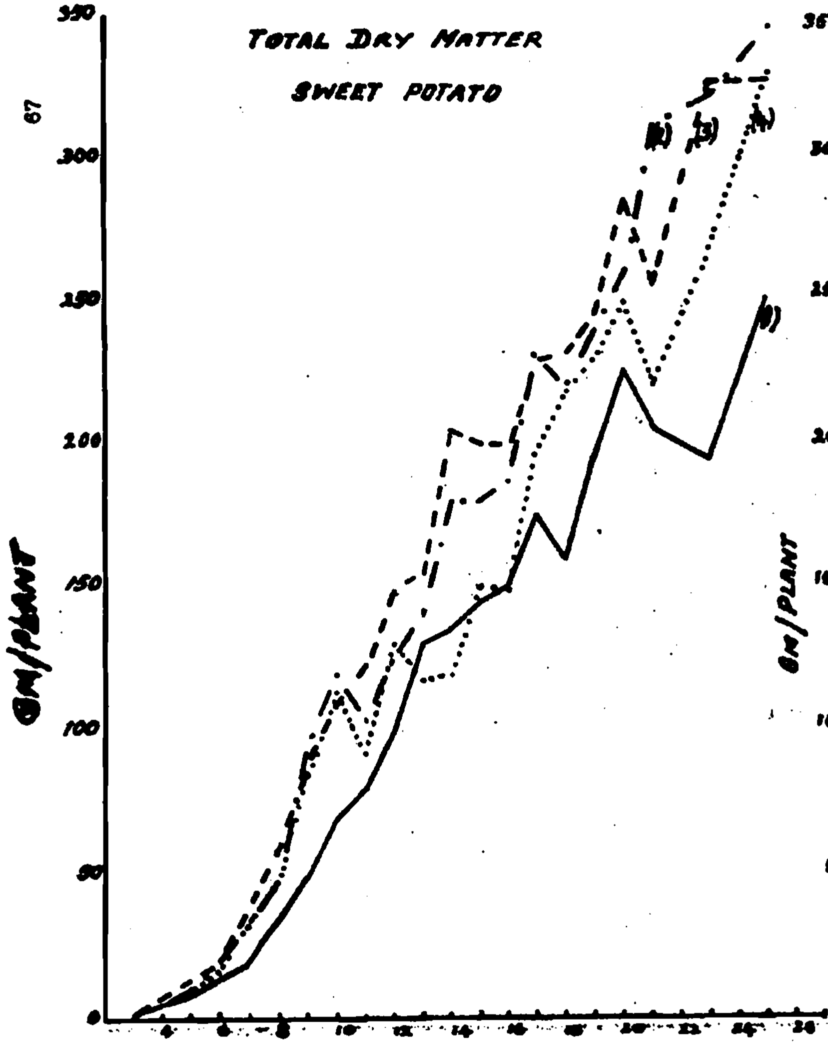
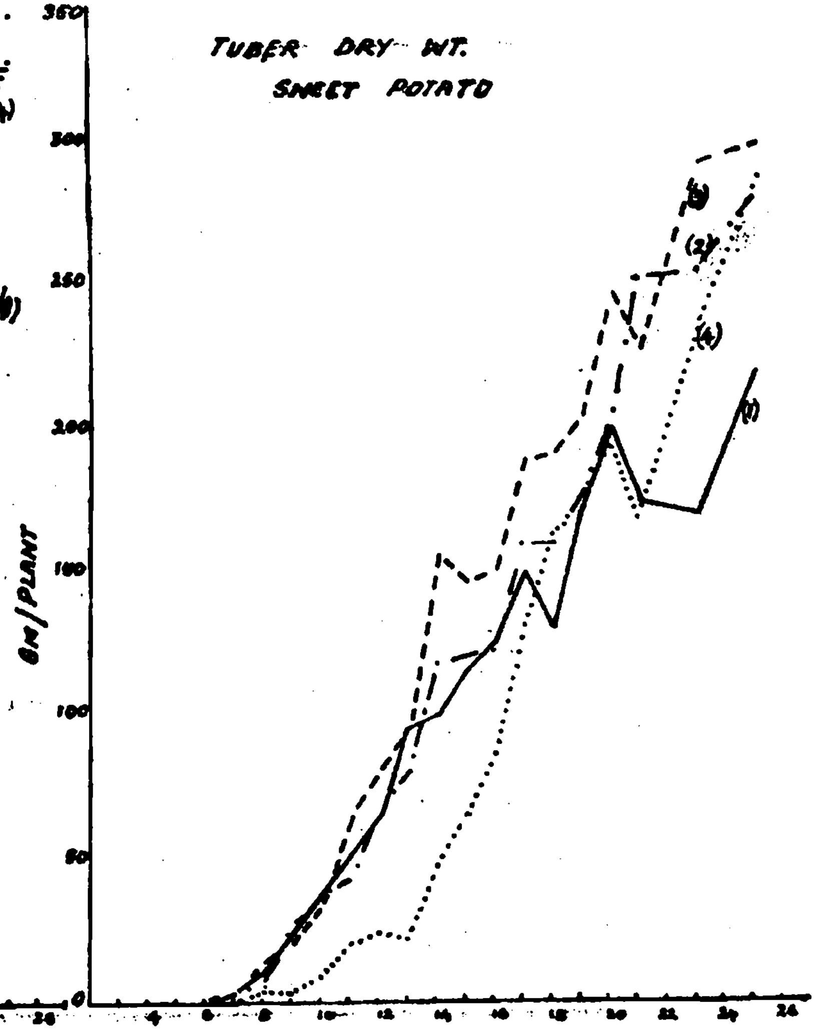
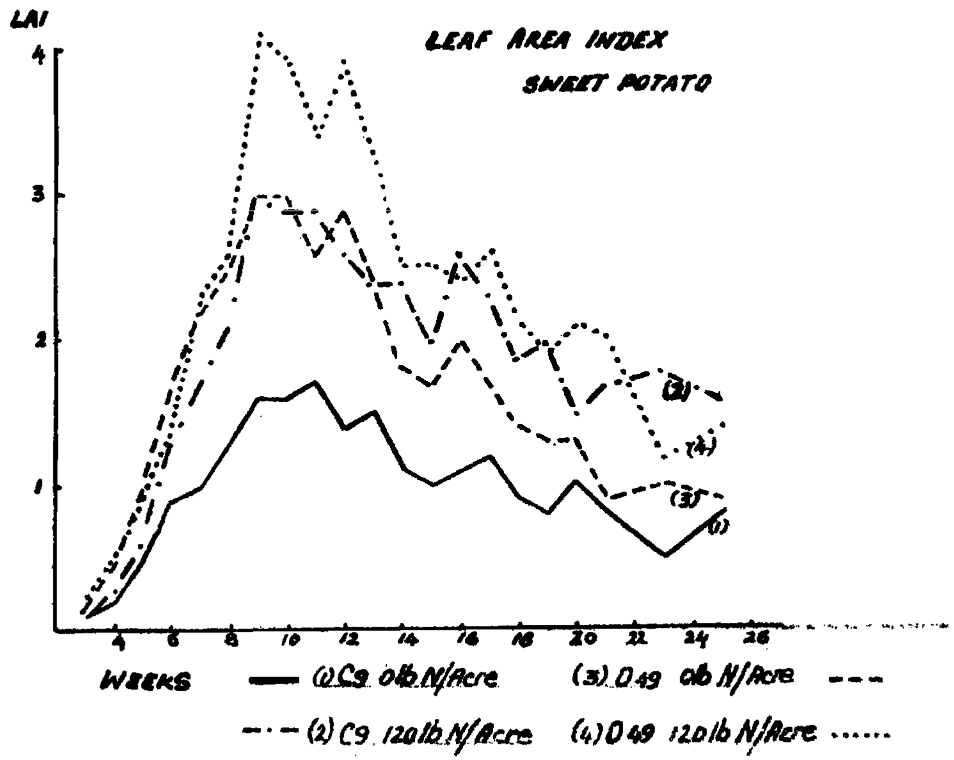


FIG. 2



WEEKS — (1) C9 0lb N/Acre (3) D49 0lb N/Acre ---
-·- (2) C9 120lb N/Acre (4) D49 120lb N/Acre ·····

FIG. 3.


LAI
4
3
2
1
LEAF AREA INDEX
SWEET POTATO
(2)
(4)
(3)
(1)
4
6
8
10
12
14
16
18
20
22
24
26
WEEKS
(1) C9 0lb N/Acre
(3) D49 0lb N/Acre
(2) C9 120lb N/Acre
(4) D49 120lb N/Acre

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, when the Leaf Area Index has fallen below maximum but this may be due to restrictions imposed on the length of the growing season by climatic conditions in Japan.

Similarly with rice low response and high response varieties (Tsunoda, 1965; Taneka, 1965) have been defined, largely depending on the inclination of the leaf surface to the vertical plane and the leaf area production at different nitrogen levels.

Gibbon (1965) in a growth analysis study at U.W.I. confirmed good response to nitrogen of the Suriname variety S.M.L. 242. Unfortunately his comparisons with Joya (a variety grown extensively in Trinidad) failed due to sever lodging of the latter under the level of nitrogen application used in his trial. These two varieties provided contrasting morphological types the S.M.L. 242 having a short stem and narrow vertical leaves, the Joya having a tall weak stem and long broad leaves suggesting mutual shading within the crop.

The cultivar differences in response to nitrogen may have significance in the breeding and selection of new varieties and this is discussed below.

DISPLAY OF FOLIAGE

Mention was made earlier of the investigations of Cowling and Chapman. A substantial increase in yield of a low yielding, high leaf area sweet potato cultivar (A138) was obtained by training the vines to climb on chicken mesh wire. An increase from 2 tons/acre to 5 tons/acre in fresh weight of tubers was obtained by this staking treatment in the absence of added nitrogen and from 1.5 to 7.3 tons with the addition to both staked and unstaked plots of 100 lb./acre calcium ammonium nitrate. The staking induced significant increases in Leaf Area Duration to which might be largely attributed the increased yield since no statistically significant differences in Net Assimilation Rate were demonstrated. In any case the substantial increase in yield due to staking in this high leaf area cultivar indicated the need for further studies on cultivars of contrasting leaf areas.

While it may not be very likely that staking in sweet potatoes will readily become a commercial practice growth analysis studies in yams (Dioscorea sp.) would be of considerable interest as this crop is grown commercially with and without staking in different areas.

TYPES OF PLANTING MATERIAL

Haynes and Williams (1966) have compared the effect of different types of planting material on final yield of tannias (*Xanthosoma sagittifolium*) and also recorded leaf area development. This comparison of the apical portion of the mother corm ('Head'), portions of the main corm with lateral buds ('Pieces') and whole cormels indicated a close correlation between Leaf Area Duration and yield. This study did not involve a complete growth analysis but the marked correlation of yield with leaf area would indicate the value of a more detailed study. Indeed this may prove a most useful crop for extensive study since the leaf area determinations are relatively simple involving only two measurements on the intact leaf. This might be carried out in ordinary field trials and if a dry weight determination is carried out at critical periods for calculation of Net Assimilation Rates a useful picture may be built up. If this is not possible then a dry weight determination at final harvest along with the leaf area measurements throughout the growth period of the crop would give an integrated value for the Net Assimilation Rate over the growth period. Thomas (1965) defines Leaf Area Duration as the 'photosynthetic potential of a plant community' - the integral of leaf area over the vegetative period, the Net Assimilation Rate for this period being the biological yield divided by this integrated leaf area.

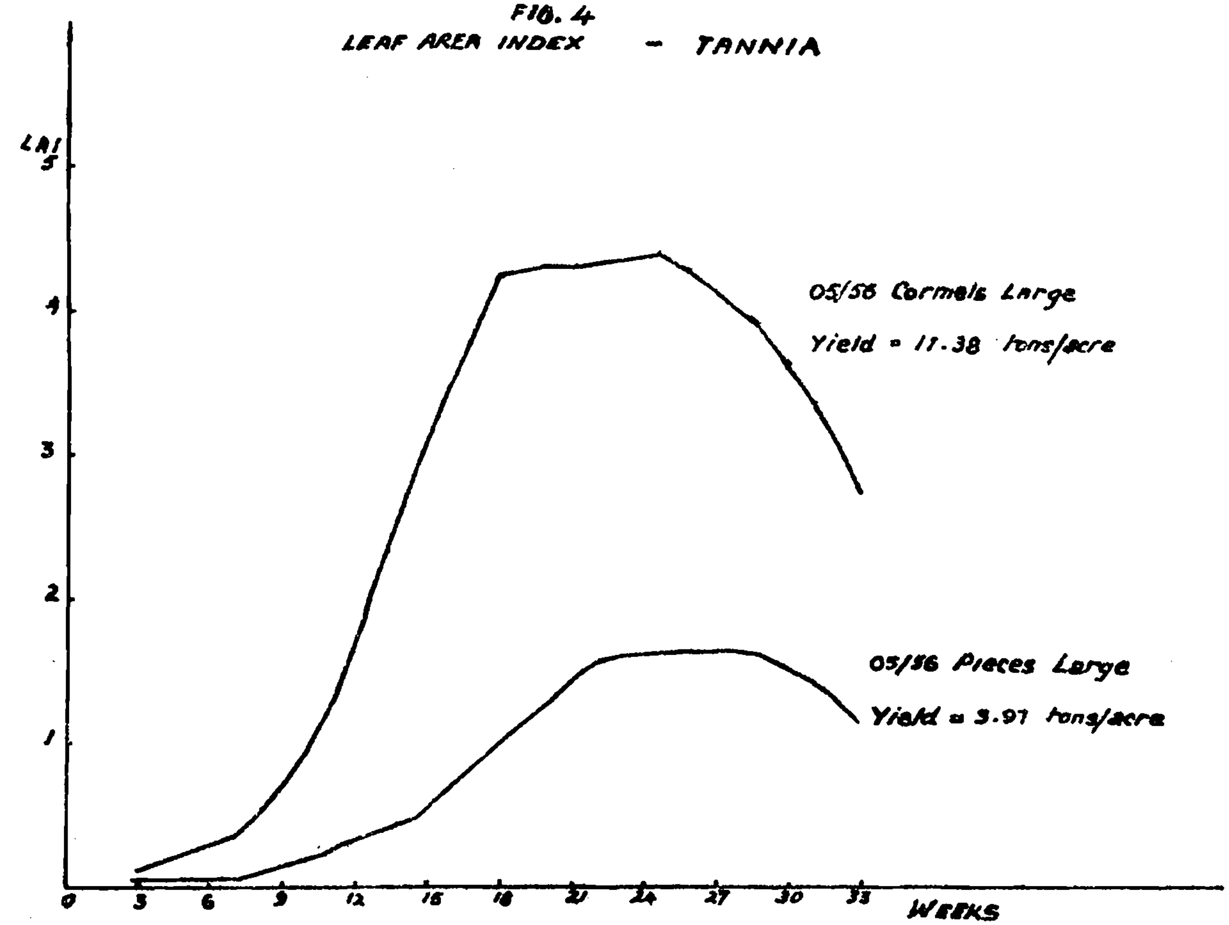
BREEDING AND SELECTION OF NEW VARIETIES

In the previous section the value of growth analysis to a fuller understanding of agronomic practice was illustrated by reference to a few specific examples. In this section the value of the information yielded by growth analysis to persons engaged in breeding and on selection of new varieties will be discussed in terms of Leaf Area and Net Assimilation Rate.

Leaf Area

Perhaps the most obvious aspect of this will be associated with the agronomic effects on sweet potato referred to earlier. Clearly if the Plant Breeder is assesing his varieties by a final harvest at a particular time in the crop growth then the effect of nitrogen and time of harvest, referred to earlier in consideration of contrasting leaf area cultivars, will greatly influence the comparative rating of the varieties. However a much more fundamental effect needs to be considered. Should the Plant Breeder breed for, and select for, particular leaf area

FIG. 4
LEAF AREA INDEX - TANNIA



characteristics and how would this be related to nitrogen response? In rice the low yields in tropical areas and lack of response to nitrogen has been largely attributed to varietal characteristics associated with leaf area and leaf disposition (Tanoka, 1965; Murata, 1965; Tsuroda, 1965). Since in these areas the level of fertility has been low varieties of rice have been selected which are able to produce a maximum leaf area with a low nitrogen supply whereas in temperate or subtropical areas the breeding and selection of varieties has been for a more efficient plant in terms of photosynthesis per unit leaf area which responds to nitrogen by increasing the leaf area to a limit that does not introduce mutual shading and so reduce efficiency.

This kind of effect may be relatively clear cut and is indeed being taken account of by Plant Breeders in rice though perhaps less so in other crops. It is often associated which characteristics that are definable in terms of morphological characters. A start has been made in designating sweet potato cultivars by growth analysis studies involving leaf area measurements and this will be extended to other tropical crops and indeed to temperate crops such as Solanum potato being grown under tropical conditions.

The next stage in the leaf area studies would be a study of those physiological processes which go to influence leaf area, for example effects on size of individual leaves, rate of leaf production, branching or tillering and so on.

But perhaps the more obvious involvement of the study of basic physiological processes in plant breeding will come under consideration of Net Assimilation Rate.

Net Assimilation Rate

The balance between dry matter produced in photosynthesis and that utilized in respiration expressed (usually) per unit area of leaf fives a measure of the efficiency of the crop in producing biological yield. While Net Assimilation Rates have been shown to vary surprising little between different species and in different environments (Thomas, 1965), there is now accumulated sufficient evidence on variations in Net Assimilation Rates to indicate that it may be a very important factor in crop yield in the field (Thomas, 1965).

Apart from mutual shading of leaves within a canopy which will affect efficiency of photosynthesis clearly the rates of photosynthesis and of respiration may markedly affect the system. This is particularly important when temperature affects are being considered since frequently rates of respiration are affected to a much greater extent by temperature changes, than rates of photosynthesis.

Murata (1965) has found varietal differences in rice in photosynthetic activity on a leaf area basis (under normal atmospheric carbon dioxide concentration and saturating light intensity). He also obtained an increase in activity due to nitrogen application but observed that this response varied with the different varieties. Differences in rates of respiration were also reffered to. Tsuno and Fujise (1965) have also shown that potassium levels will affect the efficiency of photosynthesis in sweet potato.

It is sometimes suggested that greater rates of respiration in the higher night temperatures in the tropics impose a restriction in dry matter accumulation by affecting the photosynthetic-respiration balance. Yet there are few critical studies in the tropics on rates of these processes in different varieties and as yet no relationship to breeding programmes.

It is apparent then that the crop physiologist, the plant physiologist as well as the agronomist must supply more detailed information on leaf area and its development and on the efficiency of photosynthesis for the plant breeder to include in the aims and objectives of his breeding programmes.

CONCLUSIONS AND FUTURE WORK

Growth analysis studies whether these be detailed and concentrated, as would be carried out in weekly harvestings with leaf area and dry matter determinations, or the supplementary information supplied, perhaps on a wider scale, by leaf area records on a crp such as tannia coupled with a final dry matter determination, undoubtedly open the door to a better understanding of which physiological processes influence crop yield. More detailed greenhouse studies on individual plants or on individual parts of the plant, must follow and then an assessment must be made of the inheritability of such characters. Such studies are being initiated at U.W.I. with sweet potato.

It is hoped that agronomists at experiment stations in the various Caribbean Islands will be interested in adding to the field growth analysis data. The workers in this field in the Faculty of Agriculture, U.W.I., are anxious to cooperate in such studies wherever possible.

Thomas (1965) has pointed out that by and large Net Assimilation Rates and the Crop Growth Rates that have been recorded are higher in tropical areas, the higher light intensity presumably making up for the shorter days.

Certainly, with manipulation of water supply, the growing seasons are longer.

With a better understanding of how individual physiological processes affect plant yield, and of how these characters are inherited, a rational and fundamental basis for selection of varieties in breeding programmes may be achieved. In addition a better manipulation of the crop environment will allow advantage to be taken of the larger photosynthetic potential in tropical areas.

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EVALUATION OF BLACK POLYETHYLENE MULCH PAPER FOR TOMATO PRODUCTION IN PUERTO RICO

H. Irizarry, H. Azzam and R. Woodbury

An experiment was conducted in February, 1959 to evaluate the economic use of black polyethylene mulch paper for tomato production in Puerto Rico.

Four treatments and five varieties were used in a randomized block design with 4 replications. The combined treatments used were described as follows:

1. Mulching, No staking, No weeding
2. No mulching, No staking, Weeding
3. No mulching, No staking, No weeding
4. No mulching, Staking, Weeding

The varieties included in this trial were Rutgers, Platillo, Plamar, and local breeding lines P. R. 123 and P. R. 126.