A physiological basis of yield loss in cassava due to pests

James H. Cock*

Abstract

Although mites, insects and diseases can cause heavy yield losses, cassava is more tolerant to pests than other crops because it does not have critical periods that affect yield-forming organs. The components of the cassava plant that determine yield are the storage roots, apices, leaves, stems and petioles. The ways in which pests affect these components and thus influence yield are discussed. The optimum Leaf Area Index (LAI) for root growth is approx. 3; above this level yield decreases markedly. The results are presented of a series of simulated experiments conducted in order to determine (1) the effect of partial or total defoliation on the yield of leafy and nonleafy varieties, (2) the effect of shortened leaf life caused by the attack of *Cercospora* spp., (3) the reduction of the photosynthetic rate due to mites and African mosaic, and (4) leaf damage caused by thrips. When damage to the main apex is not continuous and the other apices that become active are not destroyed, there is no reduction in yield and, in fact, yield may increase substantially in leafy varieties. Damage caused by bacterial blight, *Anastrepha* spp., *Erwinia* sp. and *Phoma* sp. always reduces yield. When varieties characterized by a flat-topped density response curve are planted, death of plants at an early age produces only minimal yield reduction if the percentage of population reduction is less than 50% and the initial plant population is high.

Diseases and pests cause severe yield losses in cassava; the extent of loss caused by single diseases may be as high as 90%, or there may even be total crop failure (9), whilst insect pests can cause losses of more than 50% (2). When one considers the enormous array of diseases and pests that attack cassava (2, 9), it becomes evident that the combined effects of these many pests may seriously reduce yields in the field. Nevertheless, cassava may be more tolerant of disease and pest attacks than many other crops because of a lack of critical periods in yield formation. After establishment, growth can be completely stopped at almost any time without destroying the yield-forming organs; this is not generally true of reproductive crops when, for example, stress during flower initiation can cause complete crop failure.

In order to develop an integrated pest management system, it is important to know how much damage a plant can suffer before yield is reduced, when damage causes greatest yield reduction, and what types of damage cause most serious losses. In this paper I have tried to present, wherever possible, quantitative data on losses.

* Plant physiologist, Cassava Program, CIAT, Cali, Colombia

The components of the cassava plant that determine yield are (a) the apices which determine potential leaf and stem growth, (b) the leaves which produce photosynthates and hence are the source of carbohydrates for root filling, (c) the stems and petioles which act as support for the leaves and as the transport system of carbohydrates to the roots and nutrients to the leaves, and (d) the storage roots which form the basic yield unit and also absorb nutrients and water.

In this paper I will discuss how diseases and pests could affect these basic components and thus influence yield. Field-simulated data refer to modification of the plant in the field; for example, leaf or root clipping and computer-simulated data are obtained using a cassava growth model.

Roots

Yield depends on the number of thickened roots and their size. These two components are related in such a way that when thick root number is decreased, individual root weight increases (3). This compensation is sufficient to keep total yield stable when root number is between 9-12 at plant populations of 1 m [2] (6). When root number is reduced below about 9 roots per plant, yield drops markedly as the roots that remain cannot compensate for the missing ones (Fig. 1). When thick root number is reduced early (1 1/2 mo after planting), the plant compensates by thickening other roots (Fig. 2), and this compensation is greater than that which occurs when root number is reduced later (3 mo after planting). These data suggest that reduction in root number to 9 does not reduce yields; furthermore, if reduction occurs early in the growth cycle the plant compensates for even greater reduction by thickening other roots.

Damage to roots in the field is caused by such pests as small rodents and grubs and by diseases like *Phytophthora* spp.. Severe reductions in thick root number (i.e., to less than 9) will reduce yield and reduction will be greater when the attack occurs later in the growth cycle. The plant does, however, have some plasticity and early damage to two or three roots per plant in a variety that has a high root number will probably have little or no effect on yield. Later damage that causes root rots or destruction of thickened roots will obviously reduce yield.

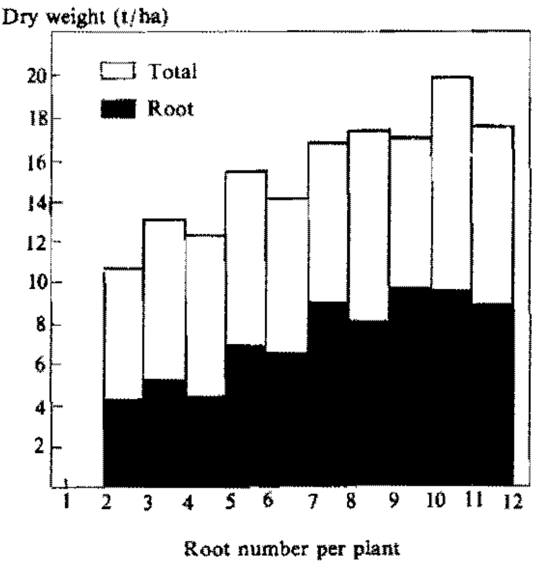

Figure 1. **Total and root dry weight as related to root number per plant. Means of all plots that fall in each range are presented. Root number was artificially reduced by cutting at 6 or 12 weeks (Var. CMC 84, harvested at 8 1/2 months)**

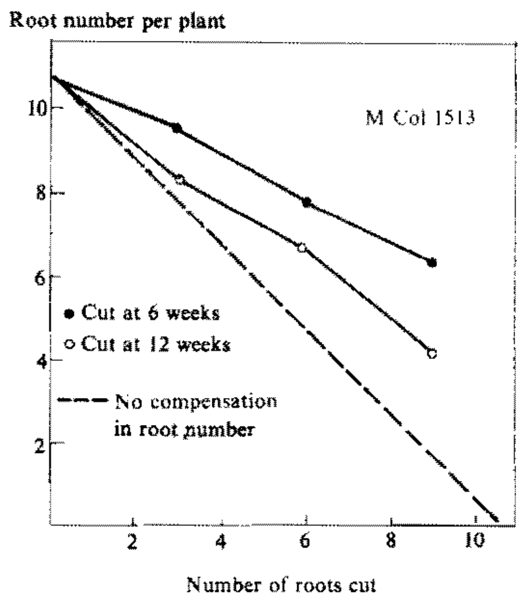

Figure 2. **Effect of cutting thickened roots on final root number.**

Leaves

As can be seen in Figure 3, cassava has a marked optimum Leaf Area Index (LAI) for root growth; this optimum occurs at approximately three, above which root yield decreases markedly (4-6, 8). Presently cultivated varieties only approach this optimum LAI for rather short periods (Fig. 4). The vigorous M Col 113 in trials at CIAT exceeded the optimum LAI from 4-9 months, was close to the optimum at 9-12 months, but thereafter had a suboptimal LAI. On the other hand, M Mex 11 approached the optimum at 4 months, but from then on was suboptimal.

Insects such as the hornworm *Erinnyis ello* consume leaves and reduce LAI. Hornworm attacks may be either sporadic and devastating, causing severe defoliation, or continuous at low levels of infestation. These two types of attack were simulated in the field by removing 50 percent of the leaves of a leafy and nonleafy variety at one time (Treatment 1) or over a period of time, removing every other leaf as it formed to represent a continued attack (Treatment 2).

In the leafy variety M Col 113, Treatment 2 had no effect on final yield from 100-200 days (Fig. 5).

During this period the controls had LAIs greater than the optimum whilst treated plants had suboptimal LAIs. At other stages yields were reduced, as even the controls had suboptimal LAIs. Similarly, nonleafy M Col 22 always had suboptimal LAIs so continuous leaf removal always

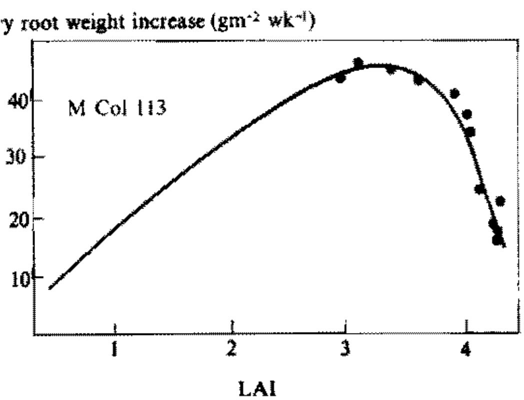

Figure 3. **Root weight increase as a function of LAI.**

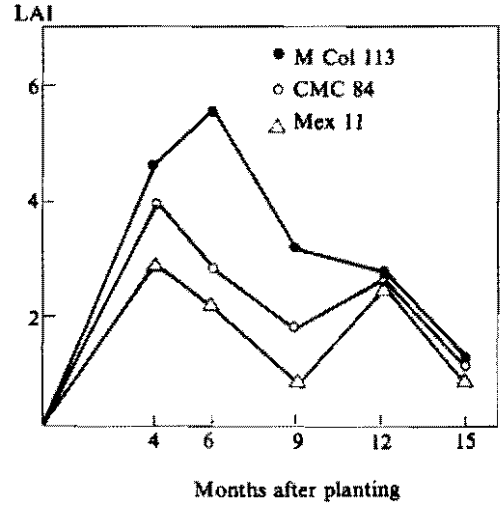

Figure 4. **Development of Leaf Area Index in three varieties.**

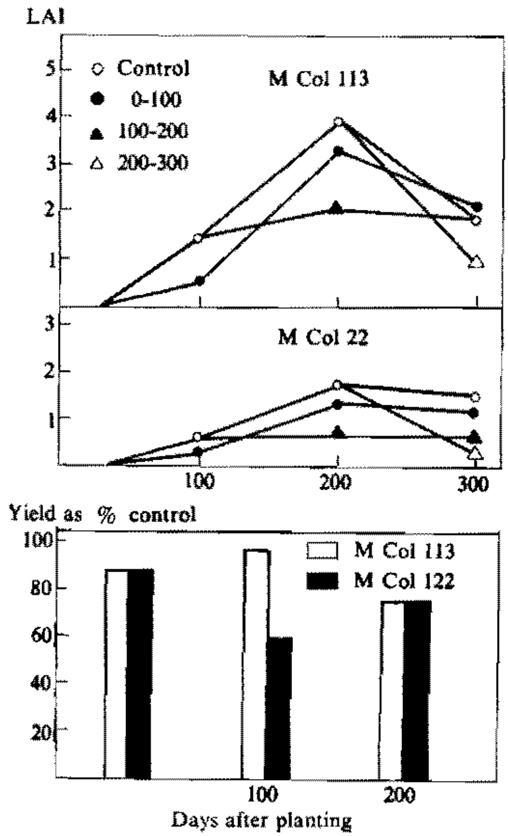

Figure 5. **Effects of removing 50% of leaves as they form at different growth stages on yield and leaf area index.**

reduced yield. Therefore, continued attacks of diseases or pests that reduce leaf number will reduce yields in nonleafy varieties but will have little effect on yield of leafy varieties during the growth stage when LAI is excessive.

In treatment 1 yield was not reduced when the attack occurred at 50 days (Table 1), suggesting that very early defoliation does not reduce yields. In nonleafy M Col 22, 50% defoliation at 50, 100 and 200 days reduced yields markedly. In M Col 113 defoliation at 200 days when LAI was excessive had little effect on yield. These results suggest that partial defoliation causes severe yield reduction in nonleafy varieties but only minor reductions in yield of leafy types at the time when they have large LAIs.

A growth simulation model (6) was modified to simulate complete defoliation effects on cassava growth. After complete defoliation, root growth ceases and LAI increases rapidly to a level similar to the control (Fig. 6). Thereafter, root growth increases as if there had been no attack. The simulated yield reductions depend on varietal characteristics but in most cases are quite small (Table 2), suggesting that complete defoliation at any time during the growth cycle will reduce yield by about 20%. It should, however, be noted that in the simulated plant types with high yield potential, the reductions are more severe. As plant improvement programs move nearer to these ideal plant types, the importance of controlling pests and diseases that reduce leaf area will increase.

Thus far we have discussed damage due to defoliation; however, diseases and pests can affect leaves in other ways. *Cercospora* spp. attack

Table 1. **Effects of defoliation (50%) at different times on yield of a leafy (M Col 113) and nonleafy (M Col 22) cassava variety.**

Time of defoliation	M Col 113*	M Col 22*
50 days	110	101
100 days	84	85
200 days	92	89
50, 100, 200 days	93	78

* Harvest data (10 mo) presented as percentage of control dry root yield

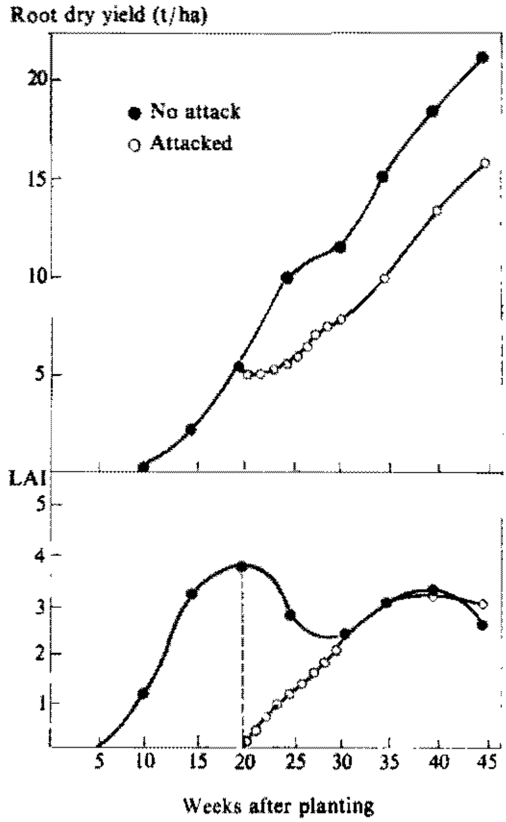

Figure 6. **Effect of hornworm attack causing complete defoliation at 20 weeks (computer-simulated data).**

cassava, producing toxins that cause yellowing, leaf spots and premature leaf fall. The effects of reduced leaf life on yield were simulated, and yield was reduced markedly when leaf life was shortened (Fig. 7). Lozano and Castaño (5) showed that healthy leaves had lives of 85 days whereas *Cercospora*- infected leaves had lives of 68 days; furthermore, yield increased by 14% in protected plots. Cock (6) suggested that one of the major breeding objectives in cassava should be to increase leaf life to levels greater than 100 days. If this becomes a reality, then losses due to premature leaf fall will be greater (Fig. 7).

Leaves with heavy mite infestations will often remain on the plant for long periods of time. Recent data obtained at CIAT (Cock and Mejia, unpublished data) show that although leaf number is not drastically reduced due to premature leaf fall, the mites severely reduce the photosynthetic rate of the individual leaves (Fig. 8). Similarly

Table 2. Effects of simulated hornworm attacks at different growth stages on a nearly ideal cassava plant and leafy type

Time of hornworm attack (weeks after germination)	Near ideal type* (% of control)	Leafy type* (% of control)
No attack	21.0 (100)	7.7 (100)
5	22.5 (107)	8.9 (116)
10	18.8 (90)	6.3 (82)
15	16.1 (77)	6.2 (81)
20	15.9 (76)	5.4 (70)
25	16.8 (80)	4.6 (60)
30	18.0 (90)	5.6 (73)
35	16.4 (82)	5.8 (75)
40	17.6 (84)	5.5 (71)

* Dry root yield (t/ha) at 11 mo

Alagianagalingam and Ramakrishnan (1) demonstrated severely reduce photosynthetic rates in cassava leaves infected with African mosaic. The reduced rates of photosynthesis in mite-infested leaves were present at all light intensities, and it must be assumed that these levels of attack will greatly reduce crop growth rate. Simulations showed that only a 10 percent reduction in crop growth rate decreases yield by more than 20 percent; hence the tremendous decrease in photosynthetic rate caused by mites has a potentially enormous negative effect on yields.

Certain pests (i.e., thrips) neither cause leaf fall nor greatly decrease photosynthesis; however, they do cause leaf distortion and reduced leaf size. Schoonhoven (4) showed yield losses of 25 percent due to thrips attack. Thrips cause leaf distortion and reduce leaf size. When the effects of leaf size on yield were determined by the simulation model,

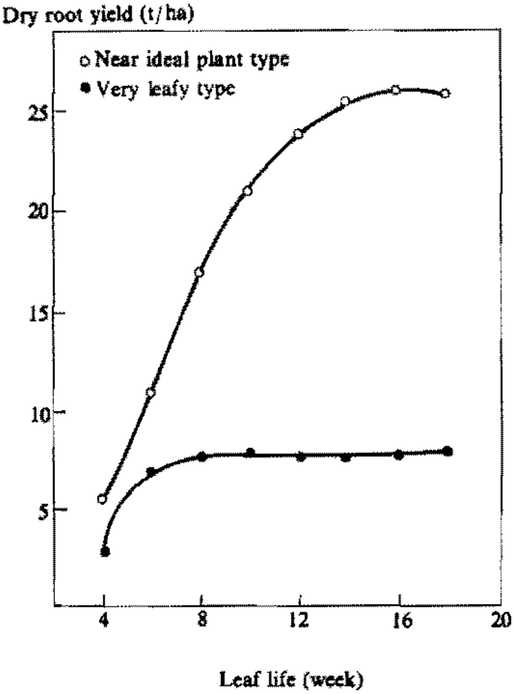

Figure 7. The effects of changed leaf life throughout the growing season on yield of a nearly ideal and very leafy plant type (computer-simulated data).

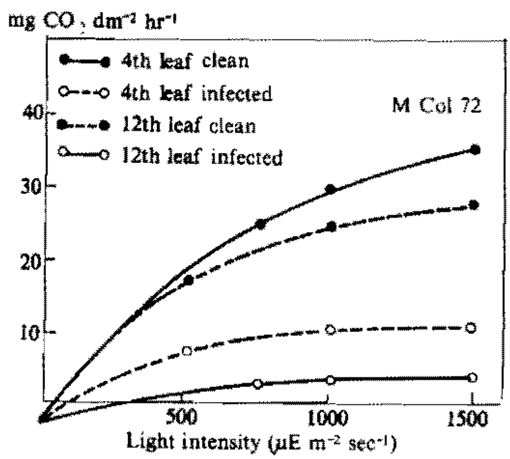

Figure 8. **Effect of heavy mite infestations on photosynthetic rate.**

it was found that yields could be severely reduced (Fig. 9); however, small reductions in leaf size (600 cm^2 maximum to 400 cm^2 maximum) in near ideal types cause small yield reductions. Hence the plant can tolerate low levels of this type of attack with virtually no loss, and in the case of leafy types, a reduction in leaf size may actually increase yields.

Apices

In the initial stages of growth, cassava has a single active main apex. As growth continues, lower axilliary buds may develop into sucker branches; or two, three or more equally sized branches develop from the axilliary buds directly below the main apex.

When apices are damaged by insects such as the shoot fly *(Silba pendula)* and thrips, apical dominance is also destroyed and axilliary buds develop. Except in very severe attacks, one of these axilliary apices becomes dominant and plant growth continues as before. Removal of apices from 6 to 8 months at two-week intervals in M Mex 11 reduced yield of dry roots by less than 10 percent; removal of up to 75 percent of the apices in the very leafy variety M Col 113 increased yields substantially (Table 3). Thus damage to the main apex, if not continuous and attacking all new apices that become active, has little effect on yield and may even increase it in leafy varieties. In fact in Costa Rica higher yields were reported from plots infested with *Silba pendula*. Furthermore, model simulation data suggest that reduction in active apex number, especially from six months after planting, has little effect on yield even in the nearly ideal plant types predicted by the model.

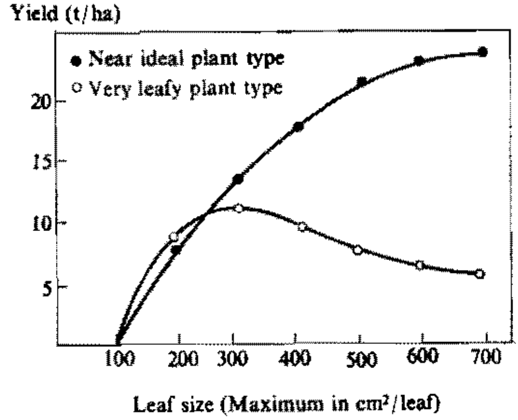

Figure 9. Effect of leaf size maximum on yield of a near ideal and a very leafy cassava variety (computer-simulated data).

Stems

The cassava stem acts as an active transport system of water and organic material and also as a support system for the foliage. Cassava bacterial blight blocks xylem transport (10), causing wilting of the leaves, which later die and fall. It is self-evident that this type of damage causes yield loss.

Anastrepha spp., in conjunction with *Erwinia* rots, weaken stems so that they are unable to fulfill their supporting role. Stems often double under

Table 3. Effects of reduction of apex number 5 months after planting on growth of M Col 113, harvested at 10 months.

Apex no. reduction (%)	Fresh root yield (t/ha)	Dry root yield (t/ha)	Dry stem wt (t/ha)	Harvest index (%)
0	33.6	11.3	12.5	44
25	38.5	13.3	12.7	47
50	39.7	13.6	12.0	49
75	40.3	14.0	11.8	49
Significant differences	**	**	NS	**

their own weight and the leaves above the break die. Obviously, yields are reduced. The same happens when *Phoma* spp. attack susceptible cultivars.

Loss of plants

In certain cases heavy disease or pest infestations may cause complete loss or death of plants. In the germination phase many fungi (9; Lozano, personal communication) and a large number of insects such as cutworms (2; Bellotti, personal communication) may reduce germination. In addition to reducing plant populations, this results in a plant arrangement that is not square. Cock et al. (6) showed that certain varieties had a flat-topped density response curve between 10 and 30 thousand plants per hectare (Fig. 10). If these varieties are used, yield reduction due to reduced plant population, when population reduction is about 50%, should be minimal if high plant populations are planted. Furthermore, recent work (Castro, unpublished data) shows that changing from square planting to a rectangularity of 1:2 has little or no effect on yield. In other works, if high initial populations are used with varieties that have flat-topped density response curves, early plant death will cause only small yield losses if there is less than 50 percent mortality. If death occurs later in the plant growth cycle, the yield already formed will be lost due to root rots and thus final yield will be reduced.

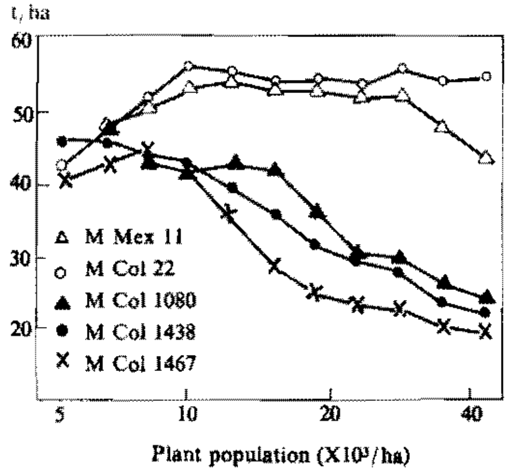

Figure 10. **Fresh root yields of five cassava cultivars harvested at 11 months.**

Conclusions

Both field data and computer simulation confirm that cassava is relatively tolerant to disease and pest attacks because of abundant chances for yield recovery after damage. Relatively minor yield losses result from (a) early plant death on a moderate scale, (b) reduction in active apex number, (c) small decreases in root number, and (d) small reduction in leaf size. On the other hand, yields are severely reduced when (a) leaf life is reduced, (b) photosynthetic rate is reduced, (c) stems are severely damaged, and (d) there is a high percentage of early plant death.

Acknowledgments

The author is grateful to Gaston Mendoza and Patricia Juri for their help in modifying the growth model to simulate pest attacks; to Sara Mejía for the photosynthetic measurements; and to Carlos Lozano, Tony Bellotti and Kazuo Kawano for help in preparing this paper.

Literature cited

1. ALAGIANAGALINGAM, M.N. and RAMAKIRSHNAN, K. 1970. Studies on a virus disease of tapioca (*Manihot esculenta* Crantz). II. Carbohydrate metabolism. Madras Agricultural Journal 57:55-62.
2. BELLOTTI, A. and SCHOONHOVEN, A. VAN. 1978. Mite and insect pests of cassava. Annual Review of Entomology 23:39-67.
3. CENTRO INTERNACIONAL DE AGRICULTURA TROPICAL. 1975. Annual Report 1974. Cali, Colombia. 260p.
4. ______ 1976. Cassava Production Systems. *In* Annual Report 1975. Cali, Colombia. pp.B1-B57.
5. ______ 1977. Cassava Production Systems. *In* Annual Report 1976. Cali, Colombia. pp. B1-B76.

6. COCK, J.H.; FRANKLIN, D.; SANDOVAL, G. and JURI, P. 1978. The ideal cassava plant for maximum yield (In press).

7. ______ WHOLEY, D.W.; and GUTIERREZ, O. 1977. Effects of spacing on cassava (*Manihot esculenta* Crantz). Experimental Agriculture 13: 289-299.

8. IRIKURA, U.; COCK, J.H.; and KAWANO, K. 1978. The physiological basis of genotype-temperature interactions in cassava (In press).

9 LOZANO, J.C. and BOOTH, R.H. 1974. Diseases of cassava (*Manihot esculenta* Crantz). PANS 20:30-54.

10. ______ AND SEQUEIRA, L. 1974. Bacterial blight of cassava in Colombia: etiology. Phytopathology 64:74-82.