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~~CASSAVA~~

James H. Cock, Coordinator and Physiologist, Cassava Program,

Centro Internacional de Agricultura Tropical

AA 67-13,

Cali,

Colombia,

S. America

4859

THE CASSAVA CROP

1.1. Botanical Description

Cassava (Manihot esculenta Crantz) is a perennial shrub that grows up to 2.4 metres tall. The crop is normally propagated from stem cuttings. The primary shoot formed from the planting piece is a series of nodal units. Each nodal unit consists of the internode, the node, an axillary bud and a palmate leaf subtended on a petiole that is normally equal to or larger than the largest leaflet. The primary shoot normally shows marked apical dominance and growth of side branches is restricted. Side branches are sometimes formed, particularly when the apex is damaged or the main shoot nearly horizontal. When the main apex becomes reproductive two to six of the axillary buds immediately below the main apex develop into similar sized branches. These new branches may later branch in a similar fashion. This branching is normally synchronized with all plants branching at about the same time.

Cassava roots form from the callus at the base of the original stem cutting and the nodal areas. Roots may also form from the base of the new primary shoot. Starch deposition is first observed as early as three to four weeks after planting (Cours 1951, Sinha and Nair 1972). The starch is mainly stored in masses of xylem parenchyma cells formed in the central part of the root.

1.2. Ecological Adaption

1.2.1. Temperature. Cassava is grown between 30 N and 30 S latitudes at elevations up to 2,300 m above mean sea level. In Colombia, Peru and Ecuador, especially selected clones are grown in the highland areas where mean annual temperature is greater than 16-17 C. These areas are characterized by very small fluctuations in mean temperature. In areas with marked

seasonal temperature changes cassava is only grown when annual mean temperature is more than 20 C. Temperatures may reach 0 C with light frosts in cassava growing areas: frost causes necrosis of all the expanded leaves and may cause death of the younger green stem tissue, however, with higher temperatures the axillary buds in the woody lower nodes form new shoots.

1.2.2. Rainfall and soil moisture. The cassava crop is found in areas with as little as 750 mm/year to more than 3000 mm/year rainfall. Highest yields are obtained in areas with no pronounced dry season, nevertheless the crop can be grown in areas with up to six months without rain. During the dry period the crop ceases to produce new leaves, and as the older leaves senesce and abscise, becomes essentially dormant; at the onset of the rains root reserves are used to produce new foliage (Cours 1951).

While cassava will tolerate long periods with minimal amounts of water it is extremely susceptible to excessive water. Standing water for as little as 24 hours may kill the crop and growth is greatly reduced under waterlogged conditions. In areas with heavy rainfall and poor drainage cassava is frequently planted on ridges or mounds so as to improve the drainage.

1.2.3. Soil Conditions. Cassava is grown on a vast array of different soils throughout the tropics. It grows best and gives greatest yields under highly fertile conditions, however, most is grown on the poorer soils of the lowland tropics. Cassava is frequently grown as the last crop in the rotation in shifting cultivation, when fertility is very low, and in many areas is grown on the most depleted and eroded soils. Although yields are low it will still produce something under conditions of such extreme soil poverty that other food crops cannot be cultivated. Low soil fertility

status is frequently associated with extremely low soil pH and high levels of aluminum and manganese. Cassava grows better than most other crops under conditions of low pH and high levels of aluminum. It is on the other hand extremely susceptible to salinity and alkalinity; growth is greatly reduced when conductivity of the soil solution is greater than 0.5 mmhos/cm (Cock and Howeler 1978).

2. Major Physical Parameters

2.1. Leaf photosynthetic rate

Mahon et al. (1977a) measured the photosynthetic rate of attached leaves of cassava and nine wild species of *Manihot* grown in growth chambers. Maximum rates of photosynthesis ranged from 15-29 mg CO₂ dm⁻² hr⁻¹ in *M. quintipartita* and *M. dichotoma* respectively. All the cassava clones tested lay within this range; considerable differences between clones were observed with the clone M Col 22 giving rates of 29 mg CO₂ dm⁻² hr⁻¹ at saturation. This rate was 20% greater than that of any other clone tested.

At CIAT plants grown out of doors in pots gave maximal rates of 33 mg dm⁻² hr⁻¹. MCol 22 had the second highest photosynthetic rate of 32 mg dm⁻² hr⁻¹ (CIAT 1977). In general the rates obtained at CIAT were higher than those obtained by Mahon et al. (1977) with the lowest rates at saturation light intensity close to 27 mg dm⁻² hr⁻¹.

Mahon et al. (1977b) obtained the highest rates of photosynthesis of young leaves at 25 C and older leaves at 30 C suggesting that the optimal temperature for photosynthesis is 25-30 C. Young leaves of plants grown at 29/26 C day night temperature had much greater photosynthetic rates than leaves grown at 24/19 C when measured at high photon flux densities.

Cassava leaves show a light saturation response typical of C-3

plants with little increase in photosynthetic rate above 1200-1500 Einsteins $m^{-2} sec^{-1}$ (Mahon et al. 1977a, 1977b, CIAT 1976, 1978). Mahon et al.

(1977a) obtained a net efflux of CO_2 at 45 vpm CO_2 in all materials tested and Mahon et al. (1977b) estimated the CO_2 compensation point as 68 vpm at 25 C. At CIAT we have obtained similar values at 25 C increasing rapidly with temperatures up to more than 100 vpm at 35 C. These data are all indicative of a C-3 photosynthetic pathway in cassava.

The photosynthetic rate of leaves of most crops decreases markedly with leaf age. Mahon et al. (1977b) obtained much lower leaf photosynthetic rates in older than in younger leaves. Aslam et al. (1977) also found large decreases in photosynthetic rate at high light intensity as leaves aged but found no effect of plant age on photosynthesis. Some of the clones tested showed a much smaller decline than others and they suggested that this might be of importance particularly for screening purposes. Plants grown in small pots out of door showed a marked decline in photosynthetic rate with plant age, however, removal of two thirds of the leaves rapidly returned the remaining leaves to the original rate ($30 mg dm^{-2} hr^{-1}$) which was then maintained until 100 days after planting if two out of every three leaves was removed as it formed (CIAT 1979). In trials with plants grown in large plots with the clone MCol 72 no significant decrease in photosynthetic rate of individual leaves was observed with leaves up to 100 days after date of appearance (Fig. 1). Unfortunately this clone was not used by Aslam et al. in their trials, however, MCol 22 in their trials showed a marked decrease in leaf photosynthetic rate with plant age while in trials at CIAT it has maintained high rates of leaves 50-60 days after leaf emergence. Although the data on photosynthetic rate as a function of leaf age are somewhat conflicting it does appear that clones do exist that

show very little decline in their photosynthetic rate as the leaf ages.

The photosynthetic rate of leaves of cassava plants grown in sand culture was reduced at lower nitrate levels in the culture solution (Mahon *et al.* 1977). Plants grown in a very infertile oxisol with and without fertilizer showed a relatively small reduction in photosynthetic rate of individual leaves (Fig. 2) although total dry weights per plant was markedly reduced (Watana and Cock unpublished data, CIAT 1978).

2.2. Crop Growth Rate and Leaf Area Index

2.2.1. Maximum reported crop growth rates. Enyi (1972) reports crop growth rates of $200-300 \text{ g m}^{-2} \text{ wk}^{-1}$ from trials in Sierra Leone and Zandstra (1979) states that cassava has maximum crop growth rates of $210-280 \text{ g m}^{-2} \text{ wk}^{-1}$, but gives no details on how these figures were obtained. Williams (1972) estimated crop growth rates of $315 \text{ g m}^{-2} \text{ wk}^{-1}$ from plants grown in polyethylene bags but with field grown plants maximal crop growth rates were close to $150 \text{ g m}^{-2} \text{ wk}^{-1}$. In a series of trials at CIAT and the surrounding area the author has repeatedly obtained values of $100-120 \text{ g m}^{-2} \text{ wk}^{-1}$ with solar radiation of $400-450 \text{ g cal cm}^{-2} \text{ day}^{-1}$ and values up to $140 \text{ g m}^{-2} \text{ wk}^{-1}$ were recorded in one trial (CIAT 1972). The weight of the fallen leaves, which may reach $3 \text{ g m}^{-2} \text{ day}^{-1}$ (Cock 1976) was included in the calculation of these crop growth rates. In other trials, reported data do not include fallen leaves and hence crop growth rate is underestimated. Enyi (1973) obtained values of $100-120 \text{ g m}^{-2} \text{ wk}^{-1}$ and there are a number of reports of values of $80-100 \text{ g m}^{-2} \text{ wk}^{-1}$ (Cours 1951, Holmes and Wilson 1976, Cock 1976, Cock *et al.* 1979). Unfortunately most of the reports make no mention of the solar radiation during the measuring period and hence it is difficult to compare different data sets. Nevertheless the reports of crop growth rates above $200 \text{ g m}^{-2} \text{ wk}^{-1}$ are difficult to reconcile with the report-

ed rather low photosynthetic rates of cassava leaves. The author suggests that the maximum crop growth rates under conditions of moderate insolation are of the order of $100-150 \text{ g m}^{-2} \text{ wk}^{-1}$. These values are not high when compared with other crops, however, cassava can maintain rates close to the maximum for rather long periods. Holmes and Wilson (1976) reported an average crop growth rate of $83 \text{ g m}^{-2} \text{ wk}^{-1}$ over a 10 1/2 month period and Cock (1976) obtained $98 \text{ g m}^{-2} \text{ wk}^{-1}$ over an 8 month period. In neither of these cases was leaf fall assessed and so real values would have been even greater.

2.2.2. Crop growth rate as a function of leaf area index.

The extinction coefficient of cassava is 0.7-0.86 (Veltkamp, pers. comm.) which corresponds to 95% light interception at LAI 3.5-4.3. Hence, it would be expected that crop growth would increase with leaf area index up to LAI 3-4 and then level off. Enyi (1972) found a fairly flat relation between CGR and LAI over the range of 3-6. The two varieties CMC 39 and CMC 84 both showed an increase in CGR with increasing LAI up to LAI 3-4 after which CGR showed no change with increasing LAI (CIAT 1972). Cock *et al.* (1979) found a slight tendency for crop growth rate to decrease above an optimum LAI of 4 in the clone MCol 113 when planted at very high plant populations. The data from a whole series of trials in CIAT and its substation Quilichao have been used to compile figure 3. Although there is considerable scattering of the data points it is clear that CGR increases with LAI up to LAI 3-4 and then remains nearly constant as LAI further increases.

Williams and Ghazali (1969) measured large differences in leaf orientation between different clones. The upper leaves fold downwards towards midday, thus assuring a more erect disposition, then throughout the

afternoon gradually assume a more horizontal position (CIAT 1973). This leaf angle change is most marked on bright sunny days. The leaf angle change does not appear to be associated with wilting as the stomata continue open throughout the process (CIAT 1973). Cock (1976) could not detect any difference between the crop growth rate of clones with a large leaf angle change and those with little changes. As most of this data was collected at leaf area indices of 2-4, when leaf angle theoretically has little effect on crop growth rate (Duncan *et al.* 1967) this result was not surprising. The changes in leaf angle could be useful to increase crop growth rate at the highest leaf area indices, attained by cassava, however, there is good reason to believe that this would not necessarily lead to higher yields of roots.

2.2.3. Maximum leaf area index. Leaf area index of most cassava clones increases rapidly in the first 4-6 months after planting and then declines (Cours 1951, Williams 1972, Enyi 1972, Enyi 1973, CIAT 1972, 1973, 1974, 1975, 1976, Cock 1976, Tan and Cock 1980). The maximal leaf area indices recorded are between 6-8 (Cours 1951, Enyi 1972, 1973, Cock 1976, CIAT 1978, CIAT 1979). However, these levels are peaks normally observed over a very short time. Rosas *et al.* (1976) found that shading of leaves reduced their life and that fully shaded leaves abscised ten days after the treatment began. Cock *et al.* (1979) found that shading to 95% had little effect on leaf life of leaves more than thirty days old, however, when shading was greater leaves abscised rapidly. As 95% shading occurs when there is a leaf canopy of LAI 3.5-4.3 (see section 2.2.2) then leaf production has to be very high for larger LAIs to be maintained for any length of time. Irikura *et al.* (1979) obtained a mean leaf area index of 5.6 for 8 months with a variety that is heavily branched and has very large leaves.

Thus although quite high leaf area indices can be obtained in cassava, they can only be maintained at the cost of very heavy leaf fall and very high leaf production rates.

2.3 Total Dry Matter Production. Cours (1951) in a classic study of 41 clones grown over a period of four years found an average total dry matter production of over $40 \text{ t ha}^{-1} \text{ yr}^{-1}$. Cock et al. 1977 obtained harvestable dry matter yields of $45 \text{ t ha}^{-1} \text{ yr}^{-1}$ at very high plant populations. Enyi (1973) grew plants for nearly 15 months and obtained a total dry matter production of close to $47 \text{ t ha}^{-1} \text{ yr}^{-1}$. Holmes and Wilson (1976) obtained the equivalent of $43 \text{ t ha}^{-1} \text{ yr}^{-1}$ total harvestable dry matter after 46 weeks. These data all underestimate the total dry matter produced as fallen leaf weight was not measured. Nevertheless the reported dry matter yields fit well with those estimated from crop growth rate. If we allow six weeks for crop establishment and 46 weeks for growth close to the ceiling LAI of 3-4 with a CGR of $120 \text{ g m}^{-2} \text{ wk}^{-1}$ then the total dry matter yield would be approximately $52 \text{ t ha}^{-1} \text{ yr}^{-1}$. Assuming an average leaf life of 80 days and that the plant maintains an LAI of 3 then during the 46 weeks of growth the plant will lose 9 m^2 of leaf/m² of land which is equivalent to 6 t/ha . Hence the harvestable dry matter would be expected to be about $46 \text{ t ha}^{-1} \text{ yr}^{-1}$, which agrees very closely with the field data reported above. These data suggest that cassava, although it has relatively low photosynthetic rates of individual leaves, a low ceiling LAI and low maximal crop growth rates has rather high total productivity for a C-3 crop. Loomis and Gerakis (1975) from an extensive review of the literature obtained maximal values of annual production of the standing crop of close to $40 \text{ t ha}^{-1} \text{ yr}^{-1}$ for C-3 plants and more recently Loomis (in press) suggests that cassava is one of the most productive C-3 plants in terms of annual

production of standing biomass.

2.4. Harvest Index. The harvest index is a crude measure of the distribution of biomass to the economically useful plant parts. In crops with a phasic growth cycle, where the vegetative phase essentially terminates before the filling period, harvest index is normally only measured at the end of the crop cycle. Crops such as cassava, sugar beets and oil palms simultaneously develop the economically useful plant parts and their leaves and stems. Hence, in these plants harvest index is often measured during the growth cycle (CIAT 1973, Corley 1973). This growth difference of phasic and simultaneous development is of great importance; in the phasic plants there is little competition between the development of the source and the filling of the economically useful sinks, while in the simultaneous plants there is normally competition for the development of source and sink. Thus in most phasic crops a ceiling LAI for yield is expected while in the simultaneous development crops the competition between source and sink for available substrates will lead to an optimum LAI for growth of the economically useful parts. Ceiling LAIs have been found in rice (Yoshida, Cock and Parao 1971) and optimal LAIs in cassava (Cock et al. 1979, Irikura et al. 1978) and oil palms (Corley 1973).

The harvest index can be determined on a fresh weight or a dry weight basis: unless otherwise stated the term will be used in this paper to describe harvest index on a dry weight basis. In cassava the harvest index, as measured in field experiments after a long growth cycle, does not give a true picture of the economic yield relative to the total biomass yield. The discrepancy is due to the large amount of biomass often present in fallen leaves and the fact that the fibrous roots are normally not included. The fallen leaves, maybe equivalent to several tons per hectare

of biomass. At very high plant populations I have observed leaf fall of more than $30 \text{ g m}^{-2} \text{ wk}^{-1}$. When leaf fall is allowed for in the estimate of harvest index the term "corrected harvest index" will be used.

Tan while at CIAT measured both harvest index and corrected harvest index and found the two to be closely related with surprisingly little difference between the two measurements. When corrected harvest index was 0.50, harvest index was 0.52 (CIAT 1977). In these trials LAIs never exceeded 3.7 and most values were less than 3, hence leaf fall would not have been as large as in experiments with high LAIs. Simulation of cassava growth using a computer model (Cock et al. 1979) has indicated that the corrected and measured harvest index can be very different in some cases, hence care should be taken with interpretation of harvest indices.

Enyi (1972) with single shoot plants found an average harvest index of about 0.55 with little effect of plant population. With multishoot plants harvest index decreased from 0.37 to 0.45 as plant population was doubled from 6 to 12 thousand plants/ha⁻¹. Cock (1976) obtained harvest indices of a number of clones ranging from less than 0.30 to 0.57 with 20 thousand plants/ha after one year. Harvest indices of over 0.7 were obtained in one trial with M Col 22, but the harvest index decreased as population increased above twelve thousand plants ha⁻¹ (Cock et al. 1977). These high harvest indices are consistent with data of Hume (1975) who found up to 60% of the assimilated ¹⁴C in the thickened roots. Boerboom (1979) has suggested that after bulking begins a constant proportion of the new dry matter formed passes to the roots, and that the proportion depends on both the variety and the growing conditions. The data of Tan and Cock (1979) were reworked and supported this conclusion, however, when the

simulation model was used it was found that while Boerboom's conclusions were normally applicable certain combinations of plant characters that result in high LAIs would lead to a poor fit to his hypothesis. Irikura et al. (1979) showed that a very high leaf area indices, which result in high crop growth rates, root growth rate was minimal. Similar conclusions can be drawn by reanalysis of the data of Enyi (1972a,b,c). This suggests that Boerhooms hypothesis may not hold at very high leaf area indices.

Cock et al. (1979) found that shading had little effect on top growth but a marked effect on root growth rate. Tan and Cock (1979) showed that reduction of top growth by apex clipping or branch removal increased the root growth rate and concluded that top growth has preference for available substrates and that root growth occurs when the substrate available is greater than that required for the tops to reach their growth potential.

Crop growth rate increases with LAI and then reaches a plateau (section 2.2.2, Fig. 3). When LAI is not changing then it would be expected that the dry matter for leaf and stem growth required to maintain a given LAI will increase approximately linearly with LAI if leaf life is constant. This is shown schematically in figure 4. (The crop growth rate curve is the same as that shown in fig. 1.) The root growth rate is obviously the difference between the dry matter required for leaf and stem growth and the total crop growth and shows a marked optimum (Fig. 4). From this schematic relationship the distribution index (root growth rate divided by crop growth rate) was estimated as a function of LAI and then compared with data from field experiments (Fig. 5). The close relation between the schematic representation and the field data suggest that the basic hypothesis is correct. Furthermore, it can be seen that maximum root growth rates occur at LAIs of 2.5 to 3 when the distribution index is close to 0.6. Cock et

al. (1979), Inikura (1979), CIAT (1976) have all shown optimum leaf area indices for root growth rate of 2-3.

The distribution index should be closely related to the harvest index and recently harvest index has been used as a selection tool by cassava breeders (Kawano 1978) and maximum yields under good conditions have been obtained at harvest indices (fresh weight basis) of 0.5-0.7. The fresh weight harvest index tends to give higher values than corrected harvest index due to no account being made for leaf fall but this is partially offset by the higher water content of leaves and young stems. Hence fresh weight harvest index approximates to the corrected harvest index. The harvest index and the fresh weight harvest index of M Col 22 were found to be 0.52-0.54 and 0.58 respectively in one experiment (D. J. Connor, pers. comm.).

2.5. Economic yield

De Vries et al. (1967) estimated that cassava had the highest potential production of calories per hectare per year of various food crops. The high potential economic yield of cassava is based on a long root filling period rather than a particularly rapid growth rate. The maximum root growth rates obtained over short time intervals at CIAT are between 40-50 g of dry roots $\text{m}^{-2}\text{wk}^{-1}$ (CIAT 76, CIAT 1978, Cock et al. 1979). From the data of Cours (1951) the maximum rate of starch accumulation in the roots is close to 50 g starch $\text{m}^{-2}\text{wk}^{-1}$. Kawano has recently obtained a yield of 79.2 t/ha/year fresh weight at 0.375% dry matter that is equivalent to 28 t dry roots/ha yr or 54 g $\text{m}^{-2}\text{wk}^{-1}$. The maximum root growth rate must have been somewhat greater than this figure as there is little root production in the first two months after planting, suggesting that maxima of 60-70 g $\text{m}^{-2}\text{wk}^{-1}$ must have been reached.

3. Response to Major Climatic Factors.

Cassava is grown over a wide range of temperature and rainfall conditions between 30 N-30 S latitude. The response of the crop to water stress and temperature has been observed in major field studies while relatively little information from field studies exists on photoperiodic or solar radiation effects.

3.1. Temperature Effects

3.1.1. Germination. The germination of cassava cuttings is greatly delayed at lower temperatures (Cock and Rosas 1975). Some varieties failed to germinate at all at temperatures of 16-17 C. Keating and Evenson (1979) examined the germination response of two varieties at different soil temperatures and found that time to emergence decreased with increasing temperature up to 28.5-30.0 C depending on variety and then increased at higher temperatures. Time to 50% shoot appearance was reasonably determined by 210 degree days above a base of 13 C. These data also showed that cassava would not germinate when soil temperature was less than 12-17 C.

3.1.2. Growth and yield. Irikura et al. (1979) did an exhaustive study of the growth and development of cassava at different nearly constant temperatures. The different temperatures regimes of 20, 24 and 28 C were obtained by growing plants at different altitudes. Site differences in fertility and rainfall were blanketed by raising fertility level and supplying irrigation at all sites. Differences in solar radiation may also have existed, however, these effects are probably small compared with those attributable to differences in temperature.

The four varieties used in the experiment ranged from very vigorous (Popayan), medium vigor (M Mex 59 and M Col 113) to very low vigour (M Col

22). Yield at the lowest temperature was greatest with the more vigorous varieties and least in the lowest vigor line while at high temperature this trend was reversed (Table 1). Leaf area index and vigor are closely related and a close relation was found between root dry weight increase from 8-16 months after planting and LAI over all sites and varieties (Fig. 6). A marked optima leaf area index of 2.5-3.5 exists for maximum root bulking rate. Similar optimum for one temperature regime have been reported by Cock et al. (1979) and CIAT (1976) using several different clones.

The major effect of temperature on leaf area index was to increase it at the intermediate and higher temperatures. At higher temperatures leaf formation rate per apex was increased and total number of apices (i.e., branches) was increased. Leaf size was slightly less at lower temperatures and maximum leaf size was reached somewhat later. Leaf life was, however, markedly increased, up to 200 days, at the lowest temperature. The increase in leaf life did not, however, offset the greater leaf production at higher temperatures.

Irikura et al. (1979) concluded from this experiment that there is tremendous variety x temperature interaction for yield and that maximum yield will be obtained at different temperatures by phenotypically similar plants, even though they may have to be genotypically different. This phenotype must be such that an LAI of about three is maintained throughout the bulking period.

The data of Irikura et al. (1979) are only for a constant temperature and do not take into account seasonal effects. Cours (1951) did follow the growth of cassava over a seasonally changing temperature regime, however, his plots were not irrigated and the cool period and the dry period occurred at similar times. Nevertheless his data do suggest that leaf life was greater at lower temperatures but that leaf area development is slower at

lower temperatures as leaf expansion rate was greatly reduced.

3.2. Day Length. Various greenhouse studies have shown that root production is decreased by long days (Bolhuis 1966, Mogilner et al. 1967, and Nair and Sinha 1968). No differences in top growth were observed. Cock and Rosas (1975) in a field experiment with supplementary light, that provided insignificant amounts of extra total radiation, found a lower harvest index at 15 hr days than with twelve hr days and Lowe (quoted by Hunt et al. 1977) found the same effect in a growth cabinet study. More recent data obtained by the author showed reduced root weight in plants grown at 18 hr days for the first three months and no effect on another variety. Furthermore, long days from three months after planting had no measurable effect on root weight. These data suggest that cassava is photoperiod sensitive in the first 3 months after planting with a reduction in yield by long days, however, insensitive lines may exist.

3.2. Solar Radiation. There is little direct data on the effects of solar radiation on cassava. Over short time periods (e.g. 2 months) reduced radiation by shading has little effect on top growth but a marked effect reducing root growth (Cock et al. 1979). In most crops increased radiation leads to increased crop growth rate; simulation using the model of Cock et al. (1979) suggests that for every 10% increase in crop growth rate root yield should increase by approximately 20%. This suggests that cassava yields will be rather sensitive to changes in radiation receipt.

3.3. Water Relations. Cassava has a reputation for being highly drought tolerant (Jones 1959, Montaldo 1977, Onwueme 1978 and Conceicao 1979). However, until recently little serious research effort had been placed on cassava water relations.

Cannon et al. (in press), Connor and Cock (in press) and Connor and Palta (in press) compared the growth of a vigorous clone M Mex 59 and a

low vigor clone (M Col 22) during a period of 76 days when rainfall was excluded by covering the ground with plastic and then followed the recovery of the stressed plants. During the stress period rate of leaf formation per apex, apex number (i.e. branching) and leaf size were all reduced. The leaf life was if anything increased by the stress treatment, presumably due to less shading by the reduced upper leaf canopy in the stressed plots. The net effect of the treatment was, however, to markedly decrease the leaf area index (Fig. 7). The crop growth rate was markedly decreased by the treatment and to an extent greater than what would have been expected from the reduction in LAI. Root growth rate was decreased to a much lesser extent and particularly in M Mex 59 the proportion of assimilate accumulated in the roots was markedly increased. In the recovery period leaf formation rate increased to levels similar to that found in the controls and branching resumed but total branch number never reached the same level as in the controls. Leaf size increased rapidly after the stress and was somewhat greater in previously stressed than in control plants. By final harvest 10 months after planting LAI of M Mex 59 in previously stressed plants was equal to that of the controls while in M Col 22 it was still less. During the recovery period growth rate of roots of M Col 22 was similar in treated and untreated plots and final dry root yield was 11.2 t/ha in the controls and 7.6 t/ha in the previously stressed plots. In M Mex 59 yield of previously stressed plots at 10.7 t/ha was greater than that of the controls 7.3 t/ha. Connor et al. (in press) suggest that the restriction in branching during the stress period reduced stem and leaf growth in the recovery period leading to a more favorable balance between top and root growth in M Mex 59 but with still sufficient leaf area to obtain acceptable crop growth rates. In M Col 22 LAI was so reduced that crop growth rates were lowered

far more by the stress period and its subsequent effects on LAI than could be compensated for by a slightly increased distribution index.

Connor and Palta (in press) found that the stomata of the stress plots closed resulting in extremely low stomatal conductance and that leaf water potential was maintained at levels comparable or slightly less negative than the well watered plots. Leaf water potentials reached minimum levels of around -14 bars and stomatal conductances in the stressed plots were reduced to less than 1 mm sec^{-1} at midday.

Campus and Sena (1975) studied the root system of cassava and found roots concentrated in the top 30 cm with some roots down to 140 cm. However, Connor et al. (in press) found roots down to 250 cm. Connor et al. (in press) also observed root characteristics and found that cassava has rather thicker roots than most species (0.37-0.67 mm dia) but has very low root lengths of less than 1 km/m land surface. These low root densities would be expected to cause low water potentials and increased hydraulic conductivity in the root zone resulting in a high resistance to water flow to the roots. The sparse root system, closure of the stomata at relatively high water potentials and the reduction in leaf area produced during the stress period point to a strategy of water conservation. The cassava plant on encountering stress immediately reduces its water uptake but conserves the carbon and nitrogen invested in leaves so that when water is again available it can rapidly begin growth again. Under more extreme drought conditions when LAI is effectively reduced to zero root and stem carbohydrates are used to rapidly develop a new canopy with the onset of the rains (Cours 1951).

Nutritional Stress. Cassava has the reputation of being a crop highly tolerant of low fertility conditions. In solution culture Edwards et al.

(1976) have shown that cassava has quite high nutrient requirements for maximal growth, particularly for phosphorus. However, they also showed that at low nutrient levels the growth was less reduced than in several other crop species (Table 2). Continued work by this group at the University of Queensland has confirmed this (Spear et al. 1978). Furthermore, maximum root yield is obtained well before maximum biological yield is reached (Fig. 4). Although low fertility may markedly reduce total assimilation the distribution to the roots is markedly increased (CIAT 1978, CIAT 1979, Cock and Para, pers comm.) and hence cassava is able to produce well at very low nutrient levels.

Edwards et al. (1976) and Cock and Howeler (1978) have suggested that cassava tends to maintain the nutrient status of its leaves at low fertility levels by reducing growth and leaf area development. Thus leaf area indices at Quilichao, a low fertility station of CIAT were reduced from 5.4 to 1.6 by low fertility while nitrogen and phosphorus status of the leaves were little changed but potassium showed a marked decrease (Table 3). The following hypothesis suggests that this may be an optimum strategy for obtaining good yields under low fertility conditions, particularly where nitrogen is limiting.

Photosynthetic rate of individual leaves of most crop species is closely related to nitrogen content (see review by Nair 1972). If there is only a limited amount of nitrogen for leaves then leaf nitrogen content will decrease with increasing LAI according to figure 8. Data from Cock and Yoshida (1973) in rice show that this does in fact occur. If we make the simple, and reasonable, assumption that below a certain nitrogen level photosynthetic rate decreases approximately linearly with nitrogen content and also that this effect occurs to a similar extent at all light intensi-

ties than we can use data from Duncan's model (Duncan et al. 1967) to describe the crop growth rate at different levels of nitrogen available to the leaves (Fig. 9). This clearly shows that maximal crop growth rates will be obtained under nitrogen limiting conditions by plants that reduce LAI so as to maintain high nitrogen concentrations in the leaves. In cassava an added advantage of this strategy is that at low LAIs the distribution index is also greater.

Recent studies have shown that cassava under low fertility conditions does reduce its LAI mainly by decreasing leaf size and branching while also maintaining a high unit photosynthetic rate (CIAT 1978).

4.5. Varietal Characters Associated With Yield

Several authors have suggested a close relationship between yield and leaf index (Doku 1965, Sinha and Nair 1971 and Cock 1976). This relation appears to hold when LAI is small but does not hold at higher LAIs (Irikura et al. 1979, Cock et al. 1979) and a marked optimum LAI is obtained.

Cock et al. (1979) studied and reviewed a large number of different morphological and development characters of cassava with special emphasis on their genetic variability and also possible interactions between them. From these data they concluded that root sink was not normally limiting unless root number was less than 7 or 8 per m², and that yield was largely determined by the excess of carbohydrates over those needed for top growth. This conclusion is supported by Tan and Cock (1979) and grafting studies (Veltkamp unpublished data).

As has been shown earlier crop growth rate is largely determined by LAI. The development of LAI is controlled by leaf formation rate per apex, apex or branch number per unit land area, leaf size and leaf longevity. Little varietal difference in rate of leaf formation per apex was found,

however, leaf formation rate declines with time after planting. Branching is a varietal character with early and late branching types. Branching interval also differs between varieties, however, for any one variety, in the absence of stress, under given conditions branching interval is constant. Leaf size increases to a maximum about four months after planting and then declines. The decline in leaf size is modulated by the branching habit (CIAT 1977) however, it occurs in all clones tested. The maximum leaf size is, however, a varietal character. Leaf life of spaced plants was found to be nearly constant for leaves formed from two months after planting and varied from 60-120 days for different clones. Under conditions of competition leaves were found to fall within 10 days after being shaded so that they received less than 5% of incoming solar radiation. All the parameters of leaf area development were studied with different levels of root sink activity effect. The root sink effect was altered either by root clipping or by ring barking. Root sink changes in no case altered the overall trends observed in normal plants.

These data enabled Cock et al. (1979) to construct a model for leaf area development, furthermore, from node weights, specific leaf weights, node production per branch and branching it was possible to determine top growth rate. In addition from the LAI the crop growth rate could be predicted, the top growth rate subtracted from this and root growth rate simulated for a number of different genetic combinations. For a full description of the model the reader is referred to the original text (Cock et al. 1979).

This model predicted that yield under good conditions with approximately $45 \text{ g cal cm}^{-2} \text{ day}^{-1}$ maximum yield could be obtained from a variety that had a leaf size maximum at four months of approximately 500 cm^2 , leaf

longevity in the absence of shading of 15-20 weeks and three point branching at 30 weeks or 30 and 45 weeks. Potential productivity of such a variety was slightly less than 30 t dry root/ha/yr under CIAT conditions. Recently under these conditions yields of more than 28 g/ha/yr have been obtained (CIAT 1978).

Unfortunately the real world is somewhat different to that of the disease and pest free environment encountered in a computer simulation. The model has, however, been used to test for the reaction of these ideal plant types to diseases and pests (Cock 1978). Complete defoliation by an insect pest will reduce yields by about 20% on the ideal plant type, which is very comparable to data obtained in the field with local varieties (Bellotti pers. comm.). However, the variation of yield with diseases that reduce leaf life such as *Cercospora* (CIAT 1976) is much greater than that of traditional varieties (Fig.). These data serve to show that the physiologist in his role of designing new plants should also be aware of the hazards of proposing a plant type that may require much greater levels of disease and pest control than those currently acceptable.

Reaction to Stress. Cassava is particularly well adapted to survive conditions of water stress and grows well at low fertility levels (sections 3.3 and 3.4). In addition it is extremely tolerant to soil acidity and associated high aluminum levels. CIAT (1978) showed no response to lime when percent aluminum saturation was less than 80% and Howeler (pers. comm.) has obtained good growth of cassava in solution culture with up to 30 ppm of aluminum. Cassava also grows well in solution culture at pHs as low as 5.5 and still grows at pH 3.3 in solution culture (Edwards et al. 1977). No response to lime was found above pH 4.7 in field trials on an acid infertile soil in Colombia (CIAT 1978). Thus cassava is very tolerant

to low pH and high aluminum saturation.

CONCLUSIONS

Cassava is a C-3 plant which reaches maximal crop growth rates of about $120-150 \text{ g m}^{-2} \text{ wk}^{-1}$ at LAI of 4 under conditions of solar radiation of about $450 \text{ g cal cm}^{-2} \text{ day}^{-1}$. Annual production of standing biomass at 40-50 t/ha is high for a C-3 crop and these high figures are obtained by a long growth duration at near maximal crop growth rate rather than through very high crop growth rates.

Cassava forms new leaf and stem at the same time as it fills the economically useful part, the roots. This results in a delicate balance between top and root growth for maximum root yield with maximal root growth rate occurring at LAIs of 2.5-3.5. These values of LAI can be most effectively maintained through most of the growing season by varieties that branch late (6 months after planting), have large maximum leaf size and a remarkably long leaf life of 100 days or more.

Cassava grows yields well at low fertility levels. Growth is reduced so as to maintain a high nutrient status in the leaves, furthermore as overall growth is restricted a greater proportion of the total dry matter is distributed to the roots. Under conditions of water shortage the crop reduces water use, and growth, by reducing leaf area and closing the stomates. Leaves already on the plant are not shed any faster under stress conditions and may become active after the stress period is finished.

Hence the cassava crop will readily survive a drought period but will produce very little during that period.

The cassava crop is grown in areas with mean annual temperatures above 20 C when annual temperature shows seasonal fluctuation and 17 C when temperature is relatively constant. Germination is delayed greatly by lower

temperatures and ceases below 12 C. At higher temperatures leaf areas tend to be greater and low vigor types are preferable whereas at low temperature the converse is true.

Table 1. Fresh and dry root yield of four contrasting cassava genotypes at different times after planting at altitudes with three different mean temperatures.

	Avg. mean temperature								
	20 C			24 C			28 C		
	Harvest date (months)	Harvest date (months)	Harvest date (months)	Harvest date (months)	Harvest date (months)	Harvest date (months)	Harvest date (months)	Harvest date (months)	Harvest date (months)
	8	12	16	8	12	16	8	12	16
Fresh yield (t/ha) ^{1/}									
M Col 22	2.7	9.3	13.3	22.1	22.7	48.3	23.9	39.4	53.1 ^{2/}
M Mex 59	9.2	22.8	32.8	25.3	38.8	57.0	21.3	30.4	60.3
M Col 113	14.2	24.2	28.6	16.4	26.1	51.3	20.2	23.9	55.0
Popayan	10.7	28.9	39.7	6.3	15.7	13.3	4.6	9.4	13.2
Dry yield (t/ha) ^{1/}									
M Col 22	0.9	3.3	5.6	8.5	11.5	18.0	8.8	14.2	18.4
M Mex 59	3.0	8.2	12.9	8.2	14.2	18.1	7.5	10.1	19.7
M Col 113	4.5	8.4	15.6	5.4	10.0	19.1	6.2	7.5	17.0
Popayan	3.1	10.7	16.2	1.9	5.1	2.6	1.1	2.2	3.0

^{1/} For fresh and dry root yields temperature x variety interaction was significant at P = 0.01

^{2/} This yield was reduced due to robbery in the experimental plot.

Source: Irikura et al. (1979).

Table 2. Percent of maximum yield of cassava and other crop species at low constant solution concentrations (Edwards et al., 1977).

	K 0.5	Ca 0.5	NH ₄ 0.4	NO ₃ 0.4	P 0.05
	(Solution concentration: mole/liter)				
Cassava	52	26	40	20	18
Soybean	--	2	--	--	34
Maize	36	2	7	6	21
Sorghum	--	3	5	2	--
Sunflower	43	0.2	9	3	--

Table 3. The effect of high medium and low fertility level on leaf area index and nutrient content of leaves + petioles of H Mex 59 six months after planting.

Fertility level	LAI	Nutrient content as % dry matter			Nutrient content as mg/dm ² leaf surface		
		N	P	K	N	P	K
High	5.39	3.69	0.25	2.00	18.9	1.28	10.3
Medium	3.54	3.68	0.19	1.40	20.2	1.04	7.7
Low	1.65	3.52	0.18	0.73	21.7	1.11	4.5

Source: Cock, J. H. and Parra G. (unpublished data)

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