Productivity of Root Crops

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The presence of an underground storage organ introduces a unique dimension to the productivity of plants. This dimension concerns the role of the organ as a sink for photosynthates in competition with leaf and stem growth. The extended periods of time over which bulking may occur, and its indeterminant nature, means that the competition for substrate influences the dynamics of plant growth over much of the life cycle. It is important then that we understand the controls by which bulking is balanced with other growth activities of the plants.

Although root crops involve special problems in partitioning of photosynthates, other aspects of their production processes seem to be similar to most other higher plants. This discussion of productivity in root crops first examines production processes of plant communities and then considers the dynamics of partitioning to storage organ growth, and its control.

Primary Production in Plant Communities

The radiation regime is a key factor in productivity. Above the earth's atmosphere the flux of short wave radiation averages 2.0 cal $cm^{-2}min^{-1}$ on a surface normal to the sun's rays. In the tropical regions, where solar altitudes vary between 66 and 90° elevation at solar noon, the diurnal totals of solar radiation on a horizontal surface outside the atmosphere range from 800 to over 900 cal $cm^{-2}day^{-1}$ throughout the year. With clear skies of low humidity, up to 80% of this radiation would be transmitted to the earth's surface. Most of this would be direct beam radiation and only a relatively low fraction (perhaps 16%) would be received as diffuse skylight. Thus, the peak irradiances in the tropics can be very high, exceeding 1.2 cal $cm^{-2}min^{-1}$. Radiation levels of this sort are observed in the desert environments of the arid subtropical regions where irradiances of 700–800 cal $cm^{-2}day^{-1}$ are common. When irrigation is possible, these regions will support very high levels of crop production. However, the potential receipt of solar energy is greatly modified by atmospheric conditions and high radiation levels are less common in the tropics because of cloudiness and humidity. Diurnal totals for solar radiation usually fall in the range of 300–500 cal $cm^{-2}day^{-1}$ of which 30–40% may be diffuse skylight. Values of 500 or more are achieved only during the dry season when moisture supply may limit the extent that the plant communities can benefit from the high radiation. Tropical environments are further limited by the short days, which range from 10.5 to slightly over 13 hours. At higher latitudes in the temperate zones, daily radiation totals of 500 or more cal $cm^{-2}day^{-1}$ are relatively common during the summer season. The lower solar elevation and longer days of these environments result in smaller values for peak irradiance and this can be of considerable advantage to the plant community.

The low irradiances of tropical regions are associated with smaller net radiation exchanges at the earth's surface. Net radiation is the difference between the totals of incoming and outgoing radiant fluxes and is related chiefly to exchanges of energy with latent heat and air temperature. Tropical environments thus have an advantage in low evaporative demands. In terms of primary productivity, however, the chief advantage of tropical regions lies with the length of the growing season, because other aspects of the radiation budget are generally inferior to that received during the summer season at higher latitudes. The long growing season lends an advantage to perennial crop-

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ping systems with indeterminant growth habits, i.e. to crops like cassava with underground storage organs of long growth duration.

The nature of the foliage cover is an important factor in determining the efficiency with which the available solar radiation is used in primary production (Loomis and Williams 1969). The leaf area index of most root crops increases slowly after planting, due in part to the use of relatively low plant densities. Depending upon species and environment, 6–12 weeks of growth may be needed to achieve full cover (at a leaf area index of about 3). Leaf area development may change with the onset of storage organ development. Haynes et al. (1967) show for yams (*Dioscorea alata* L.) that leaf area declines as tuberization begins. A similar response occurs with potato (*Solanum tuberosum* L.) (Moorby and Milthorpe 1975). In contrast, sugar beet (*Beta vulgaris* L.) (Loomis and Bennett 1966; Campbell and Viets 1967), sweet potato (*Ipomoea batatas* L.) (Tsuno and Fujise 1965) and cassava (*Manihot esculenta* Crantz) (Enyi 1972) continue to add new leaves to the canopy during tuberization and thus are able to maintain a reasonable leaf area index throughout the season.

One way to quantify these differences is to calculate the leaf area duration (the integral of leaf area index over time). Enyi (1972) found that 75% of the variation in cassava yields related to single and multishoot treatments could be ascribed to differences in leaf area duration. Similar correlations are found with other crops. However, crop growth rate is a nonlinear function (either plateau or parabolic; Loomis and Gerakis 1975) of leaf area, and leaf area duration, as a linear integration of leaf area with time, is not the most fruitful approach. A number of studies (Williams et al. 1965; Shibles and Weber 1966) suggest that the time integral of percentage light interception may be a better index. Crop growth rates increase as a linear function of percentage interception. The slope of the relationship and the maximum rate are dependent upon canopy architecture, photosynthesis capacity of the leaves, and environment.

The length of time before full cover is achieved after planting can be a major limitation to seasonal productivity. For this reason, evergreen foliage canopies of complete cover usually attain the highest annual production rates. The period of partial cover can be shortened with species that have a high allocation of photosynthate to foliage production, or through dense plantings (a large number of apical meristems per unit area). However, with either of these approaches, the allocation to storage roots or tubers later in the season may be less than would be achieved with a less dominant foliage system.

The production rate also depends upon the manner of leaf display relative to the sun. A great deal has been learned about these problems through the use of light distribution simulation models (Duncan et al. 1967; Allen et al. 1974; Lemeur and Blad 1974; Monsi et al. 1973). These models are now well developed. They have been validated in a wide range of crops and environments, and can be used in predictive simulations for other environments and situations. Models have been particularly useful for analyzing the efficiency of different canopy arrangements because genetic and mechanical manipulations of leaf display generally confound photosynthesis responses with other aspects of growth and development.

Some simulations with the Duncan model (Duncan et al. 1967; Duncan 1971) are illustrated in Fig. 1. With less than full cover, plants that display their leaves horizontally in regular arrays are found to be more efficient in light interception and more rapid in the development of full cover than those with inclined leaves distributed in clumped or random distributions. With a full cover canopy of leaf area index of 3, however, productivity is nearly independent of leaf angle. With very high foliage densities, simulations for a wide range of canopy architectures show clearly that there can be a marked increase in primary productivity using erect rather than moderately inclined leaves in the top of the canopy. In tropical regions, with very long growing seasons for the accumulation of leaf density, it seems that it might be desirable to attempt to achieve erect-leaved communities of very high foliage density. The advantage of erect leaves derives from distributing a high irradiance over a large area of obliquely displayed leaves. This reduces the frequency of light saturation of leaf photosynthesis, which occurs with high irradiance per unit leaf surface. However, with the characteristic low, diffuse irradiances of the humid tropics, the advantage is not nearly as great as is shown in Fig. 1 for clear skies in the temperate zone.

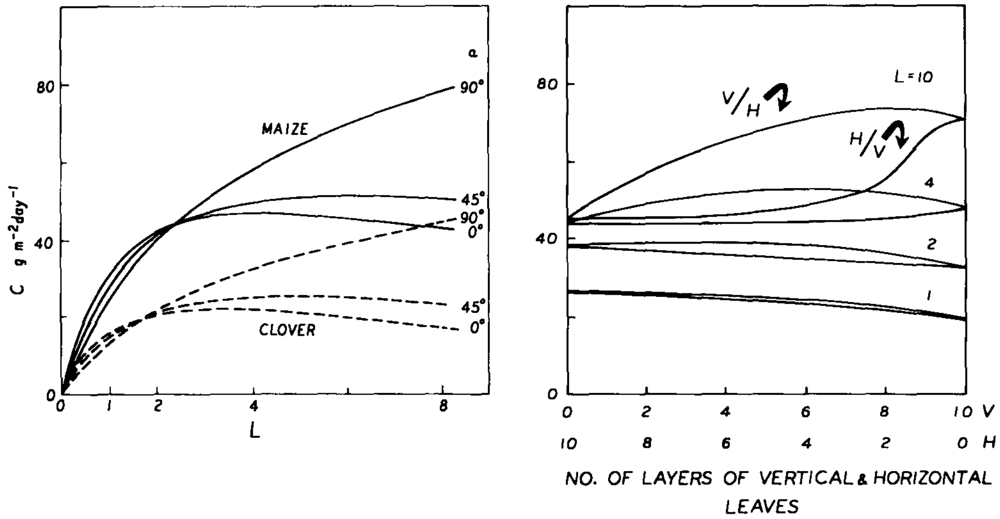

Fig. 1. (Left) Simulations with the Duncan model of crop growth rates (C) for communities of C_3 and C_4 plants of various leaf area index (L) and leaf elevation angle (α). The canopies are composed of 10 strata of randomly dispersed leaves. Solar and skylight data of 38 °N latitude, 1 July (after Loomis and Williams 1969). (Right) Simulations of crop growth rates for "best" and "worst" possible combinations of leaf angles at leaf area indices (L) of 1, 2, 4, and 10. Each canopy has 10 strata of leaves; the horizontal axis indicates the number of strata with vertical (V) and horizontal (H) leaves. The best canopies (upper lines in each case) have V leaves on top and H leaves in the lower strata. The worst canopies have H in upper strata, V in lower. C_4 plant; solar and skylight data of 40 °N latitude, 1 July (after Duncan 1971).

The influence of diffuse radiation on productivity has been considered in detail by Allen et al. (1974). Our own work with the Duncan model is illustrated in Fig. 2. The proportion of diffuse radiation (H_D/H) increases with increasing cloudiness, but this is associated with a sharp decline in the fraction of potential radiation that reaches the earth's surface (H/H_0) (Fig. 2, left). At any given radiation level (Fig. 2, right) simulated production rates increase as the proportion of diffuse radiation increases, but this effect is more than offset by the reduction in total radiation (connecting line). Although less pronounced with canopies of horizontal leaves and with zenith-bright skies, the decline was found for all canopies, dates, and latitudes.

There are several other difficulties associated with the achievement of dense foliage canopies in the tropics. With a specific leaf area of 2–3 dm^2g^{-1}, the dry matter of a hectare of leaves will range between 375 and 500 kg in blade material alone. With a protein content of 15–18%, 9–15 kg N ha^{-1} are required for each unit of leaf area index. Foliage canopies with leaf area indices of 8–10 thus require cycling of 70–150 kg N $ha^{-1}yr^{-1}$ for leaf blades alone. This is a difficult proposition in most tropical environments. Very high annual productivities have been achieved in tropical regions with certain grass species with net production in the range of 50–80 or more MT ha^{-1} (Loomis and Gerakis 1975). These crops involved the development of extremely dense foliage canopies but 1000–2000 kg N ha^{-1} of supplemental fertilizer were required. This suggests that photosynthetic capability is not the principal limitation to yields in the tropics.

There are a number of reasons, then, that point to the use of relatively low leaf-area indices for optimizing the production of root crops in tropical environments. With a low leaf area index, a high proportion of the leaf surface will be exposed to irradiances sufficient for saturation of leaf photosynthesis. And if water and nitrogen are not limiting, the question of the photosynthetic capabilities of root crops assumes some importance. Photosynthetic gas exchange in sugar beet, potato, and sweet potato have been studied rather well, but very little information has been developed for other root crops. In general, these plants all

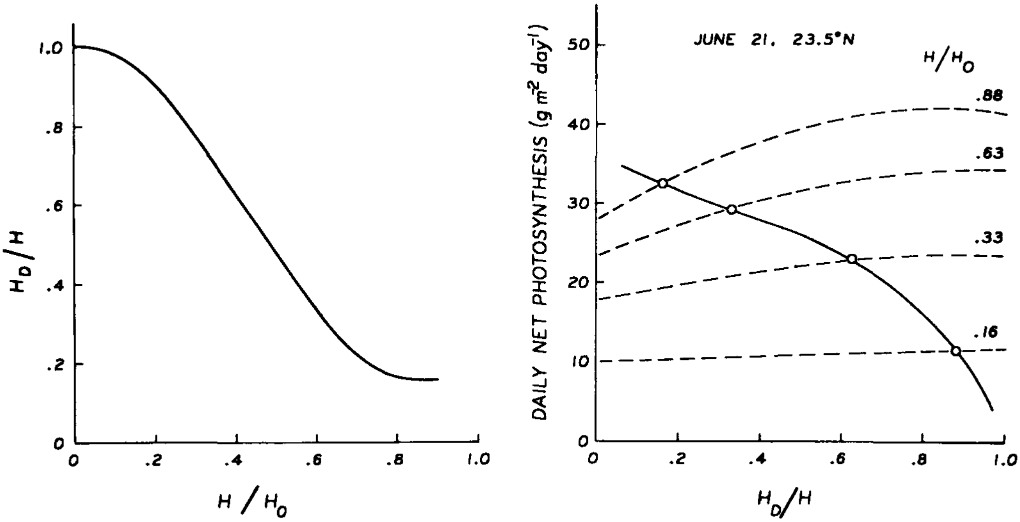

Fig. 2. (Left) Liu and Jordan's (1960) observations of the fraction (H_D/H) of daily total radiation on a horizontal surface (H) received as diffuse skylight (H_D) as a function of H/H_0, the fraction that daily total radiation was to that received outside the atmosphere (H_0). The observations were made throughout the year in the northern hemisphere; a high proportion of diffuse radiation occurs with high cloudiness and hence with a low proportion of daily total radiation. (Right) Simulations with the Duncan model of community photosynthesis rates with varying proportions of diffuse skylight (H_D/H) from a uniform overcast sky. Photosynthesis rate increases at each radiation level as H_D/H increases. The points and connecting line indicate the situation for "real" skies using the Liu and Jordan relationship shown to the left. The reduction in radiation offsets the more efficient distribution of radiation within the canopy and photosynthesis decreases as cloudiness increases. Solar data for 23.5 °N latitude, 21 June, C_3 plant.

have a C_3 pattern of carbon metabolism. They can achieve a high quantum efficiency at low irradiances, but they are susceptible to light saturation with 0.4–0.5 cal cm^{-1}min^{-2} of sunlight. The ribulose diphosphate carboxylase enzyme system of C_3 plants has a low affinity for CO_2 and assumes a role of an oxygenase enzyme under saturating light conditions (Schrader 1976). When water and nutrients are not limiting, such plants can achieve high levels of production, but the levels are still considerably below the records set in similar environments by tropical grasses and other species with a C_4 type of metabolism (Loomis and Gerakis 1975). C_4 species can achieve good rates of photosynthesis even when carbon dioxide concentration within the leaf is quite low, i.e. at high light or when the stomates are partially closed. This lends a capability to the C_4 species for a greater water use efficiency (Downes 1969) and many ecologists feel this may be the principal advantage of the C_4 mechanism.

It seems unlikely that the C_4 metabolic system can be easily introduced into C_3 plants; the inheritance is complex and the transfer has not been successful even in the few instances as in *Atriplex* where the two systems were found in closely related species (Bjorkman 1976). The alternative is to select for higher photosynthesis capability within C_3 plants. Little progress has been made in this direction, perhaps because environmental factors have strong influences on the system and our approaches have been relatively crude. Recent results with C_3 tomato (Augustine et al. 1977) are much more promising.

Regardless of the outlook in breeding, it would be helpful if we had more information on the photosynthetic capabilities of the root crop species. Response functions to temperature, light, and carbon dioxide concentration and their variation are needed. Good quality data on these functions can be obtained only through the use of fairly sophisticated gas exchange systems. Attempts to approach the problem through growth analyses techniques (e.g. calculation of net assimilation rates by dividing the crop growth rate by leaf area index) have been less satisfactory. NAR values are highly sensitive to environment since they integrate the daily patterns of temperature and solar radiation as well as the manner and density of leaf display and the respiratory activities of nonfoliage parts. Even when extrapolated to 0 leaf area index, NAR values may bear little relationship to the photosynthetic capability of a particular plant. Comparisons of NAR rates within or between species thus have provided little information about the morphological and physiological properties of the particular photosynthetic system.

Solar radiation flux, foliage architecture, and photosynthetic capability, then, are the principal factors affecting primary productivity. In the field, there are many subtle variations in these or other factors that add to the complexity of the situation. The placement of plants in rows, the use of species mixtures, deliberately or inadvertently within the plant community, and the phototropic movement of leaves are simple examples. Fukai and Loomis (1977) have developed a photosynthesis simulator for row-planted crops. The validated model predicts a 30% greater production rate when leaves of a cotton crop are uniformly distributed over the land rather than being clumped in rows. They also found that phototropic movements in cotton, which tend to maximize the proportion of leaves displayed normally to the sun's rays, can be advantageous to production rates with a small leaf area index. Williams and Ghazali (1969) have found movements in the upper leaves of cassava, with a tendency toward vertical orientation at night and a change to moderate angles of display during daylight hours. There were differences among varieties in the average leaf angle, the amount of diurnal change, and in the occurrence of a mid-day drooping to a more vertical leaf angle. The presence of disease or insect damage and the influence of leaf age may also become important factors in production. All of these features are susceptible to study and improvement. The supply of carbon dioxide, in contrast, is much more difficult to modify, yet it is probably a limiting factor during the mid-day period in most agricultural systems. Carbon dioxide is normally limiting under intense radiation and the extent to which this limitation is enhanced by depletion of carbon dioxide from the air within the crop is strongly dependent upon the efficiency of eddy transfer and hence on wind speed. Again, this will be less of a problem in the tropics with low radiation.

Partitioning

The allocation of new assimilates to respiration, growth, and storage is the second feature of the production system. Photosynthesis may be rather intimately associated with partitioning. As we saw earlier, in considering the dynamics of foliar development, partitioning to leaf growth has a strong control on the increase with time of community light interception and hence photosynthesis. In addition, photosynthesis rates may be depressed in some cases by the lack of active growth and storage sinks. Although final yields are obviously dependent upon photosynthesis, crop physiologists have had difficulty in correlating variations in yield components with photosynthesis rate. The extensive work by Wallace et al. (1976) with bean, as an example, illustrates the difficult morphological questions that are encountered. We will look briefly at respiration as an aspect of partitioning before turning to the morphogenetic questions that lie at the heart of the partitioning problem.

Respiration

Plant biologists have had a tendency to treat respiration rather casually and to consider it primarily as a wasteful drain on assimilate supply. Our understanding and conceptualization of respiration in higher plants has been advanced markedly in the past few years. McCree (1971) identified two main components of whole-plant respiration: one part associated with the cost of maintaining the existing system; and a second part, which in his formulation is proportional to the photosynthesis rate. The second term corresponds to the energy cost of biosyntheses and growth. His formulation parallels the position that microbiologists had reached earlier (e.g. Pirt 1965).

Smith (1949) and other early workers in photosynthesis recognized that the amount of respiration would be heavily dependent upon the end products of growth and photosynthesis. Penning de Vries (1974) and Penning de Vries et al. (1974) have formulated this approach rather rigorously in a classic study. Using current concepts of metabolic pathways, they calculated the energy and material costs of synthesis from primary photosynthate for each

Table 1. Balance sheet for respiration associated with biosynthesis and growth of biomass in young corn plants. Amino acid, protein, and organic acid compositions appropriate to corn were used (after Penning de Vries et al. 1974).

Compounds	Fraction of plant $\left(\frac{\text{g}}{\text{g biomass}}\right)$	PV[a] $\left(\frac{\text{g glucose}}{\text{g product}}\right)$	Substrate use $\left(\frac{\text{g glucose}}{\text{g biomass}}\right)$	O_2 consumed (g)	CO_2 produced (g)
Nitrogenous					
Amino acids	0.023				
Protein	0.200				
Nucleic acid	0.077				
	0.230	0.620	0.371	0.00208	0.0924
Carbohydrates					
Sugars	0.085				
Cellulose	0.226				
Hemicellulose	0.226				
Pectin	0.028				
	0.565	0.853	0.662	0	0.0377
Lipids	0.025	0.351	0.071	0	0.0355
Lignin	0.080	0.483	0.166	0.00735	0.0404
Organic acids	0.050	1.104	0.045	0	—0.0023
Minerals	0.050	0	0	0	0
Respiration for additional ATP and $NADH_2$ production, ion uptake, and glucose transport	0	—	0.223	0.18000	0.3280
Total	1.00		1.538	0.189	0.530

[a] PV is the "product value", g product achieved per g glucose consumed starting with NO_3-N and SO_4-S, but unbalanced for total ATP and $NADPH_2$ needs that are balanced at the bottom of the table for the whole plant. The net product value, 1.00 g biomass/1.538 g glucose = 0.650.

type of primary plant product. For example, starting with glucose, they totaled the number of ATP and $NADH_2$ molecules required in a least-cost pathway for the synthesis of each amino acid and for the assemblage of these into typical proteins. The same process was followed with carbohydrates such as cellulose, lipids, nucleic acids, and other products. Associated with these biosyntheses were identifiable but less certainly determined costs associated with transport, gradient maintenance, and turnover of proteins and nucleic acids. Detailed tables giving product yields (g product/g glucose) for all of the important constituents of higher plants were presented. Starting with nitrogen and sulfur in reduced or oxidized forms, a summary of their calculations for the biochemical composition of typical corn plant material is shown in Table 1. Two key points are evident. First, the respiration cost for the synthesis of lipids and proteins is very high in comparison to that for carbohydrate fractions; plants with a high proportion of carbohydrates in their biomass will have a greater weight yield per unit of photosynthate. Second, even though corn plant material has a relatively low protein and lipid content, about 25% of the original photosynthate supply is consumed by respiration associated with syntheses (growth). This percentage agrees well with McCree's estimates of the growth-associated respiration of clover (McCree 1971) and sorghum (McCree 1976) plants.

Respiration budgets of this sort apply only on a whole plant basis. One of the largest energy costs, for example, is the reduction of nitrate. In many plants, this is accomplished largely in the leaves with some direct participation of photosynthetic energy sources. The growth respiration for nitrogen metabolism of a storage organ on the other hand involves only the cost of assembling these amino acid

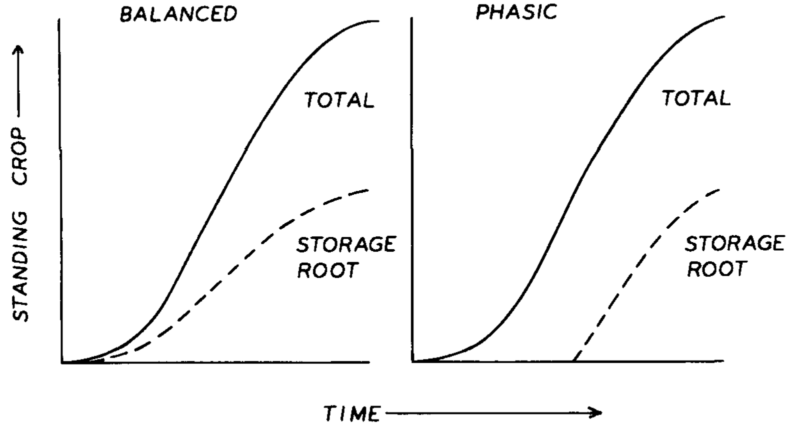

Fig. 3. The time course of two types of partitioning observed in root and tuber crops. (Left) Continuous partitioning. (Right) Phasic partitioning.

units into proteins. If the protein and lipid levels of storage organs are low, the growth respiration will also be relatively low. The maintenance respiration of storage organs also can be very low if a high proportion of the dry matter is carbohydrate and is compartmentalized in starch grains.

Source-Sink Relations

The other aspects of the partitioning process seem to centre principally on the relative activity of photosynthate sinks (Evans 1975). Agricultural crops usually are grown under conditions that result in fairly intense interplant competition and if nutrients and water are not limiting, source activity is usually the most limiting part of the system. Limitations due to sink activity and transport capacity, however, can be demonstrated. Through manipulations such as the removal of developing fruits or girdling (Humphries 1967; Neales and Incoll 1968), carbohydrates accumulate in leaf and stem tissues and photosynthesis is usually depressed. The negative feedback on photosynthesis might occur at any of several steps in the process. A direct repression of carboxylase enzymes has not yet been demonstrated and the mechanisms for assimilate control of photosynthesis remain unresolved (Thorne and Koller 1974). However, as Evans (1975) concludes, source-sink and transport systems are relatively well balanced in most crop plants to the side of source limitations.

As illustrated in Fig. 3, there are two general patterns of partitioning during the growth and development of plants with underground storage organs. In one type, characterized by the sugar beet, storage organ growth begins early in the seedling stage and continues throughout the vegetative period of the plant. There is an indeterminate competition between shoot growth (particularly of new leaves) and storage organ growth. Shoot growth retains a priority for assimilate supply even though the relative magnitude of top and root may change as root size increases. A balance between these two activities is maintained throughout the growing season. In the other type of partitioning, early vegetative growth is characterized by shoot and fibrous root development. Storage organ growth begins later, is usually more determinate in nature, and often requires an inductive environment. Examples of this type of growth include the potato and cassava, some varieties of which begin tuberization after being exposed to short days (Bolhuis 1966; Gregory 1956; Okigbo 1971). The switch to storage organ growth may be quite dramatic with a subsequent cessation and/or even negative growth of shoot tissues.

Balanced Partitioning: The Sugar Beet

The balancing mechanisms between shoot and storage organ growth in plants such as the sugar beet may be based on several functional activities. In shading or crowding experiments we can demonstrate a sequence of priorities in the utilization of a limited supply of photosynthate. The growth of new leaves clearly has priority over fibrous roots and both of these have priority over storage root growth. We do not understand how this priority series is estab-

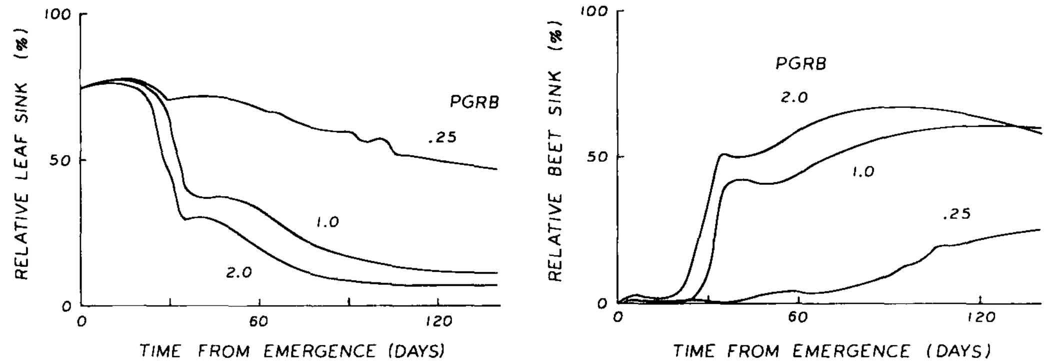

Fig. 4. Simulations with a dynamic, integrative physiology model (SUBGOL; Hunt 1974; Loomis et al. 1976) of growth sink activities for sugar beet. Relative sink activity is expressed as a percentage of the total daily allocations of photosynthate to growth, storage, and respiration. The model responded to long-term weather data for Sacramento, Calif., (38 °N latitude); emergence was on 16 May with 7 plants m^{-2}*. Possible Growth Rate of Beet (PGRB) is varied as a genetic opinion with 1.0 corresponding to sugar beet, 2.0 representing mangel, and 0.25 representing Swiss chard. (Left) Leaf growth sink. (Right) Beet growth sink.*

lished and maintained. The relationship between fibrous root and storage root growth is particularly interesting since transport to fibrous roots in the sugar beet occurs past the actively growing vascular cambia of the storage root. One direction for research is to examine the controls over phloem loading and unloading (Wardlaw 1974).

In addition to the top-down priority in photosynthate distribution, there seems to be a reverse order of influences for deficiencies of nutrients and water acquired by the roots. Stresses for these factors are usually more limiting to shoot growth than for the growth of fibrous roots and underground storage organs. Brouwer and de Wit (1969) have formulated the top-down photosynthate priority and the root-up priority for water into a "functional balance" hypothesis to explain the maintenance of root/shoot ratios in plants. Finally, correlative controls provided by plant hormones also play a key part in the allocation process. The role of auxins in apical dominance in shoots provides a classic example (Phillips 1975). Fluxes of abscisic acid and cytokinin from roots also serve to regulate shoot growth (Leopold and Kriedemann 1975). Correlative controls over the activity of underground organs will be considered later. Unfortunately for our understanding of whole-plant processes, there has been very little study of the interactions between substrate supply and hormones in the control of growth and development.

Our own research on this problem has been greatly aided by the development of a dynamic simulation model of the sugar beet production system (Fick et al. 1973, 1975; Hunt 1974). The model is based on tissue and organ level physiology and attempts to integrate the relative activity of sources and sinks into a behavior of whole plants and crops. The structure of the model and its behavior then represent a hypothesis for the controls over partitioning in sugar beet. The simulations illustrate clearly a transition from foliage dominated growth to storage root dominated growth (Fig. 4). The initial size of the future storage organ (the hypocotyl and primary root axis) is too small at emergence, even with maximal activity of the cambia, which develop very early in the seedling stage (Winter 1954; Milford 1973), to use a significant proportion of the available photosynthate. In the model, leaf growth thus wins in the early competition for the limited supply of photosynthate. As a result, photosynthate supply expands rapidly, more rapidly in fact than the capacity for root growth. This additional photosynthate allows successive leaves to reach a larger and larger size (Fig. 5, middle). The potential photosynthesis per plant is determined by density, which establishes the area of the sunlight available per plant. As the tops expand to fully occupy this area, the photosynthesis rate per plant comes to a maximum value. With a single apical meristem per plant, the capacity of the leaf sink has a ceiling determined by the (leaf initiation rate) × (growth capacity of the ex-

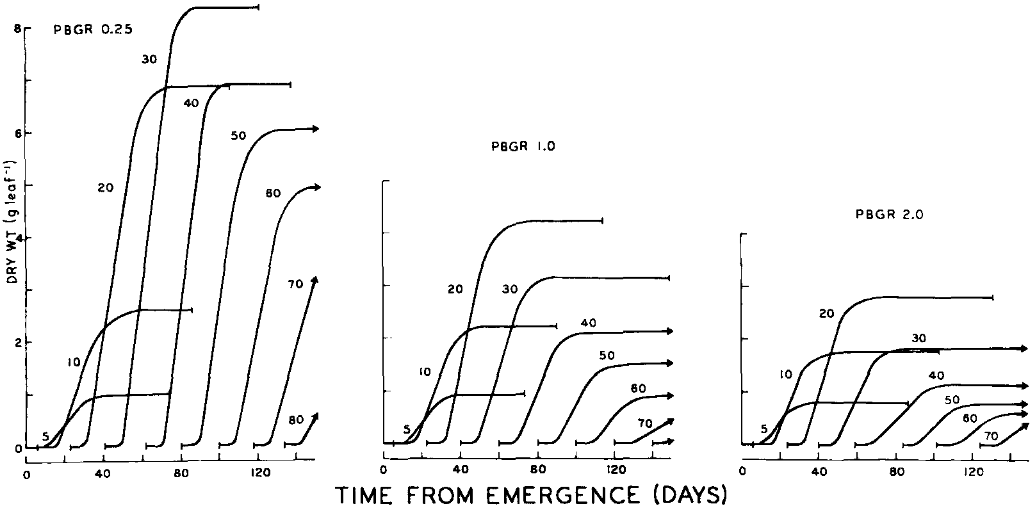

Fig. 5. Simulations with SUBGOL of the growth in weight of successively numbered leaves of sugar beet plants. Inputs are the same as in Fig. 4. (Left) Leaf growth in competition with chard root. (Middle) Leaf growth in competition with sugar beet root. (Right) Leaf growth in competition with mangel root.

panding leaves) × (the number of plants per unit area) (Loomis et al. 1976). During this period, the storage root has continued to expand and increase in its capacity for growth, which eventually exceeds not only the growth capacity of the shoot but also of the photosynthate supply. The result is the transition from shoot-dominated growth to root-dominated growth illustrated in Fig. 4.

It is significant that the shoot continues to be an effective competitor for the limited supplies of photosynthate. The explanation for this seems to be that the leaf initiation rate is relatively unaffected by competition for substrate and that the developing leaves maintain a priority for assimilates, including their own, during their initial period of growth. The final mature size of the later leaves is smaller than those that mature earlier without significant competition from the storage root (Fig. 5).

The sensitivity of the partitioning system is revealed by altering the "genetic" opinions introduced into the model. For example, we can vary the "possible growth rate" of the storage organ. In real plants, this might correspond to changes in the number of cambia in the storage organ, or in their cell division rates, or in the capacity to transport assimilates from the shoot. By reducing this possible growth rate by a factor of 0.25, we markedly delay the transition to storage root-dominated growth and also reduce the degree of root dominance (Fig. 4). Also shown in Fig. 4 is the result of doubling possible root growth, corresponding to a genetic opinion for the mangel. The results correspond to the differences observed in real plants between sugar beet and Swiss chard, and mangel, which are all members of the *Beta vulgaris* species. In the simulation, the reduced capacity for root growth allows the assimilates to be used in leaf growth and development. Figure 5 illustrates simulations of leaf growth for beet, chard, and mangel and shows clearly the kinds of leaf-size differences observed with real plants.

We do not know whether real plants control these aspects of partitioning through "possible growth rates" of roots, or by analogous controls over shoot growth (Loomis et al. 1976) although we have some confirmation for root control of partitioning in *Beta* species through reciprocal grafts of sugar beet and chard. Chard plants normally develop very large leaves, but when grafted to a sugar beet stock with a very strong capacity for storage organ growth, the resulting chard leaves are smaller, particularly in their petiole weights (Fig. 6). The reverse is true when beet shoots, which normally have smaller leaves, are grafted to chard stock. The chard root is unable to effectively use a large proportion of the assimilate and beet leaf growth is greater than when the

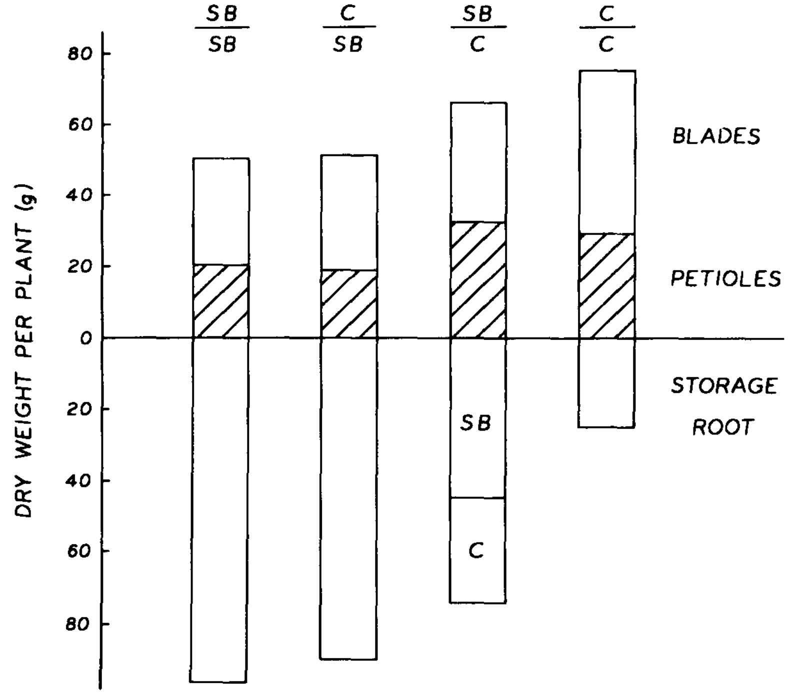

Fig. 6. Dry weights of underground storage organs and leaves, separated into blades and petioles, from grafted plants of sugar beet and chard. The grafts were made in the seedling stage with apical buds as scions. The leaves developed in competition with active thickening of the storage roots. SB/SB, C/SB, SB/C, and C/C indicate scion/stock sources as sugar beet (SB) or chard (C). With SB/C, a very small amount of hypocotyl tissue that was transferred with the apical bud developed significant cambial activity, and the proportions of those roots derived from SB and C are indicated.

beet leaves compete with the strong sugar beet storage root.

The chard-beet grafts indicate that much of the control over the *capacity* for storage root growth is an inherent characteristic of the root genotype. Similar conclusions can be drawn from grafting experiments with other root and tuber crops including sweet potato (Wilson 1967; Hozyo et al. 1971; and Hozyo and Park 1971), potato (Bunemann and Grassia 1973), cassava (Mogilner et al. 1969; de Bruijn and Dharmaputra 1974) and earlier work with sugar beet by Thorne and Evans (1964).

These experiments and simulations reveal the main features of the chard/beet, root/top partitioning system and lend support to the thesis that assimilate supply plays a role in control. Two directions for further research are indicated. One is to ascertain whether there are basic differences in cell division and expansion between chard and sugar beet storage roots. The chard plant actually has a greater number of cambia layers, so its lower capability for growth must rest with either a lower rate of cell division/enlargement when unrestrained by substrate, or with a lower priority in acquisition of photosynthates from the shoot. Again, it is unclear whether such a lower priority could also result from a higher growth capability in shoots or some limitation in phloem transport. Chard plants actually have a lower rate of leaf initiation, so the principal difference, if it rests in shoot growth potential, has to fall to the number of cells and their final size within the developing leaves. Nutritional control of partitioning could also be exercised in a number of other ways. We should not overlook, for example, the possibility that there are marked differences in these plants in the capacity or mechanisms for phloem loading and unloading (Wardlaw 1974). This would directly affect, in a nutritional sense, the priorities of shoots and roots.

The second area of research involves investigations of the correlative influences over root and shoot activity. In experiments in which we have used the radish plant (*Rhaphanus sativus* L.) as a model of vascular cambial activity in underground storage organs, we discovered that auxin must be present for the initiation of a vascular cambium, and that cell division is sustained only if a cytokinin is also present (Loomis and Torrey 1964). Peterson (1973) has confirmed and extended these findings for the turnip. In sterile culture, the thickening of excised radish roots is independent of the presence or absence of the root tip suggesting that the supply of cytokinins from this source is not a factor in vascular cambium activity. This conclusion is reinforced by the demonstration of polar transport within radish hypocotyls and root sections in which auxin and cytokinin both are preferentially transported from the shoot towards the root end of these tissues (Radin and Loomis 1974). Thickening fails to occur when the hormones are supplied from the root tip end of a root or hypocotyl segment.

We may find that hormones do not serve as quantitative control agents over the degree of partitioning. Instead, they may act as switches to initiate events and subsequent variations in cambial activity may be more strongly determined by nutrition than by the hormonal milieu. Lawrence and Barker's (1963) study on the role of the carbon source for the tuberization of potato supports this view.

Phasic Partitioning

The partitioning patterns of many root and tuber crops may be more determinate than in the sugar beet. The same aspects that we discussed for balanced partitioning (e.g. cell division and nutritional control) also apply here; the principal difference lies with *initiation* of storage organ growth. The early growth period is similarly dominated by shoot and fibrous root growth, but it is without competition from storage organs and may be of extended duration. Storage organ growth is initiated later in the life cycle, frequently in response to an environmental signal, and may completely dominate subsequent growth. In many respects, the situation is analogous to the determinate, phasic development of cereal grains. However, it is sometimes difficult to discern these differences in practical situations and the point may have utility more for ordering our thinking about physiological controls and plant breeding than for crop management. One reason is that a species may show phasic development in one environment where the inductive stimulus is seasonally present, but not in another, continuously inductive environment.

Photoperiodic induction of storage organ growth serves as one example of phasic controls. Beginning with the work of Garner and Allard (1923) we now know that fleshy root or tuber development in some varieties of potato (*S. tuberosum* L.), runner bean (*Phaseolus coccineus* L.), yam (*Dioscorea alata* L.), and Jerusalem artichoke (*Helianthus tuberosus* L.), *Dahlia*, *Begonia*, *Ullucus tuberosus*, *Oxalis tuberosa*, radish, cassava, and other species requires or is strongly stimulated by photoperiods shorter than 10–12 hours (long nights). It is interesting that both root and stem structures respond. Considerable genetic variation exists within species. Some radish varieties, for example, seem to require short days for thickening; others are neutral or accelerated by long days.

Nitsch (1971) and Leopold and Kriedemann (1975) have reviewed the present status of the physiological controls of short-day induction. The key findings include Nitsch's (1965) observation that tuber formation can be prevented in Jerusalem artichoke by a red light break during the dark period. With the same species, Hamner and Long (1939) found that the photoperiodic stimulus was perceived in leaves and that the influence was transmitted through grafts to noninduced plants (see also Gregory 1956). Most intriguing, leaves of sunflower (*H. annuus* L.) generated a short-day stimulus that induced tuberization in the artichoke (*H. tuberosus* L.) (Nitsch 1965). Induction may be quantitative; some plants are fully induced by a few photocycles but 'Sneezy' dahlia gave a linear increase in tuberization over the range of 4–28 inductive days (Moser and Hess 1968).

Hormonal control of tuberization in photoperiodic susceptible species may be complex. Palmer and Smith (1970) initiated tuberization in isolated potato stolons through an application of cytokinin. Extensive starch accumulation was the first event in the initiation process, an event that is inhibited by gibberellins. It is noteworthy that gibberellins also inhibit tuberization. They are present in elongating tips but decline rapidly with inductive treatment (Railton and Wareing 1973). Similar results have been found with *Dahlia* (Biran et al. 1974) where abscisic acid promotes root tuberization in plants on noninductive long days but gibberellin inhibits it. Forsline and Langille (1975) found that inducing conditions caused a very marked increase in cytokinin activity in potato shoots after two inductive cycles; the active cytokinins reached maximum values in below-ground tissues after 6 days and tubers were initiated after 8–10 days. It may be that transport of a cytokinin from shoot to root, parallel to that hypothesized for radish (Loomis and Torrey 1964), serves as the photoperiodic stimulus.

One other feature of phasic partitioning deserves comment. Once tuberization has begun, the competitive effects on shoot growth may be quite dramatic, even to the extent that shoot growth may be completely suppressed. Again, we find both nutritional and hormonal theories proposed for control. In potato, the haulm actually undergoes negative growth as materials are redistributed to the developing tubers (Moorby and Milthorpe 1975). Vegetative "cutout" also occurs in other systems, e.g. cotton, an indeterminate flowering plant, where apical growth ceases during heavy fruit development. Of the many relevant observations, it may be noteworthy that shoot growth inhibition occurred in some experiments with *Dahlia* when tuberization was promoted by short days or by foliar sprays of abscisic acid under noninductive long days (Halevy and Biran 1975). It remains to be seen whether storage roots and tubers release growth inhibitors that serve in the mobilization of resources from the rest of the plant.

It appears that photoperiodic control (and similarly temperature controls, which we have not discussed) may provide a functional balancing of shoot and underground organ growth, over time, for species in which tuberization, once initiated, is an over-dominant process. The control exists in many tropical root and tuber crops. Threshold daylengths are rather precise, usually in the range of 11–12 hours and the phenomenon may be important to the seasonal behaviour of some species within the tropics. Other species might carry the trait but exist always in the induced state in their native latitudes; tuberization would be continuous in the tropics (and hence balanced by other mechanisms as with the sugar beet) but highly seasonal at higher latitudes. Cassava's narrow geographical range near the equator is probably related to photoperiodic control (Bolhuis 1966; Jennings 1970). The trait should be considered in grafting studies (e.g. Wilson 1967) as well as in plant breeding and crop management.

Models in Root Crop Productivity

The production systems of crop plants involve a very large number of plastic elements. It is increasingly necessary when attempting to develop integrative explanations or predictions about systems to turn to simulation models as an aid for dealing with the complexity. We have seen that our present understanding of light interception, photosynthesis, and the partitioning aspects of plant growth have been greatly assisted through the use of such models. Many of these involve adaptive controls and thus respond to the changing nature of the plants and their environments.

A feature missing from such models has been an ability to simulate the hormonal regulation of adaptation and development. In models such as the sugar beet growth simulator, these concepts are simply entered as "genetic" rules. Radin (1970) outlined a hormonal control model for radish root development, including secondary growth and Wilson (1975) in an eloquent essay has gone further and outlined a scheme for modeling the interaction of hormonal and nutritional controls. This may be one of the tools needed, plus a great deal more information on physiology and morphology, before we can provide plant breeders and production experts with an integrated understanding of root and tuber crops.

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Total Dry Matter Production, Tuber Yield, and Yield Components of Six Local Cassava Cultivars in Trinidad

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Dry matter production, quantitative shoot morphology, dry matter distribution, tuber yield, and yield components of six representative cassava cultivars in Trinidad are presented. The results are discussed in relation to the yield performance of elite cassava cultivars and the yield potential of the cassava species. A cassava type on which improvement of the yield potential of the species might be based is identified.

Cassava production in the Commonwealth Caribbean is estimated at 26 × 10^3 t with an average productivity of 13.3 t/ha (7.8 tons/ha if the small but highly productive cassava in the Barbados is excluded). This level of cassava productivity is low compared with that in Brazil (14.6 t/ha), and cassava production represents only approximately 10% of the yam production of the region.

Cassava is grown in ecosystems ranging from the dry plains of Jamaica (annual rainfall 130 cm) to the very wet coastal plains of Guyana (annual rainfall 500 cm). However, despite the low productivity of Caribbean cassava, there have been reports of the existence of varieties with high yield potential (60 t/ha under experimental conditions). Similar productivity levels have been reported for elite cultivars in the CIAT cassava collection and a potential productivity level of 90 tons/ha/year has been predicted for the species by Cock (1974).

To increase Caribbean cassava production, two objectives must be achieved: (1) high productivity cultivars suitable for growth under the wide range of Caribbean ecosystems must either be identified or synthesized; and (2) cultural practices calculated to optimize yield of high performance cultivars must be developed.

In pursuance of these objectives, total dry matter yield, tuber yield, and other components of selected cultivars have been analyzed to study crop performance in cassava cultivars with contrasting growth habits. This was done prior to introduction of exotic germ plasm and regional testing of selected high performance types in different Caribbean ecosystems. Preliminary data on six representative cultivars are presented to place these cultivars in the profile of tuber yield productivity levels.

Materials and Methods

Six cultivars (*Manihot esculenta* Crantz) were grown on 30-cm-high ridges that were 90 cm apart. Stem cuttings (18 cm, 85 g) were planted 90 cm apart at an angle of 45° along the crest of the ridge and were each treated with 140 g of a standard 12:12:7 NPK fertilizer one month after planting. The experiment was established as a randomized split plot design with three replicates, as an out of season crop planted in the dry season on 10 January 1974. One week after shoot emergence selected

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