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THE PHYSIOLOGICAL RESPONSE OF CASSAVA TO STRESS

(La réponse physiologique du Manioc au stress)

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SUMMARY

Cassava has gained the reputation as a crop that is highly tolerant of the stress conditions found in marginal areas for agriculture.

This paper reviews the physiological basis of this tolerance. Cassava has a long growth cycle and an indeterminate growth habit. Thus short periods of stress have little effect on the overall growth. In addition it has no critical growth periods such as flowering when short stress periods affect critical processes in yield formation. Cassava simultaneously develops its source, leaves, and its sink, roots. During stress periods the balance between source formation and sink filling is shifted towards the roots. Thus although total biomass production may be reduced markedly in stress periods the effect on root production is less marked. At low fertility levels leaf area index is reduced, but the nutrient content of leaves is maintained allowing for efficient photosynthesis. Similarily under drought conditions leaf area index is reduced, resulting in reduced water loss. This effect coupled with a stomatal reaction to changes in relative humidity of the ambient air allows cassava to survive long dry periods and use limited water very efficiently.

RESUME

Le manioc a la réputation d'être une culture très tolérante aux conditions de stress des zones agricoles marginales. Cet article passe en revue les bases physiologiques de cette tolérance. Le manioc a un long cycle de développement et une croissance de type indéterminé. Aussi de courtes périodes de stress n'ont-elles que peu d'effet sur la croissance globale. De plus, le manioc n'a pas de périodes critiques de croissance, telle que la floraison, durant lesquelles de courtes périodes de stress pourraient avoir une grosse influence sur le rendement. Le manioc développe en même temps ses feuilles (organes "source") et ses racines (organes "puits"). Pendant les périodes de stress, l'équilibre "source-puits" est modifié en privilégiant le remplissage des racines au détriment de la formation des feuilles. Aussi, bien que la formation de biomasse soit réduite nettement par les périodes de stress, l'effet est faible sur le rendement en racine. Avec une faible fertilisation, l'indice foliaire est réduit, mais les concentrations foliaires restent suffisantes pour permettre une photosynthèse efficace. De même une alimentation hydrique réduite diminue l'indice foliaire ce qui conduit à une réduction des pertes d'eau. A cela s'ajoute une réaction des stomates aux changements d'humidité relative de l'air ambiant ; ces deux phénomènes permettent au manioc de survivre à de longues périodes de stress hydrique et donc d'utiliser très efficacement l'eau consommée.

INTRODUCTION

Cassava has gained the reputation of being a crop that grows particularily well on infertile soils in areas with uncertain rainfall. Furthermore in Africa where locusts are a serious problem it is recognized as extremely tolerant to attack. In this paper the physiological basis of cassava's tolerance of stress is discussed.

The cassava plant, like most root crops, simultaneously produces new leaves (the source of carbohydrates and deposits carbohydrates in the roots. This situation constrasts with the determinate crops in which the reproductive organs are the useful parts. In these crops the source is developed first and then the sink is filled. This particular characteristic of the root crops leads to two fundamental aspects of their physiology. First of all they tend to have an optimal leaf area index for yield and secondly they do not have critical periods when stress over a very short time span can have disastrous effects on yield.

CASSAVA GROWTH UNDER NON STRESS CONDITIONS

Under good conditions the cassava plant after germination rapidly produces small leaves from the apical meristems. The size of the leaves produced increases with each subsequent leaf until 4-6 months after planting and then declines. The rate of leaf production per apex initially is approximately 5 per week but declines as the plant grows older to about 1 per week. Initially one or more of the axillary buds on the planting piece grow and later when the apex becomes reproductive the development of the axillary buds directly below the reproductive organ gives the branching (forking) characteristic of cassava. The branching habit increases the number of active apices and partially compensates for the decrease in leaf formation rate per apex and leaf size in the later growth stages. Nevertheless in general in cassava LAI increases rapidly from about 1 month after planting until four to six months after planting. Thereafter the combined effects of leaf fall of the older leaves and the reduced formation of new leaf area results in a decline in leaf area index.

The crop growth rate (CGR) of cassava increases rapidly with increasing LAI reaching a plateau of about 100 g $m^{-2}wk^{-1}$ at LAI 4-5. In the early growth stages the rapid development of leaves, stems and fibrous roots utilizes almost all the available products of photosynthesis leaving little excess for storage root expansion. As the production of leaves and stems decreases a balance is reached where growth occurs both in stems and leaves and roots.

GENERAL REACTION TO STRESS

The various types of stress to which the cassava plant is subjected obviously have different effects on the plant, nevertheless there are certain general reactions of the plant that are common to several stress factors.

Under stress conditions the cassava plant tends to restrict its top growth. This results in a reduction in Leaf Area Index and hence crop growth rate. However as can be seen schematically (Fig. 1) a decrease in Leaf Area Index and Crop Growth Rate leads to an increase in Harvest Index. Hence the decrease in root growth under stress is less than the decrease in total or crop growth rate. In other words under stress conditions the total growth may be reduced but the efficiency of distribution of that growth to the useful parts is increased. In some cases if LAI is supra optimal under good conditions, stress can actually increase yield (Fig. 1). In field trials with branch removal (TAN & COCK, 1979) and water stress (CONNOR, COCK and PARRA, 1981) yield of vigorous varieties was indeed increased by cimposing the stress condition.

A decrease in LAI varies potential problems with reduced interception of light. The cassava plant however partially obviates this problem through heliotropism of the leaves (EL-SHARKAWY et al, 1984). Cassava leaves move in such a manner that light interception is maximized when water is not limiting. When water is limiting and stomatal closure occurs (see setion on water stress) this could lead to potential problems with excessive heat load on the leaves. Under these conditions the heliotropic movement is overridden by a drooping of the leaves that reduces light interception and hence the heat level.

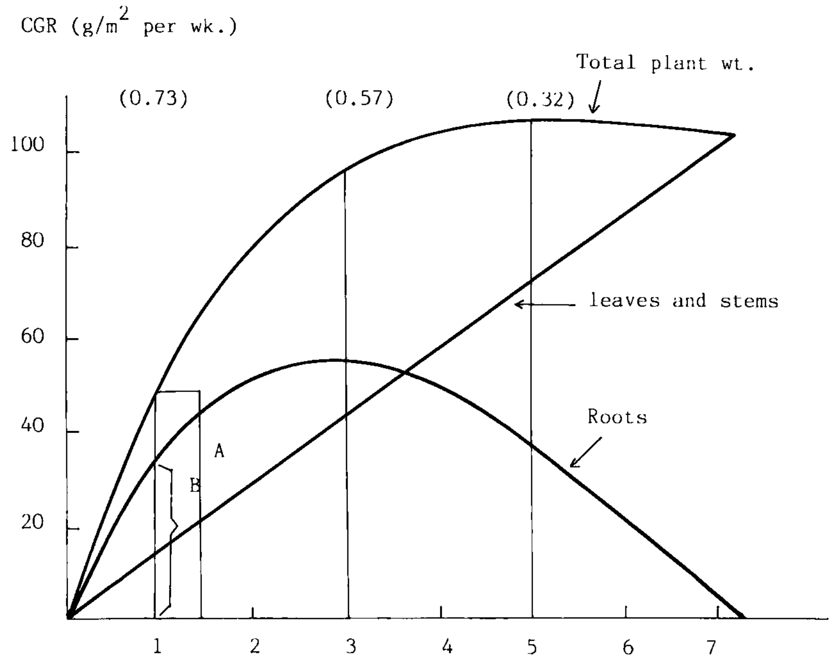

Fig. 1. Crop growth rate (CGR) and dry matter used for stem and leaf and root growth at different constant leaf area indices. Harvest index is represented in figures in brackets at LAI 1,3,5 and is obtained from B/A. (Adaptation from Cock 1983).

A second general attribute of the cassava plant is its ability to recover from damage. In those crops in which the source is formed and then the reproductive organs develop and then fill disruption of such important growth aspects as floral initiation, anthesis or defoliation after the source has developed can, even if they only occur over a very short time span, drastically reduce yields and the plants ability to recover is minimal. In the case of cassava there are no short duration critical phases. If defoliation occurs at any stage the plant can form new leaves, if some roots are damaged the ramaining roots can to a large degree compensate.

NUTRIENT STRESS

Deficiencies of the major nutrients are likely to effect yield in three major forms, through reduction of the photosynthetic rate of leaves, reduction of the leaf area index and changes in the distribution of dry matter to the different plant parts. In most crops major nutrient deficiency, particularily nitrogen, results in a marked drop in photosynthetic rate of the leaves. In pot trials we found that the photosynthetic rate of cassava did not decrease at low levels of N whereas that of corn (C4) and beans (C3) was markedly reduced (Table 1). It is commonly observed that nitrogen deficient corn and bean crops turn yellow showing typical deficiency symptoms. It is only rarely that cassava plants turn yellow due to nitrogen deficiency.
The plant tends to reduce LAI and maintain the nutrient status of the leaves (Table 2) and thus maintains the photosynthesis rate per unit leaf area. COCK (1983) using a simulation model has suggested that the optimum strategy to obtain high crop growth rate at low fertility levels is to maintain nutrient concentration in the leaves and reduce leaf area index. Cassava follows this strategy and hence is well adapted to maintain high growth rates at low levels of nutrients.

The reduction in leaf area at low fertility level should lead to a shift to the left in the curve in Figure 1 and an increase in harvest index. In field trials this effect has been observed repeatedly.

Thus under conditions of nutrient stress cassava reduced LAI and maintains high rates of leaf photosynthesis. This optimizes the use of limited nutrient resources for production of dry matter. Furthermore the reduction in LAI results in more efficient distribution of dry matter to the roots.

WATER STRESS

Cassava is extremely tolerant of drought conditions an yet until recently little knowledge existed on the mechanisms that allow the crop to survive and produce with

TABLE 1. Photosynthetic rate and nitrogen content of corn, bean and cassava leaves grown in a low nitrogen status soil. (Source : Marcio Porto, M. EL-SHARKAWY and J.H. COCK, unpublished data).

	N application level	N (%dry weight)	N (mg dm^{-2} leaf)	Photosynthesis (mg CO_2 dm^{-2} hr^{-1})
Corn	None	1.9	7.9	43
	High	3.4	14.9	57
Beans	None	3.4	11.7	26
	High	5.0	21.2	40
Cassava	None	4.6	21.5	42
	High	4.6	19.2	42

Table 2. Nutrient concentration of cassava leaves grown at different fertility levels (Source : CIAT 1979).

Fertilizer applied (Kg/ha)		Leaf area (dm^2 $plant^{-1}$)	Leaf nitrogen (% dry matter)
0	0	76	4.2
100	0	94	5.3
200	0	119	5.0
0	300	163	5.0
100	300	198	5.1
200	300	156	5.0

extremely limited availability of water. Once the crop is established it is remarkably difficult to kill by witholding water ; often in dry areas cassava and deep rooted tree crops are the only species that remain green throughout the dry period. Cassava's ability to survive is not however related to a particularly extensive and deep root system. Recent data obtained by us suggest that cassava takes little water from depths of greater than 1-1.5 m and that it reduces soil water potential to levels of only -10 to 15 bars. Thus cassava's ability to survive drought must depend on its capacity to conserve and use water efficiently.

When water is with held from cassava the rate of leaf production per apex and the leaf size of new leaves rapidly decrease (CONNOR and COCK, 1981). Branching is subsequently reduced or delayed but leaf fall is apparently not accelerated. The net result is a decrease in leaf area index. This alone should decrease the transpiration or water use of cassava. However CONNOR and PALTA (1981) showed that stressed plots also had much lower leaf conductances further reducing the transpiration. An interesting aspect of the data of CONNOR & PALTA (1981) is that stomatal closure, which reduces leaf conductances, occurs in stressed plots at similar leaf water potentials to those with open stomata plots in unstressed plots. This suggested that the stomata were reacting to external factors rather than sensing the internal stress within the plant. Later EL-SHARKAWY et al (1984a, 1984b) showed that this was indeed the case. The stomata of the cassava plant are extremely sensitive to the water vapour pressure difference (VPD) between the leaf and the air and the sensitivity is greatest in stressed plots where water has been withheld. This mechanism is a key factor in the drought survival ability of cassava. The plant senses when evaporative demand is high and stomatal closure occurs. This reaction conserves water ; the more common reaction (at least the more popular explanation among scientists !) in crop plants is to maintain stomata open until the water potential reaches a thresh hold value and then stomata close. This latter reaction is like shutting the barn after the horse has escaped.

The sensitivity of stomata to air humidity or VPD not only conserves water allowing the crop to survive drought periods but also leads to very efficient use of available water. During periods when potential evapotranspiration is high and water use efficiency is low (e.g. midday) the stomata close. The crop actively photosynthesises when potential evapotranspiration is low and water use efficiency is high. This leads to very efficient use of water in cassava as compared to other C-3 plants (Table 3). The values in fact are in the range commonly found in C-4 plants. This high water use efficiency of cassava in terms of total dry matter production is coupled with the high harvest indices associated with low LAI under stress conditions making cassava extremely efficient in terms of economic yield per unit of water transpired.

TABLE 3 : Simplified estimates of water use efficiency of C C species with insensitive and highly sensitive stomatal reaction to VPD. Calculations for a 12 h day.

	Beans		Cassava		Sorghum	
VPD (KPa)	2	4	2	4	2	4
WUE (mol CO mmol H O	5	2.3	6.8	3.3	10.3	3.9
Average WUE (mol CO mmol H O)	3.9		5.1		7.1	
Transpiration rate (mmol m s)	3.9	6.8	3.9	2.9	3.9	6.8
Transpiration (mol m)	168	294	168	126	168	294
Transpiration (mol m) (Average of 2 days)	231		147		231	
Photosynthesis (mmol CO m)	908	676	1142	416	1730	1146
Photosynthesis (mmol CO m) (Average of 2 days)	792		779		1438	
WUE (mol CO mmol H O) Average of 2 days)	3.4		5.3		6.2	

TEMPERATURE

Cassava is not normally found growing when average temperature is below about 17-18°C. KEATING and EVENSON (1979) showed that cassava varieties differed in their germination below about 13°C. The photosynthetic rate of cassava has a plateau between 25-40°C with the rate declining to essentially zero at 50°C about 40 per cent of maximum values at 12°C (EL-SHARKAWY et al, 1984). It appears that low temperature in general limits cassava growth more through reduction of leaf area than through direct effects on photosynthesis. IRIKURA et al (1979) have shown that leaf area is greatly reduced at 20°C whilst EL-SHARKAWY et al (1984) show that photosynthesis at 20°C is reduced by less than 20 per cent of its maximum level. There are large varietal differences in the ability to develop leaf area at low temperature.

In some areas where cassava is grown in the sub-tropics there are short term periods when temperatures drop to 0°C or slightly less. These low temperatures cause defoliation and death of the non liquified shoots. In southern Brazil farmers normally prune plants before the cold periods. In spring the plants produce new shoots and grow normally.

DISEASES AND PESTS

In a long season crop, such as cassava, grown with limited chemical inputs the potential losses from diseases and pests are large. Traditional cassava varieties often possess high levels of host plant resistance to pathogens and pests ; at the same time they also possess physiological mechanisms of tolerance. COCK (1978) indicated that yield in cassava is determined by the the following parameters : (a) the apices which determine potential leaf and stem growth, (b) the leaves which produce photosyntates and hence are the source of carbohydrates for root filling, (c) the stems and petioles which act as support for the leaves and the transport system of carbohydrates to the roots and nutrients and water to the leaves, (d) the storage roots which form the basic yield unit.

Pests or diseases which destroy the apex will not normally cause severe damage unless they are present for a prolonged period. If the apex is destroyed axillary buds immediately below the apex immediately develop and compensate for the loss. TAN and COCK (198) have shown that apex removal can on occasions increase yield.

Damage to the leaves can be of several different types. Leaves may be reduced in size, their efficiency may be reduced or they may be eaten or fall prematurely. Simulation data suggest that cassava is relatively tolerant of substantial reductions in leaf size, particularily in the more vigorous varieties (COCK, 1978). However as less leafy higher yielding varieties are developed they will be more susceptible to this type of damage.

COCK (1978) has shown that a similar situation exists in the case of premature leaf fall. This has little effect on vigorous varieties but more efficient types will be more seriously affected. Cassava is however rather tolerant of defoliation. The plant rapidly produces new leaves and yield losses can be of the order of 20 per cent under fertile conditions (CIAT, 1984). Under less fertile conditions and with repeated attacks the plant is however not able to compensate with sufficient new leaf growth and yield losses can be very severe (CIAT, 1985).

Defoliation by such pests as the cassava hornworm (*Erynnis ello*) is extremely noticeable and causes a great impression on farmers. Damage by insects such as mites are however often much less noticeable and yet they may cause very severe yield losses. Any disease or pest that causes a marked reduction in photosynthetic rate will greatly decrease yields. COCK (1978) estimated that a 10 per cent decrease in photosynthetic rate could decrease yields by 20 per cent. Recently HOLGUIN and COLLAZOS (1984) showed that a latent virus in cassava that causes no visible symptoms can decrease photosynthesis by 18 per cent.

The stems of cassava are attached by several pathogens and pests. When these are damaged and broken the effects are rather similar to those that occur when apices are damaged. In the case of frog skin disease it appears likely that the phloem transport system becomes blocked and yield losses can be 100 per cent. The plant has no mechanism of tolerance to this type of damage.

The number of thickened cassava roots is generally determined early in the growth cycle. If this number is reduced due to disease the roots that remain have a considerable capacity for compensatory growth.

Certain diseases or pests may cause plant death. Obviously if this occurs later in the growth cycle losses will be large, however the losses normally occur in the establishment phase. As cassava has a relatively broad plateau in the yield/density curve the yield loss due to minor loss of stand is normally minimal.

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