SOME PHYSIOLOGICAL PRINCIPLES DETERMINING THE YIELD OF ROOT CROPS.

— *by* —

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In this paper, the usual liberties taken by agriculturalists with botanical terminology will be accepted: the term 'root crop' will be used to denote a crop grown for some underground organ irrespective of its morphology. The adjective 'tropical' poses greater restrictions — mainly because most of the intimate aspects of the physiology and ecology of strictly tropical root crops are unknown. During the next decade there will surely be a vast extension of enquiry within this field — particularly concerning the description of responses to the main environmental factors and deeper understanding of the correlated functioning of species such as the sweet potato *(Ipomoea batatas),* cassava (*Manihot esculenta*) and yams (*Dioscorea spp*). In the present context the most useful purpose may be served by examining relevant features of two species which are much more fully documented: one, the (Irish) potato (*Solanum tuberosum*) originated in the tropics, has been rigorously selected for growth in temperate climates, and is now finding its way back into the tropics; but for even mentioning the other, sugar beet (*Beta vulgaris*), the indulgence of the more ardent tropical agriculturalists must be sought.

GENERAL FEATURES OF GROWTH

Three phases of growth may usually be recognized : (i) that of pre-emergence, which involves the establishment of an autotrophic plant from materials stored within the mother organ (tuber or seed); (ii) that in which leaf growth is predominant and (iii) that, overlapping with the preceding, in which growth of the storage organ occurs (Fig. 1). The potato and sugar beet represent two extremes of plasticity in respect of internal control of differentiation. Differentiation of tubers on the distal parts of the diageotropic stolons of the potato depends on a particular internal state of the plant; this state is a function of age and of the environment. Usually, there is appreciable development of stems and leaves before tubers are initiated; once the tubers commence to grow, no further leaves are initiated and the leaf surface senesces rapidly. On the other hand, differentiation of the storage root of the sugar beet is peculiarly insensitive to environmental control. The concentric cambia are initiated at a very early stage of ontogeny in a very wide range of environments and the root and leaves develop more synchronously. Root growth eventually dominates over leaf growth — but never completely, there being only a slow decline of the leaf surface over a long period of time. Here, the leaf area is in excess of that required but in the sub-species mangold, where a higher ratio of root to leaf area has been selected (Watson and Baptiste, 1938) a commercially adequate concentration of sugar has not been achieved. The sweet potato — the only other species for which limited growth data are available — would appear to be intermediate: apparently the root tubers commence to store materials relatively late in ontogeny but they grow slowly and the leaf surface, which may be in excess of requirements, declines slowly. There is possible

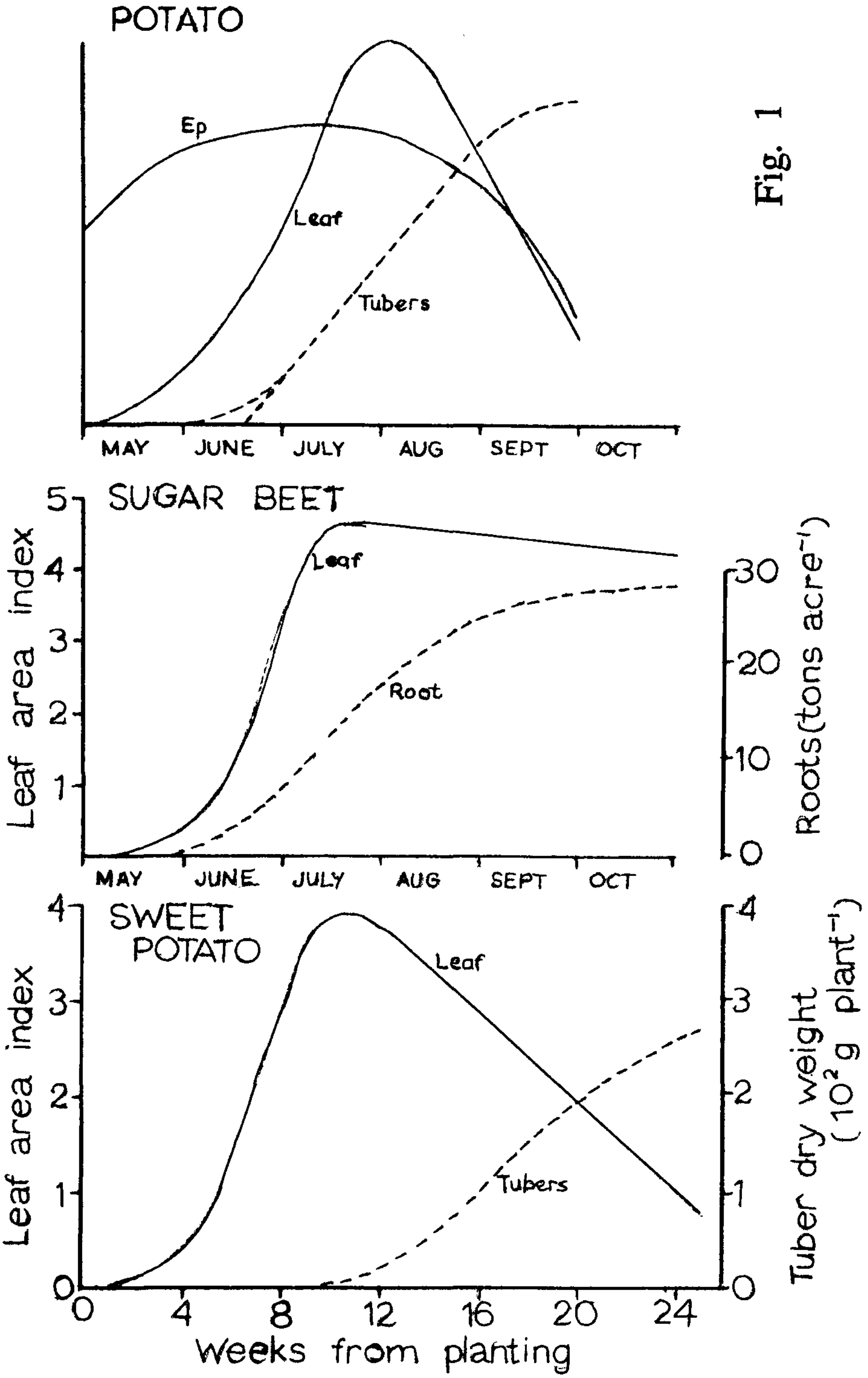

POTATO
Ep
Leaf
Tubers
MAY
JUNE
JULY
AUG
SEPT
OCT
SUGAR BEET
Leaf area index
5
4
3
2
1
Leaf
Root
Roots(tons acre⁻¹)
30
20
10
0
MAY
JUNE
JULY
AUG
SEPT
OCT
SWEET POTATO
Leaf area index
4
3
2
1
0
Leaf
Tubers
Tuber dry weight (10² g plant⁻¹)
4
3
2
1
0
0
4
8
12
16
20
24
Weeks from planting

Fig. 1

scope for selection of varieties with earlier initiation and with a better balance between leaf and root growth than existing varieties.

Agricultural production is primarily concerned with manipulating the responses represented by these curves to achieve certain results within particular environments. The aim may be to obtain the highest yield within the available growing season, as with main-crop potatoes, or to obtain a marketable yield very early, as with first-early potatoes in the United Kingdom. The dominant environmental factor may differ between environments; in Britain and much of Europe low temperatures determine the length of the growing season, whereas in tropical regions shortage of water is often the overriding factor. In Fig. 1, a crude description of the seasonal variation of the adequacy of the environment is given by the potential net assimilation rate; that is, the net assimilation rate of young plants. This probably varies little between species at the same stage of ontogeny whereas growth rates vary much more widely; a more sensitive index would be given by relative growth rates during the one or two weeks following emergence. The curve is smoothed to remove weekly fluctuations; this cloaks the fact that the limits of the season are determined mainly by the probability of occurrence of catastrophic values (from severe frosts or prolonged droughts).

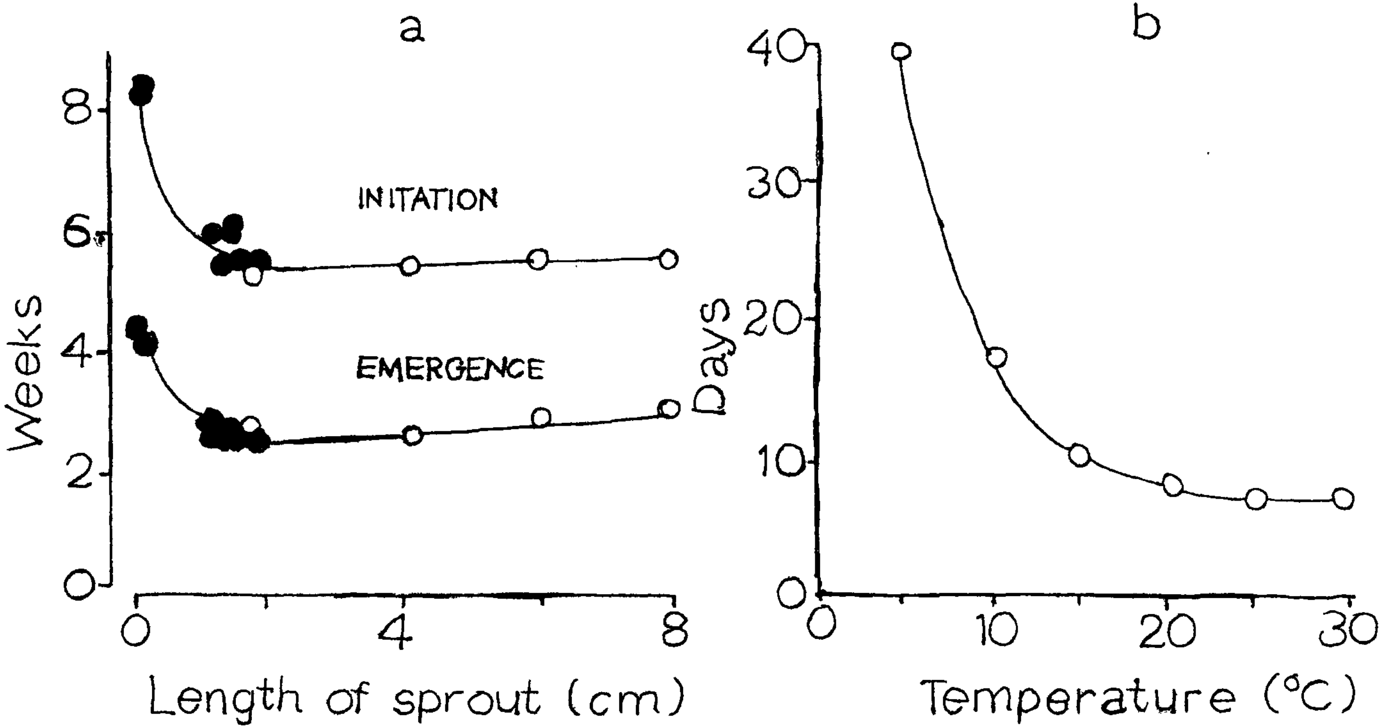
THE PRE-EMERGENCE PHASE

Pre-emergence growth of the potato

The tuber at planting bears a population of dormant, correlatively inhibited and growing sprouts; only those in the last category continue to grow after planting (Morris, 1966a). The mother tuber provides the main source of substrate until the plants have a leaf surface of 200—400 cm2 (Headford, 1961; White, 1961) although the external supplies of mineral nutrients influences growth at earlier stages than this (Moorby, 1967). Provided there is an adequate supply of water, growth during the pre-emergence phase is controlled by soil temperature and by the degree of development at planting. Generally, the rate of emergence of potato is faster the higher the soil temperature and the greater the degree of development of the sprouts at planting (Fig. 2). Plants grown from tubers with well-developed sprouts also initiate tubers earlier but there is a limit to which these responses can be used in practice. Well-developed sprouts if subjected to low temperatures after planting may initiate tubers before emergence and greatly delay the establishment of the haulm; this is the condition known as 'little potato'. Moreover, proneness to the abnormality known as 'coiled-sprout' is related to the size and degree of development of the sprout (Moorby and McGee, 1966).

There is little advantage to be gained, therefore in planting tuber with sprouts greater than 1—2 cm. In general, the smaller the sprouts at planting the higher will be the yield at natural maturity but the longer is the growing season; sprouts longer than 2 cm give rise to plants which emerge earlier, initiate tubers and give a higher yield early in the season but not at maturity (cf.p 5). The yield and size distribution of tubers is also influenced by the number of sprouts which are growing at the time of planting; the greater the number of these the higher the yield but the proportion in the smaller size grades is also higher (Toosey, 1963).

Fig. 2


a
Weeks
0
2
4
6
8
INITATION
EMERGENCE
0
4
8
Length of sprout (cm)
b
Days
0
10
20
30
40
0
10
20
30
Temperature (°C)

Development of potato sprouts during storage.

The number and size of growing sprouts at planting depends partly on size and variety but mainly on the storage history of the tuber. The many issues involved have been reviewed by Milthorpe and Moorby (1967) and need only be briefly mentioned here. Provided a period of more than three months is available between harvest and planting, the appropriate storage environment can be provided, and the tubers are free of virus and other diseases, conditions during the growth of the mother tubers are of little consequence (Goodwin, *et al.*, 1966). Dormancy, although an intriguing physiological phenomenon possibly involving a balance between gibberellins and inhibitors such as abscisin (cf. Milthorpe and Moorby, 1967), is also of little significance under European conditions of culture. It can, moreover, be readily broken by exposure to gibberellin A3, ethylene chlorhydrin or water (Goodwin, 1966) or prolonged by treatment with nonyl alcohol or other inhibitors (Burton, 1961). The pattern of subsequent growth is, however, of the utmost importance.

The environmental factors exerting the largest effects on growth during storage are light and temperature. There are large differences between darkness and light supplies of about 1 cal cm $^{-2}$ day $^{-1}$; amounts of light greater than this have little further effect. Little or no growth occurs at temperatures less than 5°C. If tubers are stored from harvest at temperatures of 15° — 25°, the apical bud loses dormancy first and starts to grow rapidly. It soon establishes dominance and only 1—2 buds continue growth (Goodwin, 1967; Goodwin and Cansfield, 1967). If, however tubers are stored at temperatures of 7° — 10°, or if dormancy is broken artificially, many buds commence growth. Gradually, the smallest buds are correlatively inhibited and with the passage of time only 2—4 buds will continue to grow. These are direct apical dominance influences in which complex growth-substance interrelationships are involved (Goodwin, *loc. cit.*). The rate of growth also involves mobilization of tuber reserves and competition for these between the growing sprouts; these interrelationships have been discussed by Morris (1966a, 1966b). By using these responses and manipulating the temperature appropriately during storage, the number and size of *growing* sprouts at planting can be varied within certain limits.

Vegetative propagation of other root crops.

Most of the tropical root crops are propagated by stem cuttings but I am not aware of any studies relating to the effect of the source of the cutting on the performance of the subsequent plant. Arguing from the scattered information gleaned from other species and generally presented under the terms "juvenility" and "ageing" — abstractions embodying a general mysticism to cloak our ignorance — it seems likely that time to initiation of storage organs will be increasingly delayed in plants propagated from the following sources: old whole tubers, young whole tubers, main-stem cuttings from plants bearing tubers, main-stem cuttings from young non-tuberizing plants, axillary-branch cuttings. However, variation attributable to differences in previous history of parent material free of disease is usually frequently less than that which can arise from differences in environments during growth (Goodwin, *et al*, 1967).

INITIATION OF STORAGE ORGANS

The potato

The initiation of tubers arises from changes in a number of metabolic reactions occuring at the sites of tuber formation; i.e. in the elongating internodes of the tubers. The actual reactions involved have not yet been explored; studies have been confined to describing the morphological changes, to indirect experiments concerning possible transmissible stimuli and to ascertaining the environmental factors which accelerate tuber initiation.

The first evidence of tuber initiation appears to be that cells of the extending internodes of stolon commence to expand radially rather than continue to elongate (Booth, 1963). This change in the direction of cell extension is soon followed by secondary cell division throughout all tissues (Fig. 3.). The apical meristem continues during some 12 — 14 plastochrons to provide new primary tissue in which extensive secondary division occurs; although secondary division continues in all parts of the tuber over an extended period, continued growth and division appears to depend on the production of new primary tissue from the apical bud. This observation may simply mean that both primary and secondary division are controlled independently by some other factor (such as provision of substrates), but the evidence from studies on second-growth of tubers (Bodlaender, *et al.,* 1964) suggest that soon after the expanding internodes at the tuber apex change from a state of radial expansion to longitudinal extension — i.e. reverts to "stolon-type" growth — secondary division ceases in the primary tuber. These data also suggest that the "tuber-forming" state of the terminal bud of a stolon is not permanent or irrevocable but requires the continued maintenance of a certain (unknown) metabolic state.

It would be pleasing within our present superficial knowledge of growth substances to ascribe the non-tuber state to high gibberellin and low abscisin contents and the tuber-forming state to low gibberellins and high abscisin [See Addicott, *et al.,* (1964), Cornforth, *et al.;* (1965) and Thomas, *et al.* (1965) concerning abscisin]. A case for this general thesis, with some experimental support, has been made by Booth (1963). One inadequate exploration of gibberellin contents, measured by the Paleg test, showed that apices of non-tuberized stolons, apices of stolons in the earliest stages of tuber initiation and minute tubers contained 1.1 x 10^{-10}, 2.0 x 10^{-10}, and 2.4 x 10^{-12} g equivalent GA_3 per apex respectively; if substantiated these results would indicate that tuber initiation is not associated with a marked change in gibberellins but that tuber growth is.

It should be emphasized that it is the changes in the extending internodes of the stolon which must be considered. It is conceivable that a decrease in the ratio of gibberellin to abscisin, say, or changes in balance of other growth regulators, may arise both from differences in rates of production and transport from other organs as well as differences in rates of production *in situ.* The association of tuber initiation with high carbohydrate contents may indicate that sucrose is here the transmitted "stimulus", as suggested by Borah and Milthorpe (1962) — leading to possible changes in balance and concentration of different growth substances localized in the terminal bud of the stolon — or it may mean that in this state less gibberellin and more inhibitors are produced in the foliage and transported to the stolons.

It is well established that tuber initiation is associated with slow growth of the haulm; there is also, in plants of European varieties with similar rates of haulm growth, a rather weak short-day reaction (Slater, 1963). The much stronger short-day reaction in *Solanum andigena* favours the suggestion that growth sub-

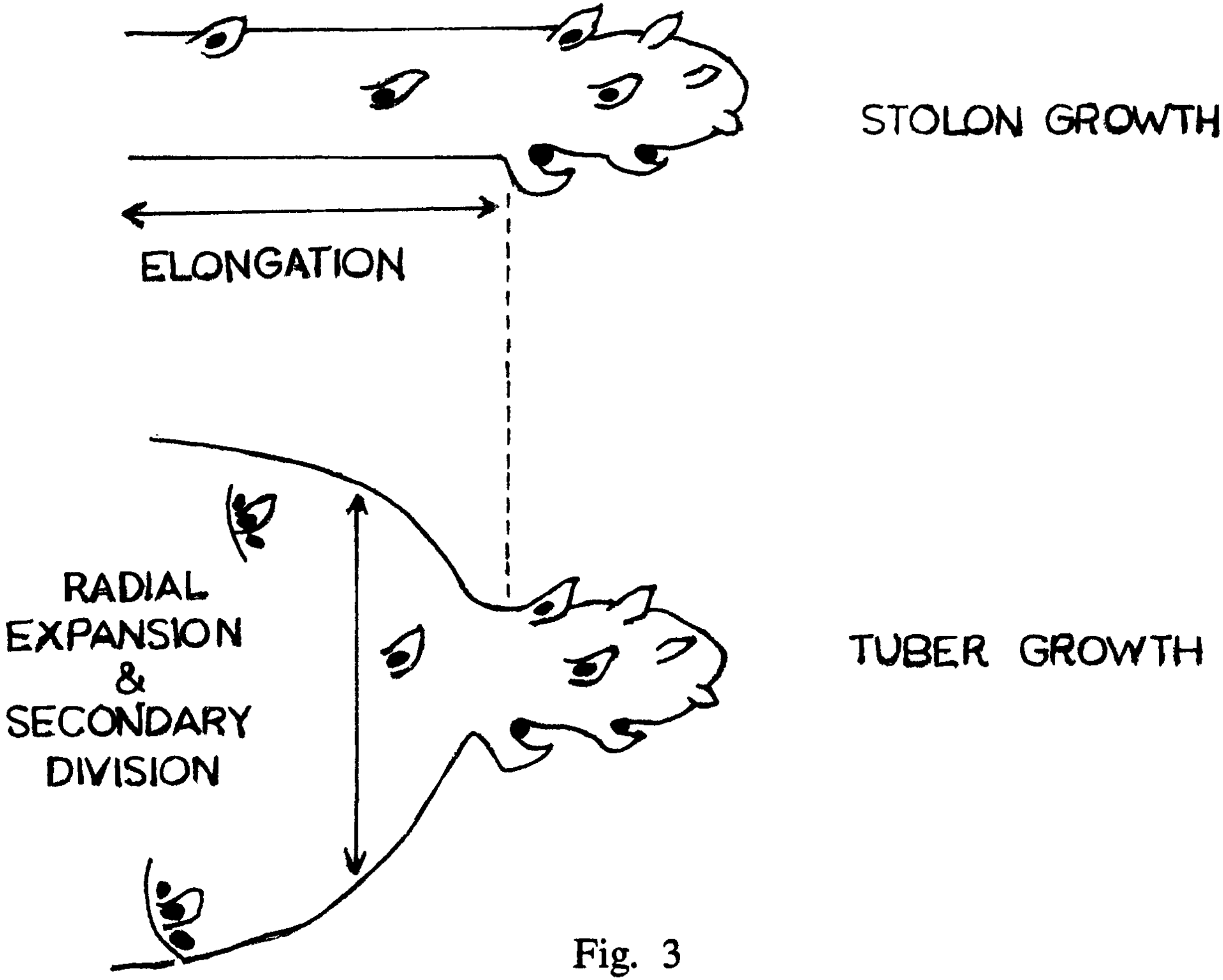

STOLON GROWTH
ELONGATION
RADIAL EXPANSION & SECONDARY DIVISION
TUBER GROWTH

Fig. 3

stances are transported. The conditions which favour initiation are low temperatures, short days, high radiation, low mineral nutrient supply and growth-retarding chemicals such as CCC and B995 (Krugg, 1964; Dyson, 1965; Dyson and Humphries, 1966; Bodlaender and Algra, 1966; Gifford and Moorby, 1967). Reversion from radial or tuber growth to elongation or stolon growth is favoured by high temperatures (Bodlaender, *et al.*, 1964) and periods of water deficit followed by relief from the deficit (Sabalvoro, 1965; McCorquodale, 1966).

b) *Other species*

In sugar beet, the storage root appears to be much more intimately associated with the growth of the leaves and much less subject to change by environmental or experimental treatments than is the potato (Milthorpe and Terry, 1967). The numerous secondary cambia are all initiated at a very early stage and these develop more or less in step with the growth of the leaf surface. Decapitation does not influence cambial initiation although it does stimulate the activity of the cambia once formed. Little is known (at least, by this writer) about the formation of root tubers in species such as the sweet potato and dahlia. In these species only a few of many apparently similar adventitious roots become storage organs; this intriguing response indicates a very localized control and is surely worth detailed study.

INTERRELATIONSHIPS BETWEEN GROWTH OF STORAGE ORGANS AND HAULM

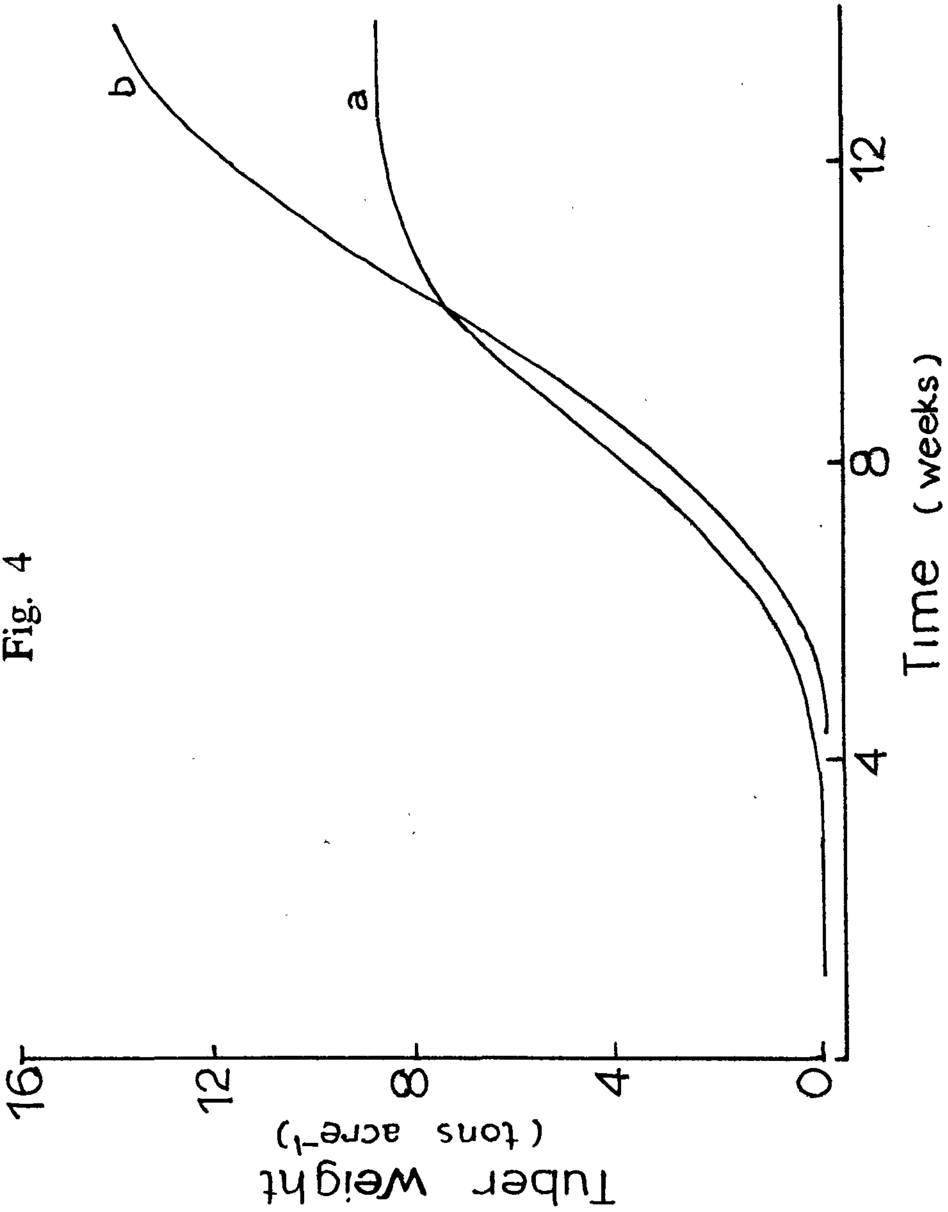
The potato

Those tubers which eventually grow to significant sizes appear to be initiated during the two weeks or so following the appearance of the first tuber. The total weight of tubers during and shortly after this time follows a gradually increasing rate of growth with time; it then enters a long phase of almost constant rate of bulking. Generally, the longer tuber initiation is delayed (i.e. the larger the haulm at the time of initiation), then the shorter is the duration of the phase of increasing rate of growth and the higher and more prolonged is the rate of bulking during the phase of 'constant' rate (Fig. 4). Manipulations, therefore, which result in very early initiation do not usually produce higher eventual yields; much that is gained in earliness is lost in the subsequent lower performance (Burt, 1965; Milthorpe and Moorby, 1967).

Much evidence (cf. Ivins and Milthorpe, 1963) shows that the bulking rate of any one crop in any centre remains constant with time despite appreciable weekly fluctuations of temperature and light. (Severe shortage of water can disrupt this pattern). This behaviour suggests that there is a large measure of internal control during this phase of growth. However, the rates of bulking vary largely between plants subjected to differing conditions prior to initiation (sprout development at planting, cultural conditions, weather, etc), thereby suggesting that the subsequent rate of bulking is largely determined by the state of the plant (reflecting previous history) and the weather conditions near the time of initiation. A clear definition of these conditions, however, is still awaited.

The constancy of the bulking rate in any one crop does not necessarily mean that individual tubers maintain constant rates. Much evidence suggest the contrary: that the rates vary irregularly with time and relative to each other. For example, in one experiment in which $^{14}CO_2$ was supplied to the whole of the foliage, the ^{14}C imported by individual tubers varied by as much as ten times and

Fig. 4



the largest tubers did not always have the largest content of ^{14}C(Table 1). An interesting feature of this experiment is that it showed that the mother tuber was importing, exporting and metabolizing carbon at this extremely late stage of its existence.

As the tubers increase in size, branch and leaf production gradually cease and the existing leaves senesce leading to the decrease in the total leaf area illustrated in Fig. 1 (Milthorpe, 1963). The rate of decline of leaf area is usually slower the greater the leaf area at the time of initiation. Finally, when little green leaf area remains, the rate of tuber growth declines and ceases. These observations could be claimed to support the general contention that the rate of tuber growth depends on the supply of photosynthate, which is mainly controlled by the extent and duration of the leaf surface (Watson, 1952, 1963). Indeed, Bremner and Taha (1966) and Bremner and Radley (1966) have found a close relationship between tuber yield and the integral of leaf area during the period of bulking assuming all leaf area of 3 cm^2 per cm^2 soil or more to be 3. Other investigators (e.g. Goodwin *et al.,* 1967) have been unable to establish any relationship.

A large amount of evidence, including the relationships with intensity of the sinks (cf. Humphries, this symposium), changing rates of photosynthesis with age, higher net assimilation rates following tuberization, and the constancy of bulking rates in varying environments, suggest that, over wide limits of leaf area, rates of tuber growth are controlled by factors other than the supply of assimilate. As competition effects are pronounced, it is likely that supplies of mineral nutrients to the growing tubers may be involved; it is also conceivable that more subtle growth-substance controls occur. These aspects still await investigation.

All available evidence would suggest that senescence and eventual death of the individual plant results mainly from lack of substrate supply to potential growing points of the haulm. That this senescence is *Erschöpsungstod* (Molisch, 1938), or death by exhaustion, is suggested by the appreciable migration of nitrogen, phosphorus, and potassium from the haulm to the developing tubers; this in turn probably results in decreasing potential rates of photosynthesis which, with the increasing flow of carbohydrates to the tubers, leads to lower and lower supply to the haulm meristems and absorbing roots. New leaves fail to differentiate and the existing leaves decline and die consecutively. There is no evidence of the "flowering senescence" described by Krizek, *et al.* (1966) for *Xanthium* and which is obvious in determinate flowering stems of cereals, grasses, raspberry and some other species. This phenomenon is distinguished by profound metabolic changes initiated concurrently with those metabolic reactions which lead to flower induction and is shown by the eventual *browning* of tissues progressing *basipetally*. In the potato, senescence throughout is shown by *yellowing* of leaves progressing acropetally; flowers are often initiated prior to planting; and removal of tubers has long been employed by plant breeders to prevent flower and fruit abscission and in which situation plants continue stem and leaf growth over a much longer time.

The potato in the tropics

In view of the special interests of this symposium, it may be appropriate, albeit dangerous, to speculate briefly on possible manipulations of the physiological responses of the potato in tropical regions. The two environmental components which most influence tuber iniatation are temperature and photoperiod, the former being the most important. It would seem essential for adequate tuber initiation that potatoes be grown in a climate in which the temperature is below 20°C for an appreciable proportion (say, 8—10 hours) of each day. High temperatures during the period of tuber growth will also tend to make the terminal buds of the stolons revert to elongation rather than to continued radial expansion but possibly higher temperatures during this phase could be tolerated than around the time of tuber initiation. Although it matters little in respect of physiological responses whether the period of lower temperature is experienced during the light or dark period (Slater, 1964), the most appropriate environment would appear to be one of appreciable incoming radiation but with sufficient night re-radiation to give the required low temperatures.

Provided the temperature requirements are met, the generally shorter photoperiods will tend to accelerate tuber initiation compared with those of more temperate regions. It may often be found that the relative lengths of growing season of different varieties will change compared to those found in temperature regions. Generally, in cool temperate climates, 'early' varieties are less responsive to short days and more responsive to low temperature than are 'late' varieties (Krug, 1963; Caesar and Krug, 1965). As temperature responses are certain to be the more critical in marginal tropical climates, those varieties which are late maturing in temperate regions may be more successful than those which are early; in tropical areas with long periods of low temperatures, the "temperate-early" varieties may tend to be later than in strictly temperate regions.

It will be remembered that there are appreciable differences in the temperature responses of different wild species; *Solanum commersonii,* for example, appears to tuberize well at relatively high temperatures (Davies, 1941). There is therefore ample basal material from which to breed and select new varieties suited to tropical conditions. The appreciable variation in the responses of European varieties (Bodlaender, 1963; Krug, 1963) also allows choice in selecting suitable varieties from existing high-yielding ones.

Another aspect which may be of considerable importance in tropical regions concerns dormancy and storage conditions for seed tubers. There are probably a number of regions where two crops can be produced annually and there will also be a desire to use locally-grown rather than imported seed. Storage, with high ambient temperatures (say, greater than 5 —7°C), may require expensive refrigeration to provide the necessary control; selection of varieties with a long dormant period may then prove advantageous. Frequently in regions where two crops per year are possible (cf. Kawakami, 1962), suitable tubers for spring planting from autumn-grown crops can be obtained but tubers for autumn planting pose greater difficulties. The period between harvesting spring-planted crops and planting the autumn crop is usually too short and that between successive autumn crops too long to obtain suitable seed tubers (say, with 2—4 strong growing sprouts). Here, varieties with a long dormant period may prove advantageous. Cultural practices must of course be adapted to the existing environmental conditions. The general responses with age and to storage environments are enumerated in a number of papers in Ivins and Milthorpe (1963); these provide a background from which the required procedures for particular situations can be evolved.

Sugar beet

As mentioned above, sugar beet is much more closely integrated than the potato and less responsive to environmental variations. Once the "constant" phase of bulking has been established (i.e. by the time the root has achieved a fresh weight of 30—40 g), subsequent wide variations of light and temperature appear to have small effects on the growth of the root (Milthorpe and Terry, 1967). That is, the rate of growth is set by the environment during the first 8—10 weeks of growth and changes little until the environment reaches the lower limits for growth (say, mean temperatures of about 5°C and radiation of about 70 cal cm^{-2} day^{-1}). During the whole period of growth, the ratio of weight of storage root to that of the shoot follows a constant pattern (Fig. 5). This pattern is not influenced by variation in light supply. Low light simply results in slower growth; although photosynthate may then generally be expected to be short, the amount produced appears to be equally shared between all requirements including the storage of sugar in root cells (Fig. 6). Variation in temperature on the other hand influences the pattern as well as the rate of growth — at low temperatures a higher proportion of the (lower) net increase in weight goes to the root and a larger proportion is stored as sugar than at temperatures at which the total growth is more rapid. However, this effect decreases as the plant increases in size; in the later stages of growth large differences in temperatures have little effect. High concentrations of nitrogen in the soil solution appear to work in the same direction as high temperature, i.e. for a larger proportion of the current increment in weight to go into leaf rather than root growth.

There is, over a wide range of environments, a continued and ample supply of substrates from the leaves. Senescence is slow and gradual, the leaf area being maintained in excess of that required for a very long time — certainly, under European conditions, until the temperature has fallen too low for growth.

With sugar beet, as all crops, shortage of water leads to an immediate decrease in the rate of growth of all parts of the plant (Owen and Watson, 1956). However, unless the period of water deficit is unduly prolonged, restoration of the water supply leads to an immediate resumption of growth at a rate higher than that pertaining before experiencing the water deficit. The loss in growth is thereby compensated to an appreciable degree. Sugar beet appears to have, to a greater extent than most other plants, this capacity to make good potential losses induced by water deficits.

Flowering in sugar beet is, of course, induced by prolonged exposure to very low temperatures, old plants being more responsive than young plants. Although there is appreciable varietal variation, young plants may frequently be induced to flower; the resultant "bolting" and diversion of photosynthate to stem and flower growth results in greatly reduced rates of growth of the storage root.

CONCLUSIONS

Young plants of all species are always much more responsive than old plants to variation in the environment and generally root crops are less responsive than leaf and fruit crops. the extremes of stability found in the general category of "root crops". Exploration of the truly tropical species, both in terms of degree of response during ontogeny and in respect of mechanisms involved, is sure to be rewarding — leading to clearer understanding and control in agricultural production and providing more precise understanding of the physiological bases of plant morphogenesis. Generally, very little is known about these species and they provide a rich field for investigation. Even with the

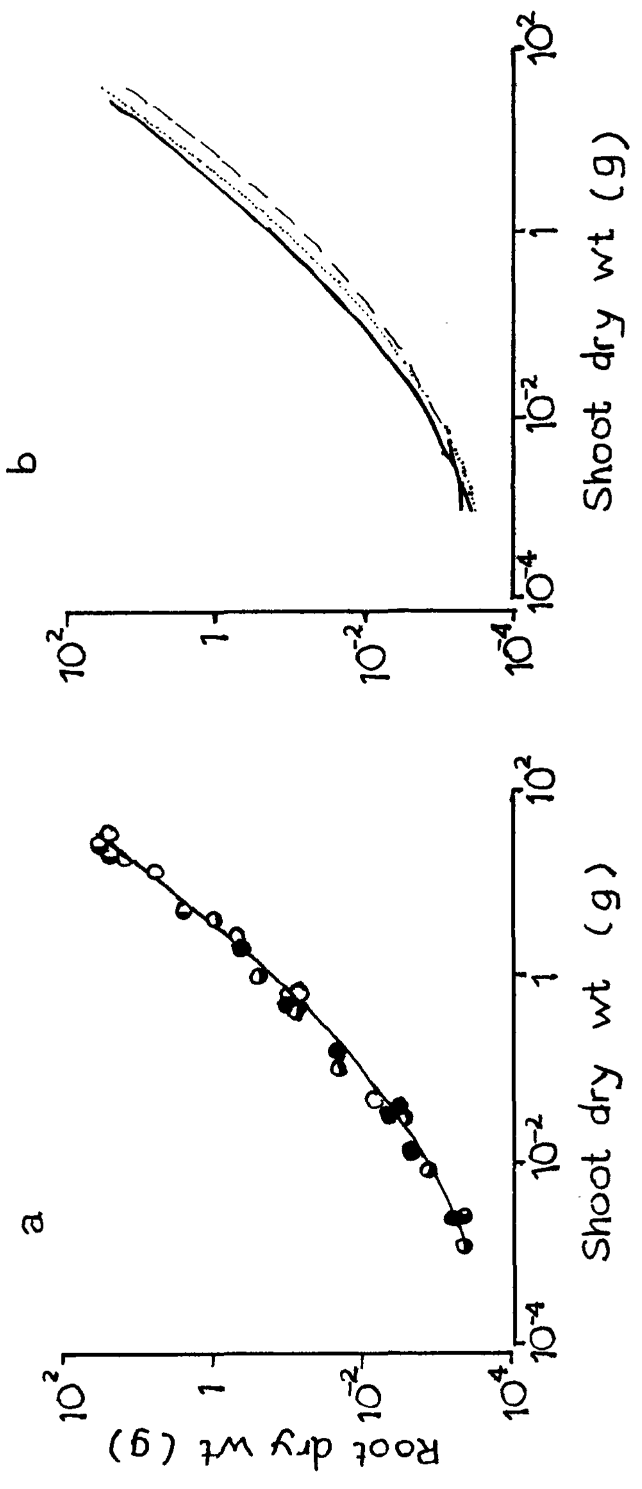
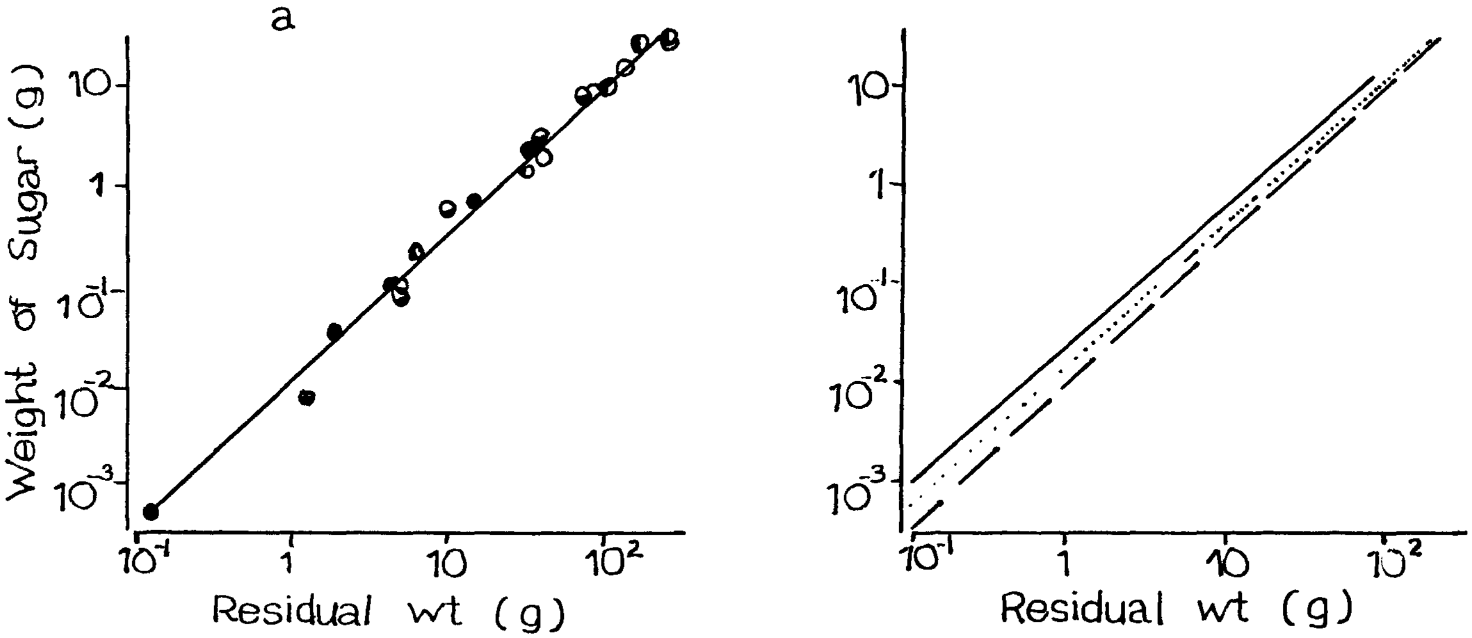

a
Root dry wt (g)
10^2
1
10^{-2}
10^{-4}
Shoot dry wt (g)
10^{-4}
10^{-2}
1
10^2
b
10^2
1
10^{-2}
10^{-4}
Shoot dry wt (g)
10^{-4}
10^{-2}
1
10^2

Fig. 5

Fig. 6


a
Weight of Sugar (g)
10
1
10⁻¹
10⁻²
10⁻³
10⁻¹
1
10
10²
Residual wt (g)
10
1
10⁻¹
10⁻²
10⁻³
10⁻¹
1
10
10²
Residual wt (g)

temperate crops, which have been investigated more extensively, there is but a fragmented and quite inadequate understanding.

One conclusion emerges clearly from agronomic experience during the past few decades. This is that knowledge of the varying responses of a species to its environment throughout all stages of its ontogeny is essential for efficient agricultural production. The era of the costly, inefficient, and strictly limited field experiment in which the final yield only is measured is now ended. It is now recognized that these provide too little information for the effort expended; progress is more rapid where every attempt is made to study the system as thoroughly as possible by analysing sequentially the relevant physiological and morphological responses. This information must be married to the increasing appreciation of the soil and aerial environment; it is only in this way that the agronomist can progress towards a clearer understanding of this complex ecological systems and thereby to contribute to the achievement of higher yields and more efficient agriculture.

Table 1. Content of ^{14}C in mother and daughter tubers of a growing plant

Tuber	Dry weight (g)	^{14}C-content (10^5 counts per minute per tuber) Ethanol-soluble compounds	Ethanol-insoluble compounds
Mother	1.76	1.91	2.21
Daughter 1	5.22	1.16	1.41
2	4.47	7.03	10.02
3	4.06	1.21	1.28
4	3.30	10.62	12.36

Figure 1. Diagram showing the general development of leaf surface and storage organs in potato, sugar beet and sweet potato. The data for potato are generalized to cover the Midland region of England and show the potential net assimilation rate (Ep) (After Milthorpe, 1963). The data for sugar beet are from Scott (1964) and those for sweet potato are from Walter (1966).

Figure 2. (a) Time to emergence and to tuber initiation in relation to length of sprouts at planting and (b) time to emergence as influenced by temperature.

Figure 3. Diagram illustrating differences between stolon growth and tuber growth.

Figure 4. Relation between rate and duration of bulking to time of tuber initiation. Plants such as (a) which tuberize early have a long period of slow bulking and mature quickly; plants such as (b) which tuberize late have a rapid rate of bulking which is maintained for a long time (After Burt, 1965).

Figure 5. Relationships between root dry weight and shoot dry weight of sugar beet when (a) grown under a range of light intensities at 10° and (b) when grown at 10° (continuous line), 17° (dotted line) and 24°C (dashed line). (After Milthorpe and Terry, 1967).

Figure 6. Relationships between sugar content and residual weight of root of sugar beet when (a) grown under a range of light intensities at 24° and (b) at temperatures of 10° (continuous line), 17° (dotted line) and 24°C (dashed line). (After Milthorpe and Terry, 1967).

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