# THE USE OF ROOTED LEAVES AND GRAFTED PLANTS FOR THE STUDY OF CARBOHYDRATE METABOLISM IN *SWEET POTATO*

— *by* —

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## *Introduction*

In a review of some of the physiological determinants of tuber yield in different sweet potato varieties, (Wilson 1967) it became evident that the direction of photosynthate to tubers was perhaps more important as a determinant of tuber yield than the total amount of dry matter produced by the plant. The direction of photosynthate to tubers, (organs of perennation) was considered to be an attribute of plant morphogenesis, as opposed to the photosynthetic attributes of the plant which were more related to total dry matter production. Final tuber yield was considered to be the end result of a series of morphogenetic changes associated with the direction of photosynthate to sinks connected with leaf production, leaf expansion, lateral bud development, decreasing specific leaf area and, at a certain critical point in the sweet potato life cycle, the tuber sink. The final balance established between the tuber sink and the several alternative leaf sinks at harvest time, is therefore, the ultimate determinant of yield in sweet potato species.

Three aspects of carbohydrate metabolism are involved in effecting these morphogenetic changes.

(a) carbohydrate production

(b) carbohydrate transport

(c) carbohydrate immobilization in tuber tissue, thus creating a sink capable of accepting more transport carbohydrates

Carbohydrate transport and carbohydrate immobilisation in the tuber sink, are considered to be more important factors affecting tuber yield than carbohydrate production per se and these factors are now further examined, using plant models, conveniently referred to here as photomodels.

## *Materials and Methods*

Definition of Phytomodels

A phytomodel, is here defined as a modified plant or plant organ, which has both a root system and a photosynthetic surface and is therefore an independant autotrophic, metabolic unit, capable of integrated growth by cell division cell expansion, and cell differentiation.

The design and use of phytomodels e.g. rooted leaves, petioles and laminae and grafted plants, provide simple and easy to handle mechanisms for the study of physiological pathological and biochemical problems. In such phytomodels, internal and external factors in the plant environment can be varied independently, on a scale not possible in conventional studies using intact plants. Phytomodels

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are also considered to have a wider application than tissue cultures, which are neither independent nor autotrophic metabolic units, nor do tissue cultures approximate any morphogenetic condition in the intact plant. Phytomodels are also preferred to systems using leaf discs or tuber discs, which are of limited viability and uncertain metabolic significance.

The use of what is here defined as a phytomodel is not new and such systems have been previously used in physiological studies. Thus Thorne (1962) described the use of sugar beet/spinach beet grafts for examination of factors affecting yield differences between these two species. Humphries and Thorne (1961), (1963), (1964) also used rooted dwarf French bean leaves for the assessment of the size of the root sink on leaf photosynthesis.

Attention is drawn, however, to the wider application of such phytomodels, provided that they can be calibrated against biochemical and physiological changes known to occur in the intact plant. Preliminary experiments here described are concerned with the calibration of rooted leaf and grafted plant phytomodels of several sweet potato varieties, against changes in dry matter content associated with carbohydrate transport and immobilization, known to occur in the intact sweet potato plant. Similar phytomodels are also being used in this laboratory for the study of physiological and biochemical aspects of intervarietal susceptibility to the pathogenic fungus, *Ceratocystis fimbriata,* responsible for the *Ceratostomella* wilt disease in cacao.

*Rooting of Sweet Potato Leaves*

Sweet potato leaves can be rooted by immersing their petioles in moist sand or in water, and keeping the leaves in a humid atmosphere. Rooting takes place in from five to ten days. Growth substances e.g. indole acetic acid (IAA), indole butyric acid (IBA) and naphthyl — acetic acid (NAA) all increase the rapidity with which root initiation takes place, and the number of root initials formed. IAA, however, tends to increase the length of growing root whilst IBA and NAA tend to induce the production of short thick roots. Rooting also varies with the age and variety of the leaf used. Mature leaves root more easily than young leaves. Leaves from pigmented varieties of sweet potato also tend to root more easily than leaves from non pigmented varieties.

In varieties in which rooting takes place with difficulty, rooting is facilitated by allowing stem cuttings with leaves attached, to stand in a humid propagation bin for two to three days. After this period of incubation, lateral buds and roots develop at each node, and root initials may already be formed at the base of leaf petioles. Such leaves, with or without root initials, root easily when severed and placed in water. In the present experiments, mature sweet potato leaves were rooted without auxin treatment, either by simply dipping the roots in water in a suitable container (100 ml conical flask) or by so doing after a preliminary incubation period in a propagation bin as described above. Leaves from the following sweet potato varieties collected from Mr. B. Williams of the Faculty of Agriculture, University of the West Indies, (St. Augustine) have been successfully rooted. 049; C9; C104; A138; F2; 01/59; R38; 14/60; A26/16.

*Grafting of Sweet Potato Cuttings*

Effective graft unions of sweet potato cuttings from different varieties can

be made by cleft grafting of cuttings from the respective varieties. (Wilson and Dawlet 1967). Cuttings used for grafting, should be about six to ten inches in length including at least three nodes and should be of similar diameters. Once joined together by a typical cleft graft and secured with polythene grafting tape, the stem cutting needed as the root stock is defoliated and placed in a sand/ coconut fibre dust rooting medium, in a propagating bin.

Rooting of the root stock, healing of the graft union and development of the lateral buds on the scion, all take place within seven days. Removal of three quarters of the laminae of leaves on the scion end of the graft, facilitates the growth of the grafted cuttings.

Satisfactory results can also be obtained by placing graft unions to root in a suitable container of water, under shaded conditions in the greenhouse. Suitable graft unions can be transferred directly to experimental containers in the greenhouse for further growth and study. The sweet potato varieties 049, R38 and C9 have been successfully grafted by this method in all possible combinations.

*Rooted leaves*

Wilson (1967) pointed out that one of the factors associated with reduced yield in staked sweet potato plants (var. A138) in the absence of applied nitrogen fertiliser (Chapman and Cowling 1956) was a relative decrease in specific leaf area in the 7th—9th weeks after planting. This decrease in specific leaf area was coincident with an increase in specific leaf area in plants supplied with nitrogen fertilizer. Increase in specific leaf area, in N-fertilised plants took place immediately prior to a critical period of N-stimulated increase in tuber dry weight, 9th—11th week). Decrease in specific leaf area in the absence of applied nitrogen fertiliser was interpreted to mean that carbohydrates were stored in the alternative leaf sink because of the restriction in the capacity of tubers to accept translocated carbohydrates, during the 7th—9th weeks of growth. Carbohydrates have been shown to accumulate in the leaves of nitrogen deficient sweet potato plants. (Wilson 1964). Accordingly, the rooted leaf phytomodel was examined in order to find out whether a similar alternative accumulation of carbohydrates in the leaf could be induced, under conditions of a restricted nitrogen supply. Such calibration of a process known to occur in the intact plant is thought to be a necessary prerequisite for investigation of the process using a phytomodel.

*Experimental*

Rooted sweet potato leaves (var. C9) were grown in one half strength culture solutions (Hewitt 1965) for one week after rooting and then transferred to solutions containing plus nitrogen and minus nitrogen nutrient treatments. After selected intervals of growth, rooted leaves were completely destarched by being placed in a dark cupboard overnight. Destarched leaves were then tested for starch, exposed to sunlight and the time taken for starch to accumulate in leaves measured. Starch accumulation was estimated by first extracting chlorophyll from leaf discs (0.5 cm diameter) taken from three rooted leaves per treatment, and testing these discs for starch with iodine in potassium iodide. Colours ranging in intensity from yellow to brown to black were developed, according to the amount of starch present in leaf discs. The time taken to develop a black colour was recorded as the time necessary for maximum accumulation of starch in leaves.

*Results*

Relevant results are given in Table 1 below.

*Table I.*
*Starch Accumulation in Destarched Sweet Potato Rooted Leaves (var. C9)*

| Treatment | Time to Max. Starch Accumulation | | Root D. Wt. at 3 weeks | Specific leaf area at 3 weeks | % Total N in lamina |
|---|---|---|---|---|---|
| | 1 wk growth | 3 wks growth | | | |
| + N Discs | 12 mins. | 15 mins. | 0.75 gm. | 7.9 | 3.25% |
| − N Discs | 5 mins. | 0 mins. | 0.34 gm. | 5.6 | 2.4% |

The data (Table 1) indicated the rate of starch accumulation was more than twice as fast in nitrogen deficient leaves compared with nitrogen sufficient leaves after one week of growth. At this time, there was no observable difference in the appearance of leaves from different treatments, and the recorded root dry weights were also similar (+N-0.45 gm: - N-0.40 gm).

After three weeks of growth, leaves growing in minus nitrogen solutions could not be destarched even after seventy-two hours in the dark. These leaves had apparently attained a condition of permanent starch saturation, which was associated with cessation of the growth of their roots, the only major carbohydrate sink. At the end of the three weeks of growth, laminae of the minus nitrogen rooted leaves showed only mild symptoms of nitrogen deficiency (intervenal chlorosis). The dry weight of roots from these plants and the percentage nitrogen in their laminae were however reduced compared with leaves grown in plus nitrogen solutions. Petiole slices also gave a more positive test for starch than similar slices from plus nitrogen leaves.

Changes in carbohydrate distribution in the absence of nitrogen supply also resulted in a 40% decrease in the specific leaf area of minus nitrogen rooted leaves compared with plus nitrogen leaves.

Effects of nitrogen deficiency and deficiences of other plant nutrients on the carbohydrate saturation point of rooted leaves are being examined in eight other varieties of sweet potato. Preliminary results indicate that a pattern of carbohydrate saturation similar to that obtained with nitrogen deficiency, occurs in sulphur deficient rooted leaves. With calcium deficiency no carbohydrate accumulation could be demonstrated in petiole slices. The carbohydrate saturation point was not attained in iron deficient rooted leaves, nor did even mild symptoms or iron deficiency develop in these leaves.

*Discussion*

Carbohydrate accumulation took place in the laminae of nitrogen deficient rooted leaves and was accompanied by decreases in specific leaf area. Decreases in specific leaf area and leaf area ratio have been found to be associated with early stimulation in sweet potato tuber bulking due to limited nitrogen supply (Wilson 1964) and with decreases in final yield in staked sweet potato plants in the absence of applied nitrogen fertiliser.

Starch accumulation has also been found to take place in the leaves of nitrogen deficient sweet potato plants grown in sand culture by the author. The rooted leaf provides a simple mechanism for examining the relative distribution of photosynthate between the root sink and the alternative leaf sink as a function of root growth and nutrient supply. The absence of accepted sources of auxin supply e.g. stem apex and lateral buds, from the rooted leaf phytomodel, allows for the study of effects of various levels of externally applied auxins on the processes involved in carbohydrate mobilization and accumulation.

*Grafted Sweet Potato Plants*

It was suggested (Wilson 1967) that perhaps the most important factor affecting intervarietal differences in sweet potato yield was the inherent tendency of different varieties to tuberize. A similar conclusion was also reached by Ivins and Bremner (1965) for Solanum potatoes. The rate of tuber bulking associated with this basic tendency, however, was thought by the formed author to be a function of the capacity of tubers to accept, metabolise and store carbohydrates, at different stages in their growth cycle. This interpretation of tuber bulking pre- supposed that the factors governing the rate of this process were morphogenetic rather than photosynthetic, and evidence in favour of this interpretation was given (Wilson 1967).

The emphasis given to considerations of net assimilation rates leaf area indices and leaf area duration, by Acland (1963), Cowling (1964) and Chapman and Cowling (1965) and to total leaf area as related to nitrogen response Tsunoda (1965) implied that these authors considered the total amount of photosynthate produced by the plant to be the more important determinant of sweet potato tuber yield. References to effects of mutual shading on tuber yield also embodied the same implication.

Tsuno and Fujise (1965) classified sweet potato varieties according to photosynthetic activity into:—

(a) leaf area types, with high leaf areas and low photosynthetic rates per unit leaf area, and

(b) net assimilation types, with low leaf areas and high photosynthetic rates per unit leaf area.

These authors further demonstrated that there existed in these two types, an apparently compensating photosynthetic mechanism. This mechanism resulted in similar rates of photosynthesis per plant, midway in the growth cycle of the types examined. The relevant question is whether the rate of photosynthesis was relatively increased in the low leaf area type due to increased tuber bulking, a process shown to take place by Tsuno and Fujise, or was photosynthesis relatively reduced by mutual shading in the high leaf area type. The former effect is considered to be morphogenetic and the latter, photosynthetic.

It should be mentioned at this point, that the inverse relationship between leaf area index and net assimilation rate shown to exist in sugar beet and kale by Watson (1958) could be demonstrated neither for a wide range of sweet potato varieties of greatly differing leaf area indicies (Acland 1963) nor for a single variety of sweet potato under staked and unstaked conditions of growth (Chapman and Cowling 1965).

It was in order to attempt a separation of the above mentioned morphogenetic effects from photosynthetic effects as the primary determinent of sweet potato yield, that grafted sweet potato phytomodels were designed.

Accordingly, grafts were made of all possible combinations of root stocks and scions between sweet potato varieties of:

(a) different tendencies to tuberize

(b) different leaf areas

(c) different leaf shapes, which allowed for variations in the amount of mutual shading associated with leaf development. The photosynthetic effect is also being examined by subjecting the grafted plants to different light regimes.

The sweet potato varieties initially used were:—

(i) 049 — (high yielding - high leaf area - entire leaf margin).
(ii) C9 — (high yielding - low leaf area - entire leaf margin).
(iii) R38 — (low yielding - low leaf area - deeply lobed leaf margin).

*Experimental*

Plants of the three varieties were joined by cleft grafts in the following combinations, where the first mentioned variety is the scion and the second the root stock.

| | | |
|---|---|---|
| 049/R38 | R38/049 | C9/R38 |
| 049/C9 | R38/C9 | C9/049 |
| 049/049 | R38/R38 | C9/C9 |

In addition to these grafted phytomodels, intact plants of the three varieties were included in the experiment and all plants were subjected to two light regimes:—

(a) full sunlight

(b) 60% sunlight achieved by shading with saran netting.

Three plants per treatment were grown in four-gallon containers containing soil in the greenhouse. No fertiliser treatments were applied to the plants.

*Results*

Preliminary results reported here are concerned mainly with the calibration of the growth pattern of grafted sweet potato phytomodels against intact plants. Effects of light intensity and graft union on leaf number and lateral shoot production after two months of growth are given in Table II.

The results (Table II) indicated that intact plants produced leaves at a faster rate than grafted plants, due no doubt to growth restriction associated with the healing of the graft union. Grafts containing similar root stocks and scions also consistently produced leaves at a more rapid rate than grafts of root stocks and scions from different varieties.

Grafts containing F38 scions tended to produce more leaves than those containing 049 and C9 scions respectively. This trend was similar to that which obtained in intact plants.

*Table II. Effects of light intensity and graft union on leaf number and lateral shoot production in several sweet potato phytomodels*

| Graft | Leaf number | | No. of Lateral Shoots | |
|---|---|---|---|---|
| | Full Sunlight | 60% Sunlight | Full Sunlight | 60% Sunlight |
| 049/R38 | 74 | 78 | 3.6 | 5.0 |
| 049/C9 | 80 | 73 | 4.5 | 4.5 |
| 049/049 | 96 | 112 | 3.0 | 5.2 |
| 049 (intact plants) | 116 | 121 | 3.3 | 4.1 |
| C9/R38 | 51 | 61 | 4.5 | 5.0 |
| C9/049 | 56 | 76 | 4.2 | 5.9 |
| C9/C9 | 99 | 98 | 6.5 | 5.5 |
| C9 (intact plants) | 108 | 111 | 6.1 | 6.0 |
| R38/049 | 81 | 59 | 6.5 | 5.5 |
| R38/C9 | 92 | 65 | 5.5 | 5.1 |
| R38/R38 | 122 | 94 | 6.2 | 7.5 |
| R38 (intact plants) | 131 | 124 | 6.3 | 6.1 |

Effects of light intensity were variable, but there seemed to be an increased production of leaves in full sunlight in grafts with R38 scions, which was greater than a similar effect observed in intact R38 plants.

On the contrary, full sunlight seemed to decrease the number of leaves produced in plants with C9 tops, particularly those of C9/R38 and C9/049 phytomodels. This effect was not observed in intact C9 plants. Leaf number was not greatly affected by light intensity in models with 049 scions.

Effects of graft union and light intensity on lateral shoot development were variable, and did not show any definite trend, except perhaps than in plants with 049 tops, lateral shoot production took place more slowly than in other phytomodels and intact plants.

Results of tuber yield after eight weeks of growth (Table III) indicated that yield (tuber fresh weight) was in all cases reduced, and tuberization often completely suppressed under shade conditions. These yield reduction were associated with increases in specific leaf area (average of ten mature leaves) at the lower light intensity. In models with 049 scions, tuber yields was considerably reduced compared with intact plants. Tuber yield of 049/049 models was double that 049/C9 models. Tuberization was suppressed in 049/R38 models even infull sunlight. The increased tendency to tuberize showed by the 049 rootstock was further demonstrated by the increased yield of the C9/049 model over both the C9/C9 model and intact plants of C9. It was perhaps significant that leaf production in the C9/049 phytomodel was considerably reduced com-

pared with the C9/C9 model and C9 intact plants. Yields of R38/049 models were also increased compared with R38/R38 models and intact plants of R38. C9 was not as effective in increasing tuber yield in reciprocal grafts as was 049. Results for the comparison of final yields with leaf area ratio and specific leaf area, based on total leaf area measurements are not yet available.

*Table III. Effects of light intensity and graft union on leaf area/leaf weight ratios and tuber yield after eight weeks of growth in several sweet potato phytomodels.*

| Graft | Tuber F. Wt. at 8 wks | | Leaf Area/Leaf D. Wt. of 10 mature leaves | |
|---|---|---|---|---|
| | Full Sunlight | 60% Sunlight | Full Sunlight | 60% Sunlight |
| 049/R38 | — | — | 6.7 | 10.5 |
| 049/C9 | 8 | — | 6.5 | 10.7 |
| 049/049 | 17 | 16 | 4.5 | 6.3 |
| 049 (intact plants) | 105 | 41 | 6.6 | 8.4 |
| C9/R38 | — | — | 13.2 | 14.1 |
| C9/049 | 132 | 24 | 5.2 | 8.3 |
| C9/C9 | 80 | — | 10.0 | 6.6 |
| C9 (intact plants) | 98 | 12 | 9.6 | 12.2 |
| R38/049 | 47 | — | 11.1 | 12.2 |
| R38/C9 | — | — | 11.1 | 14.1 |
| R38/R38 | 13 | — | 8.8 | 16.6 |
| R38 (intact plants) | 27 | — | 10.4 | 14.5 |

*Discussion*

It would appear from this preliminary experiment that tuber development in the sweet potato varieties examined was a function of their tendencies to tuberize. Further, this tendency was associated with characteristics of the sweet potato root stock and could be transferred to another variety by reciprocal grafting. The calibration of reciprocal graft phytomodels against intact plants, indicated that leaf development was somewhat affected by the grafting process but that this effect did not preclude the development of what appeared to be real differences in the tendencies of different varieties to tuberize, in models examined.

*Summary and Future Work*

Two systems conveniently called phytomodels, rooted leaves and reciprocal grafts of different sweet potato varieties have been described and their use in the study of carbohydrate mobilization and carbohydrate storage, in the sweet potato discussed.

Preliminary experiments on the calibration of the phytomodels against growth changes known to occur in intact sweet potato plants have been described.

Such calibration is an important pre-requisite in the use of models for the study of factors affecting tuber development. This is so, because tuber development itself, is interpreted as the expression of a series of morphogenetic changes associated with the direction of photosynthate to the tuber sink. Since these changes are themselves not completely understood, the precise nature of the process examined with a phytomodel must be defined and its significance in relation to the intact plant established.

Rooted leaves of different varieties of sweet potato are being used for studying the distribution of photosynthate between the root sink and alternative leaf sink. Effects of nitrogen nutrition on this distribution are being particularly examined because of the variable yield responses of sweet potato varieties to nitrogen fertilization.

Reciprocal grafts are being used for examining intervarietal differences in the capacity for tuberization in the sweet potato, because previous efforts to relate tuber yield to foliage characteristics have met with limited success. Indications are that intervarietal differences in tuber yield are related to tuber growth.

The ultimate aim of this work is to find out the factors of primary importance in tuber growth. On this subject, attention is drawn to the fact that tuber cells must first be formed before they can act as a tuber sink. Expansion of these cells once formed is also a pre-requisite for the increase in size of the tuber sink with development. Factors affecting tuber cell division and cell expansion may be independent of those affecting carbohydrate production, but they certainly are important as determinants of the size of the tuber sink.

Effects of high levels of nitrogen supply (Wilson 1964) and observations on the effect of low light intensity on the restriction of tuber growth, suggested that factors affecting tuber growth were related to the morphogenetic condition of the sweet potato plant sensu Evens and Hughes (1961) and Whitehead and Myerscough (1962). The direct effect of exposure to light on the restriction of tuber development (Tsuno and Fujise 1965) also suggested that a light dependent mechanism in the tubers themselves is also a factor affecting tuber growth.

A number of regulatory functions have been ascribed to indole acetic acid in plants. Recent work suggested that auxins might also be involved in tuber growth. Thus, high levels of entodenous hormones have been shown to mediate in nitrogen increased shoot/root ratios by Wilkinson and Ohlrogge (1964). Strong evidence suggesting that the breaking of lateral bud dormancy was coincident with auxin release by the growing bud has also been supplied by Turner and Bidwell (1965). Wilson (1964) showed that nitrogen induced lateral shoot development was inversely related to tuber growth, in sweet potato plants grown in sand culture. Auxins released by lateral bud development might therefore have resulted in inhibitory levels of auxin in sweet potato roots. Rapid early growth of sweet potato tubers at low levels of nitrogen supply, in the same experiments, might simply be the reverse of this process.

Indole acetic acid has also recently been shown to control cellulase activity in the apices of etiolated pea seedlings by Fan Der-Fong and Maclachlan (1966) and these authors suggested that cellulase action played an essential role in a variety of growth processes, particularly lateral cell expansion. On the

other hand, Loewnberg (1965) found that citric acid promoted IAA destruction in tobacco callus tissue, with a concommitant inhibition of bud formation. Destruction of IAA was apparently mediated by stimulation of IAA oxidase activity. Citric acid has also been found to induce loss of rigidity in Solanum potato tuber slices, associated with depression of oxygen uptake over the period when the tissue became flaccid. (Somers 1965).

One of the prerequisites for cell expansion is cell turgidity. It is suggested, therefore, that endogenous levels of auxins and mechanisms controlling these levels, might be responsible for intervarietal differences in tendencies to tuberize in sweet potato. Accordingly, it is proposed to use phytomodels to examine the effects of citric acid and other oganic acids on cellulase and IAA oxidase activity as related to cell expansion in root cells of rooted leaves and tuber cells of grafted sweet potato plants. Precalibration of these phytomodels against processes associated with intervarietal differences in photosynthate distribution in the sweet potato, could lead to valuable information on the exact nature of the morphogenetic changes associated with tuber development.

Apart from this fundamental objective, grafted sweet potato phytomodels could provide an immediate answer to the plant breeder, with respect to the capacity for tuberization of new varieties. Such a use for these phytomodels is suggested by the increased tuberization of C9/049 and R38/049 reciprocal grafts over C9 and R38 intact plants. The capacity for increasing tuberization in models with C9 and R38 scions could be taken as a measure of the tendency for tuberization of a particular variety.

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