The Potential for Producing Root and Tuber Crops from Seed

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ABSTRACT

The physiological basis of yield of root and tuber crops will be discussed, based on a simple model for the cultivated potato Solanum tuberosum, from which a strategy for maximizing yield can be developed. The possible effects on the strategy of substituting true seed for normal methods of vegetative propagation will be discused.

The physiological basis of yield with particular reference to S. tuberosum

The basic principle of crop production is the conversion of light energy into chemical energy in the process of photosynthesis. For this to take place, the raw materials of water, carbon-dioxide and about 13 mineral elements are needed, and a green crop canopy able to intercept radiation, part of which is fixed into chemical energy. Of these ingredients, the natural supply of nutrients is rarely adequate, but can be supplemented to make them unlimiting, so too can the supply of water, however, little can be done to increase the supply of carbon-dioxide. This leaves the utilization of light, which unless intercepted by the crop canopy, cannot be converted into chemical energy.

Monteith (1977) was able to show that in Britain, the total dry matter yields of crops, as disparate as barley, sugar beet, potatoes and apples, were closely and linearly related to the total amount of radiation intercepted by these crops. The efficiency with which light was converted into dry matter was approximately 1.4 g per MJ of intercepted radiation. Total dry matter yield is therefore a function of the total amount of radiation intercepted and the efficiency with which it is converted into dry matter. For economic yield, the analysis needs to be extended into the way dry matter is distributed between the various plant parts.

The first applications of this type of yield analysis on the potato crop was made by Scott and Wilcockson (1978), followed by a comprehensive review of this analytical approach, with its implications for growers, breeders and the potato industry, by Allen and Scott (1980). The relationship using potatoes and sugar beets, between total dry matter yield and the total amount of radiation intercepted by crops over the growing season, was report by Scott and Allen (1978). Both crops show exactly the same relationship between intercepted radiation and yield, fixing radiation with an efficiency of about 1.3 g dry matter per MJ intercepted radiation.

It would seem that, at least under temperate conditions, the major yield determining factor is the total quantity of radiation intercepted by crop canopies, and that the only major factor likely to affect the efficiency of the conversion is water stress. There is some evidence from unpublished data of Tostevin, referred to by Harris (1980), that efficiency may decline with the age of the crop, but the weight of evidence suggests that the conversion efficiency remains roughly the same over the length of the growing season. It is well known that leaf age affects the efficiency of photosynthesis (Leopold and Kriedemann, 1975), but the potato crop is an indeterminate crop and presumably whether or not efficiency declines with age will depend on the capacity of the crop to produce new leaves and therefore probably upon the average age of the leaves forming the crop canopy, although there has been little or no work on this aspect of growth in the potato crop.

It is also known that efficiency of conversion of light by individual leaves (Leopold and Kriedemann, 1975) is greatest at relatively low light intensities, but that for a full crop canopy efficiency does not decline until fairly high intensities owing to the geometrical arrangement of leaves. This will assume greater significance in tropical and sub-tropical latitudes as the intensity of radiation increases.

With regard to distribution of dry matter within the crop, the extreme plasticity of the crop has been ably demonstrated by Steward et al (1981) in response to changes in temperature and daylength. However, for the normal range of cultivars grown in the field under particular environments such plasticity is unlikely to be encountered. Allen and Scott (1980) were able to show that over the normal range of treatments likely to be given to potato crops in Britain, variation in the distribution of dry matter between tubers and the rest of the plant was likely to be small.

It would follow from the preceding comments upon the relationship between total dry matter yield and intercepted radiation and upon the distribution of dry matter, that there should be a close relationship between tuber dry matter yield and intercepted radiation. This is confirmed by data from Scott and Wilcockson (1978) and from a recent experiment at Reading (Blanco White, unpublished).

Based on this analysis it is possible to define a strategy for maximizing the yield of tubers grown in temperate conditions; this is simply to maximize the amount of radiation intercepted by the potato crop, consistent with economic constraints. This resolves itself into obtaining a leaf area index capable of intercepting most of the incident radiation as rapidly as possible and maintaining this for as long as possible or desirable. A leaf area index of 3 to 4 would seem adequate to intercept most of the incident radiation.

The "tools" available to the grower to implement the strategy can be broadly classified into three groups:

(a) selection of genotype

(b) manipulation of plants
e.g. selection of tuber size, preplanting tuber treatments such as sprouting, selection of plant density and spatial arrangement.

(c) manipulation of the crop environment
e.g. additional supplies of plant nutrients, supplementation of water supply.

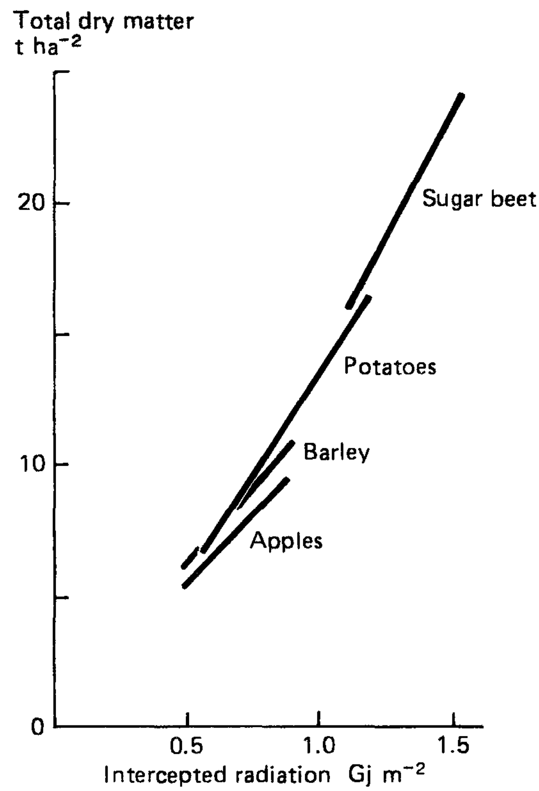

Figure 1. Relation between total drymatter yield at harvest and radiation intercepted by foliage throughout the growing season (Monteith 1977).

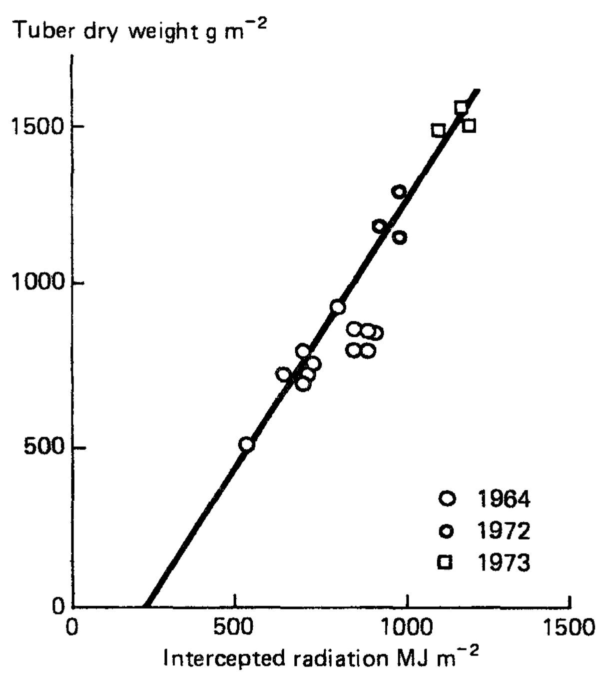

Figure 2. Tuber dry weight and intercepted radiation at Sutton Bonington (adapted from Scott and Wilcockson, 1978).

These tools may be considered to act in a positive way by increasing the amount of radiation intercepted, through effects on leaf growth, or they may operate through "negative" agencies, such as pests, diseases and weeds, which have a tendency to reduce the amount of radiation intercepted.

The grower, of course, has other matters to consider such as harvesting losses, losses during storage, and the quality of the product. A valuable feature of this type of analysis is that, given a knowledge of the radiation income and the pattern of crop growth, the potential yield of the crop can be readily calculated from the relationship between intercepted radiation and tuber yield. This makes it possible to estimate the scope for improvement under any particular set of environmental constraints.

An attractive feature of this type of analysis, particularly for agronomic research, is that the instrumentation needed to obtain estimates of intercepted radiation need only be minimal. In most of the work referred to the estimates have been made by placing solarimeters above and below the crop canopy, and their outputs measured by integrators over the growing season. However, it has recently been shown (Burstall and Harris, 1983) that there is an excellent correlation between the percent ground covered by leaves (viewed directly from above) and intercepted radiation. Simple inexpensive devices can be easily constructed to obtain these measurements. An instrument for measuring radiation receipts is the only other requirement. The height of the crop canopy will obviously affect the way such estimates are made.

Radiation interception and propagation of S. Tuberosum from seed

I am indebted to J. Shakya for the data used in this section, which were obtained from experiments carried out at Reading University in 1981 and 1982. In each year a growth analysis experiment was carried out in which the main variables were method of propagation and plant density. The percentage of incident radiation intercepted was measured directly in 1982, but in the following account it has been estimated from its relationship with leaf area index (1981) and with percentage ground covered by leaves (1982). Total incoming radiation was measured by a Kipp solarimeter. The total radiation intercepted by the crop canopy was calculated for each day from the time of crop emergence to the time of foliage death, or the final harvest.

In experiment 2 (1982) the methods of propagation compared were establishment from seed sown in the field, from seed planted in the greenhouse and subsequently transplanted, and from tuber eye plugs. Eye plugs were used in preference to whole tubers in order to establish comparable plant densities on a stem density scale. The tuber crop was the variety Désirée and the seed was derived from fruit collected from a crop established from tubers the previous year. The crop established from seed was genetically diverse, but this seemed to be a more noticeable feature in the tuber rather than foliage characters.

Tuber dry weights were plotted against intercepted radiation for each harvest of each of the three methods of propagation meaned over the density treatments. Intercepted radiation accounted for 97% of the variation in yield. Thus, in spite of the wide genetic diversity incorporated in the treatments and the widely different patterns of growth, tuber yield was accounted for by the same simple model.

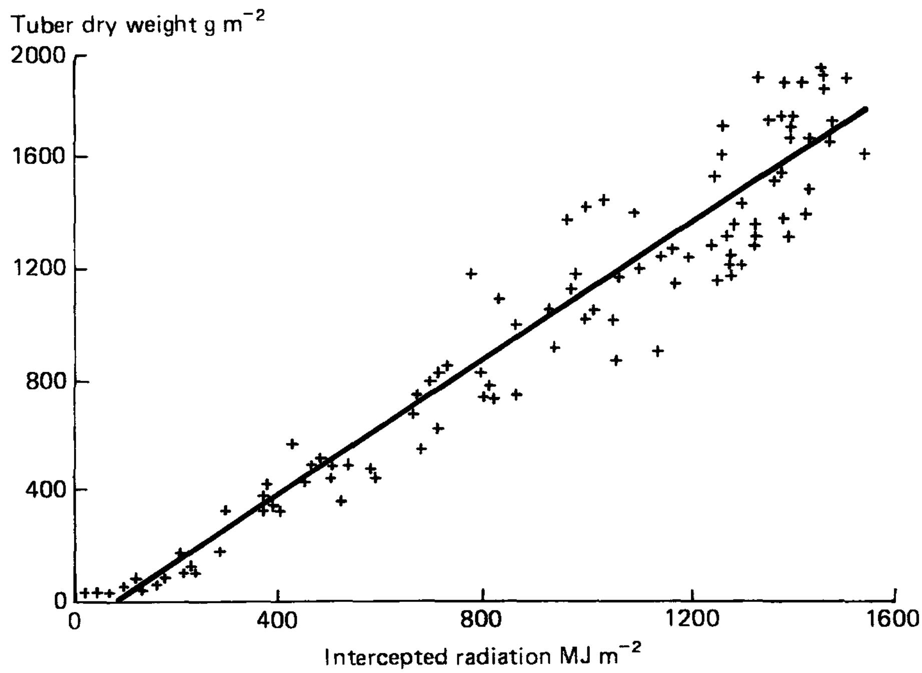

Figure 3. Relationship between accumulated tuber dry weight yield and accumulated intercepted radiation - University Farm Sonning, 1981. (S. Blanco White personal communication).

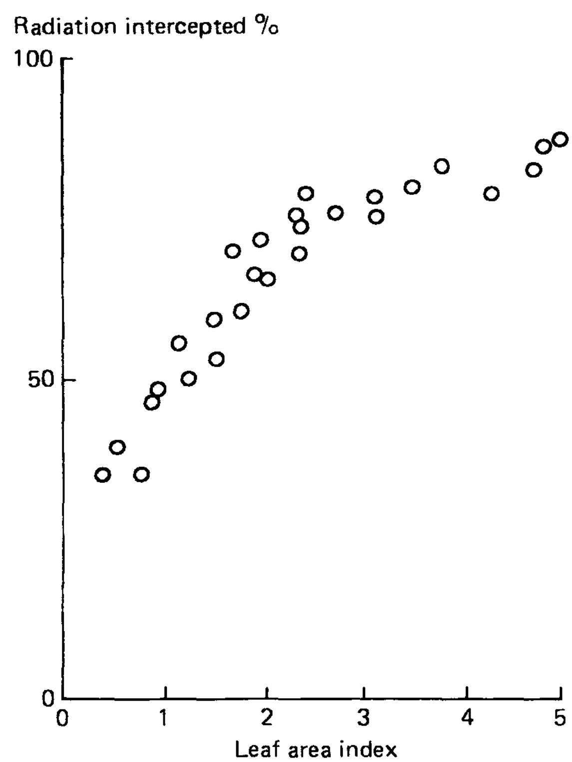

Figure 4. The relationship between leaf area index and total radiation intercepted. (Scott and Wilcockson, 1978).

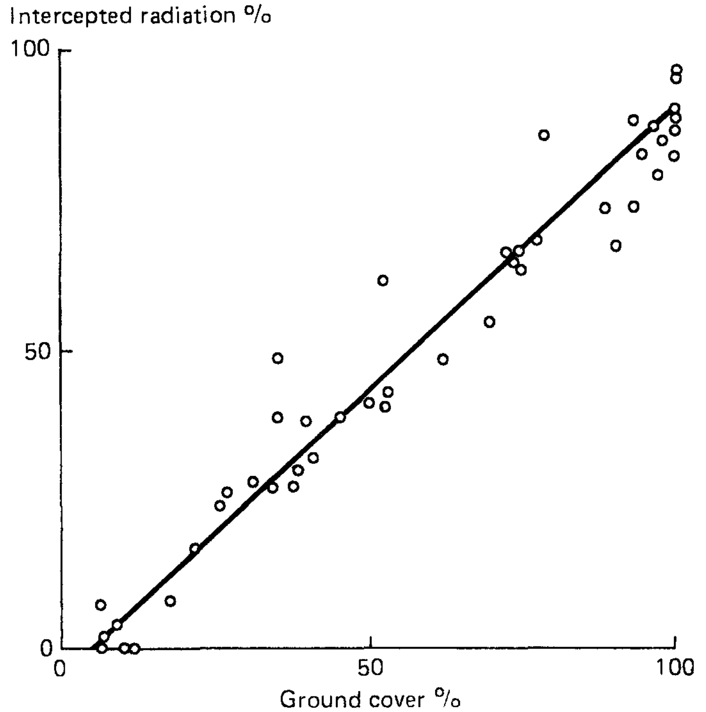

Figure 5. Relationship between percent ground cover and percent radiation interception (Burstall and Harris).

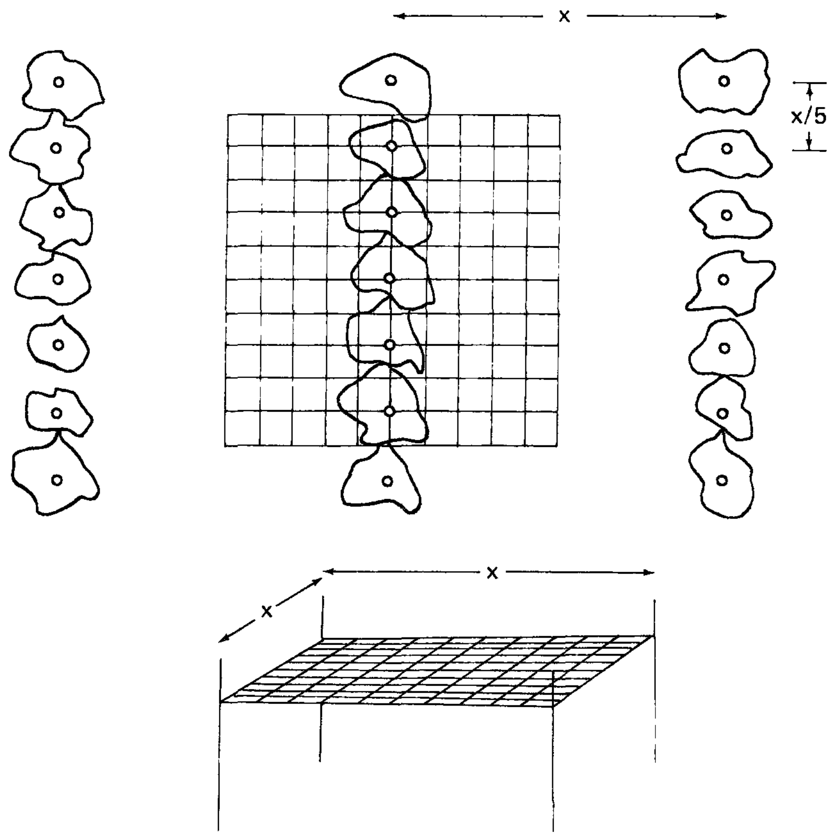

Figure 6. Simple grid for estimating crop cover.

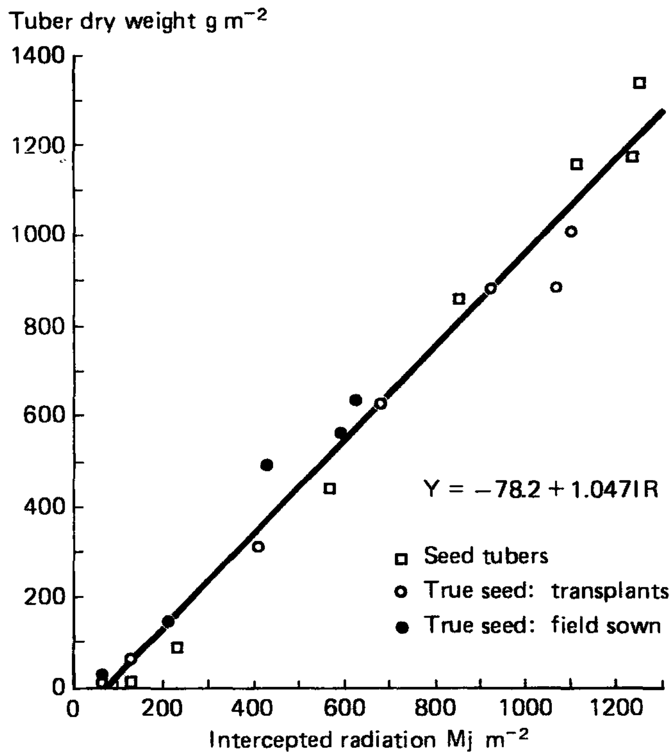

Figure 7. Relationship between intercepted radiation and tuber yield.

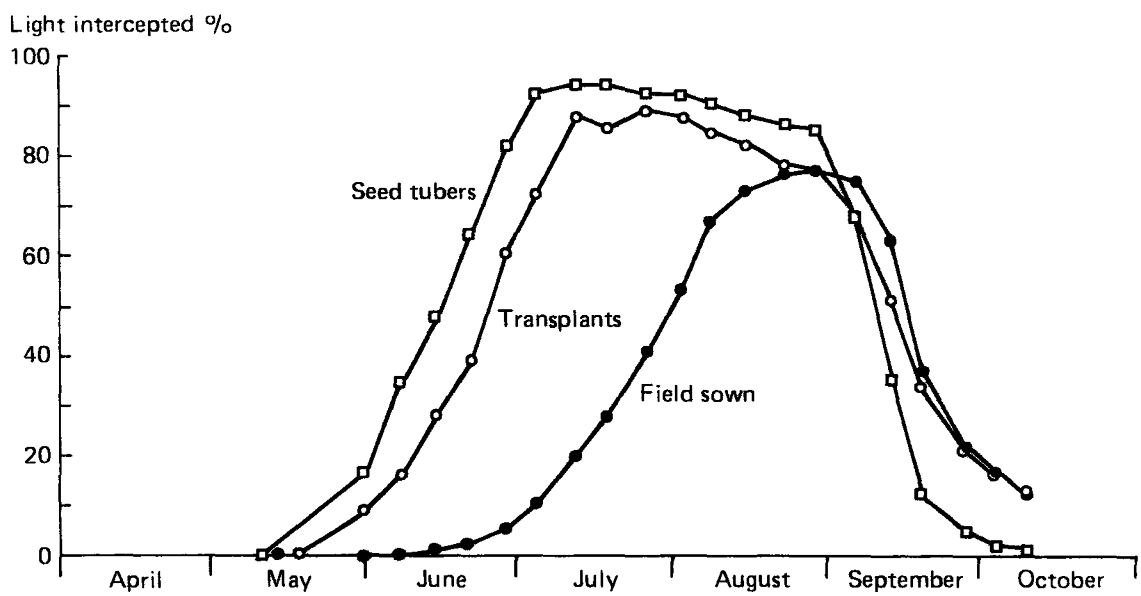

Figure 8. Method of propagating the potato crop and light interception, 1982, mean 4 densities. (Data of J. Shakya).

There were slight differences between the regressions for the three methods of propagation. These regressions together with the common regression are given in Table 1.

Table 1. Regression of tuber dry matter yield (y) ($g\ m^{-2}$) on intercepted radiation (IR) ($MJ\ m^2$) 1982 (each treatment is the mean of 4 densities)

	Treatment	Regression
1	All methods of propagation	= - 78.2 + 1.047 IR
2	Field sown from true seed	= - 49.9 + 1.101 IR
3	Transplanted from true seed	= - 51.2 + 0.950 IR
4	Propagated from tuber eye plugs	= - 171.2 + 1.165 IR

For crops propagated from seed, the amount of radiation intercepted before measurable tuber growth (45 and 54 $MJ\ m^{-2}$ for field sown and transplanted treatments respectively) was about one-third of the amount intercepted before the onset of tuber growth in the crop propagated from tubers (147 $MJ\ m^{-2}$). This is presumably a reflection of the greater chronological age of the seed propagated crops for any particular increment of radiation intercepted due to the slow development of the crop canopy.

It is immediately apparent that the slow development of the canopy from seed sown in the field offers severe limits to the potential of this particular treatment. On the other hand the pattern of light interception on the transplanted crop would suggest that this treatment has much more potential.

One way of increasing the interception of radiation, particularly in the initial stages of growth, is to increase plant density and adopt less rectangular planting patterns.

Before leaving these particular experiments attention is drawn to the patterns of light interception achieved by a transplanted crop and a crop propagated from whole tubers in experiment 1 carried out in 1981. In this experiment, the initial development of the canopy of the transplanted crop was set back by hail damage which occurred just after the crops had been transplanted into the field, and which did not affect the tuber propagated crop, however the latter showed severe leaf rolling from mid-July onwards and the crop rapidly senescenced. The crop propagated from seed completely escaped this condition. This potential effect on the incidence of tuber transmitted diseases is, of course, one of the advantages claimed for propagating the crop from true seed, and it affords an interesting demonstration of the effect that this particular method of manipulating the crop may have upon the realization of the strategy of maximizing radiation interception.

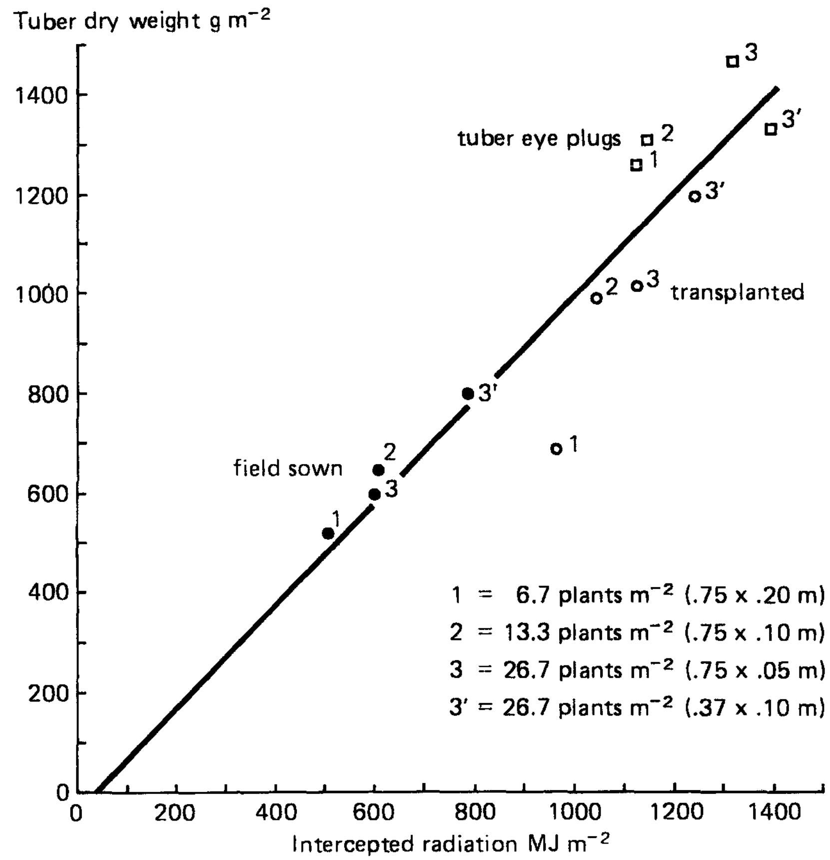

Figure 9 Effect of treatments on radiation intercepted and yield 1982.

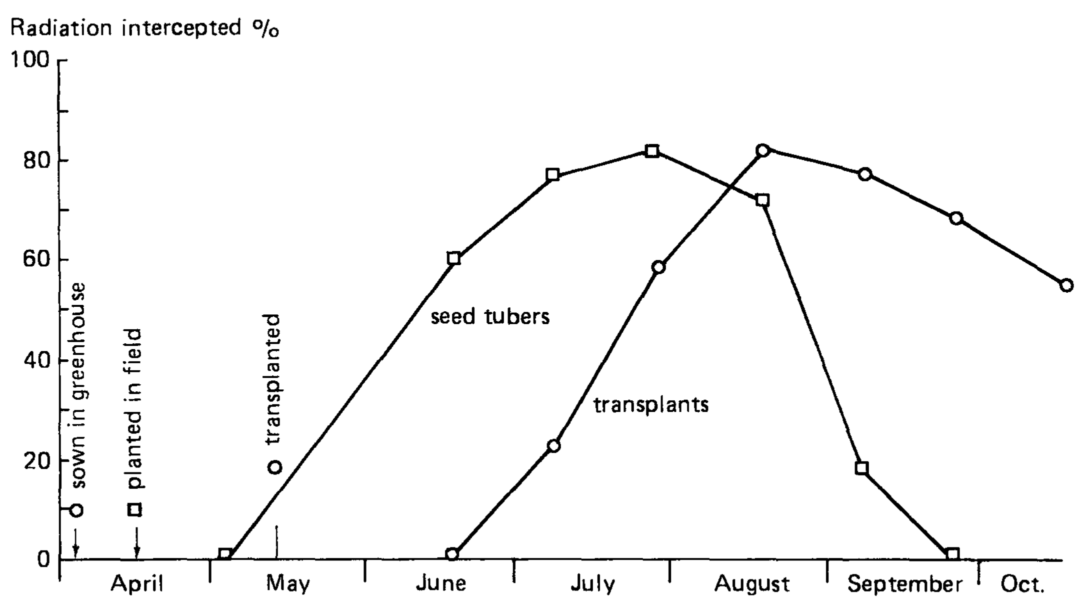

Figure 10 Percent radiation intercepted by crops propagated from tubers and seed 1981 mean 4 densities (J. Shakja).

The type of analysis described, I believe is of considerable help in interpreting the results of treatments particularly where they depart so radically from normally accepted procedures, as is the case where normally vegetatively propagated crops are grown from seed. It not only assists in interpretation but it is of considerable help in planning further work. For example, in the case of our own experiments, it suggests that field sowing true seed is unlikely to give yields approaching those of conventionally propagated crops due to the excessive wastage of radiation resulting from the very slow canopy development. On the other hand, transplanting crops grown from true seed may only be marginally inferior to tuber propagated crops in the early part of the season and may under certain circumstances be superior in the latter part of the season. The initial poorer light interception may be overcome by earlier sowing of seeds for subsequent transplanting, if the shock due to delayed transplanting can be overcome by treatments such as the application of CCC, to curtail top growth and enhance early root development.

The potential for producing tropical and sub-tropical root and tuber crops from seed

The apparent dearth of any literature on the production of the major tropical root crops from seed is interesting in that it suggests either that there is considerable potential for exploring this particular avenue, or that the difficulties of so doing are so formidable and well known that it offers an unlikely route for future development.

There can be no doubt that there are severe problems of flowering and seed production in all the tropical root crops (Simmonds, 1976; Wilson, 1977; Onwueme, 1978) which not only make any consideration of propagating these crops from seed a practical non-starter, but has also imposed a break on the progress of breeding new varieties. However, this need not necessarily be regarded as a permanent constraint either on breeding progress or on the possibility of ultimately being in a position to consider propagation from seed. Encouragement in this respect is given by research on pollination, seed set and germination in the white yam (*Dioscorea rotunda*) which has shown that these problems may be tackled successfully. Even more encouraging is the discovery that the low degree of flowering and high male to female ratio characteristic of plants produced by continuous vegetative propagation have been transformed to a much higher degree of flowering and a lower male to female ratio in second generation plants (Sadik, 1976). It has also been shown in sweet potato (Martin and Jones, 1971) that selection over six generations of open pollination increased the proportion of plants in flower, the number of flowers per plant and total seed production.

The use of growth regulators to promote flowering has been demonstrated in tannia (*Xanthosoma sagittifolium*) by McDavid and Alamu (1976), when applying gibberellic acid as foliar spray promoted flowering within 100 days when none were produced on the control plants. The same authors showed that soaking the setts in a solution of the same growth regulator before planting also promoted flowering (Alamu and McDavid, 1978).

The possibility that flowering may be restricted by pests and diseases has been demonstrated by Jones et al (1977) who found that certain insecticides gave dramatic increases in the number of seedlings per parent plant in the sweet potato.

The possibility therefore of developing new and more productive cultivars by sexual reproduction and of incorporating improved seed production capacity in such cultivars makes it perhaps worthwhile speculating on the potential advantages of propagating such crops from true seed.

It would, however, be potentially more productive if such speculations could be made in an agronomically orderly framework, and there are reviews of the physiological basis of tropical root/tuber crop production (Wilson, 1977; Loomis and Rapoport, 1976) on which such a framework may be built. These, however, like the model described above draw heavily on experiments with temperate root crops such as the potato and sugar beet. The merit perhaps of the model described here is its simplicity, and the fact that it can be tested with the minimal use of instrumentation and without complex growth analysis. It should be an invaluable aid, when considering questions of agronomic innovation, if this could be done in the light of clearly thought out and quantifiable physiological strategies.

Supposing that evidence collected in the way described suggested that there was a close relationship between intercepted radiation and the economic yield of a particular crop - what implications might this have for the production of that crop from true seed? Wilson (1977) has pointed out that if it is assumed that optimal light interception occurred at a leaf area index of 3, then a considerable proportion of the total time that tropical root crops are in the ground may be spent with indices of less than three (Table 2).

Table 2. Proportion of total crop time (%) spent with LAI less than 3.

Crop	% total crop time
Solanum (tropical)	40
Ipomoea	31
Xanthosoma	27
Dioscorea alata	50
Dioscorea esculenta	44
Dioscorea trifida	66

From Wilson, 1977

In terms of speeding up the interception of radiation, experience with *Solanum tuberosum*, outlined previously would seem to be distinctly discouraging, for the development of canopies capable of intercepting most of the incident radiation by seed propagated crops lagged far behind those of the vegetatively propagated counterpart, and especially where the seed was field sown. This is attributable both to the small amount of capital available for growth from seed compared with tubers, and to the climatic constraints which prohibited the early establishment from field sown seed because of the risk of frost damage. Earlier planting under protected conditions removed much of this adverse effect, and as outlined earlier, experiments are in hand which may make it possible to overcome this time lag completely - although obviously not without incurring extra costs.

This would suggest that in tropical root crops, similar strategies might be required to overcome similar problems, with seasonality of rainfall probably replacing the risk of frost as the most important environmental constraint.

However, the capacity to develop the crop off the field before planting could be a valuable property of seed propagation. It was shown clearly in Table 1 that the Dioscorea species are particularly slow to develop a crop canopy. Onwueme (1978) graphically describes the problem: "For the first 3 months or so after planting, the tuber is dormant and sprouting does not occur. Then for a further 1 to 2 months after emergence, the plant is almost exclusively made up of vine, the leaves remaining small and unexpanded." He points out that one way of speeding up early growth is to plant sprouted tubers; however, large losses of setts, both in moist and dry sprouting conditions is a severe drawback to the technique. With these problems in mind, it is possible to suggest that propagation from true seed might have something to offer. Seed grown in nurseries prior to the normal time of planting, where they could be watered and protected, could be ready to plant out and intercept radiation from the commencement of the growing season. Onwueme has pointed out that the foliage production from true seed may be sparse, but the possibility exists of solving this problem by early development away from the field, adjusting plant densities, and ultimately by improving early foliage development by breeding - in short by selecting a set of "tools" appropriate to this particular strategy.

Improving light interception in the early stages by appropriately managed seed propagation is, however, not the most obvious and immediately applicable way in which radiation interception might be improved to increase productivity. However, virus and other pathogens which are borne on the vegetative organs of propagation may cause serious reductions in the size of the leaf canopy and restrict the interception of radiation, propagation from seed may enable crops to be established which are free, at least initially free, from infection, and may escape or partially escape from the consequent reduction in canopy size. This possibility is illustrated in Figure 12 and Shakya (unpublished data) has shown that under these circumstances, yield of seed and tuber propagated crops were comparable. In this context it should not be overlooked that young seedlings may be particularly susceptible to infection by virus and other diseases, and will need adequate protection. This problem was experienced in some of our own experiments with seed propagation of potatoes in 1982. Whether or not this particular benefit of seed propagation will be attractive will depend upon the ease with which reasonably disease free stocks of vegetative propagules can be both maintained and obtained.

In addition to the possible effects of production from seed on the physiologically base strategy of production, this technique has other implications. It has often been pointed out that where the organ used to propagate the crop vegetatively is also the part of the plant which is consumed, then seed propagation has the obvious attraction of enabling the grower to utilize all the economic fraction of the crop, and to this extent some yield reduction due to seed propagation could be tolerated. Table 3 shows the low multiplication ratio of vegetatively propagated crops compared with seed crops.

These problems do not apply to cassava and sweet potatoes where propagation is by stem cuttings or from vines. Other considerations of no immediate relevance to the physiology of yield and vigorously canvassed as being of considerable practical importance to the production of potatoes from seed (Accatino and Malagamba, 1982) involve the relative ease and cheapness of storing, transporting and handling seed rather than vegetative material, and these considerations would apply equally well to the production of other vegetatively propagated crops.

Table 3. Ratio of fresh-weight yield to weight of planting material (multiplication ratio) for various crops.

Crop	Approximate multiplication ratio
Guinea corn	80
Maize	70
Cowpea	25
Upland rice	20
Groundnut	15
Irish potato	7
Tannia	5
Taro	5
Yam	5

Onwueme, 1978

In this paper I have attempted to give a broad outline of the potential and problems of propagating tropical root crops from seed. I have not dealt with the problems and benefits which may arise from incorporating propagation from seed into mixed cropping systems nor with possible effects on the quality - particularly with regard to size distribution of the edible products. These are important problems, but ones which need to be resolved locally.

The ideas put forward are based on studies of the potato crop, grown in Britain, by traditional vegetative methods and from seed, and it is clearly unwise to extrapolate uncritically such experience to crops and crop environments with greatly differing characteristics. It is also clear that, unlike the potato, a major obstacle for many tropical root crops is the difficulty of obtaining seed and this hurdle must be surmounted before any progress can be made. However, anyone advocating the possibility of producing potato crops from seed would, as little as 15 years ago, have been classified as an eccentric academic, and subsequent developments have made many agronomists reconsider the accepted techniques which have been developed over many generations. This experience would make it unwise to write-off the potential for using this technique for other vegetatively propagated crops.

The major point that I have tried to convey in this paper, and here I think our temperate experience may be valid to the tropics, is that it should be possible to make more rational conjectures concerning such questions as the potential value of the seed propagation of the tropical root crops if they were made in the context of physiologically soundly based production strategies. Such strategies could, in addition, suggest useful plant characters which could be incorporated into plant breeding objectives. It also seems to me that a case can be made for using the simplest acceptable physiological model available, and one which can be tested and applied without the need for sophisticated instrumentation. I hope that this paper has been able to make a reasonable case for such an approach.

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