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THE EFFECT OF A PERIOD OF WATER SHORTAGE ONTHE GROWTH AND YIELD OF CASSAVA

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Summary

A drought stress was imposed on two cultivars, M Col 22 and M Mex 59, by withholding rainfall from field plots for 10 weeks commencing when the crops were 12 weeks old. The crops were then allowed to recuperate until the experiment was terminated at 10 months. Harvests were taken at intervals through the growth cycle and were supplemented with measurements of fine root distribution, leaf production, leaf senescence, soil and plant water status and stomatal response. As a result of the stress the late developing cultivar M Mex 59 actually improved its yield at 10 months over the controls. An explanation for the behaviour of both cultivars is sought in the relative effects of water shortage ondry matter production and allocation, canopy dynamics and internal plant water relations.

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THE EFFECT OF A PERIOD OF WATER SHORTAGE IN THE GROWTH AND YIELD OF CASSAVA

Introduction

The seminar reports aspects of an experiment carried out at Santander de Quilichao over the period April 1979- February 1980. The purpose of the experiment was to evaluate the response of two cultivars of cassava, M Col 22 and M Mex 59, to a period of drought imposed when the crops were 4 months old. The drought was arranged by placing plastic covers over the soil surface. They were maintained for 10 weeks and were removed when M Col 22 was showing signs of imminent desiccation. The recuperation phase lasted a further 3 months. The total duration of the experiment was thus 10 months.

The following sequences of measurements were maintained.

a) Five harvests during the growth cycle. One at the beginning of the stress, a second more or less in the middle and a third at the end of the stress. The fourth harvest was taken after 6 weeks of recuperation and the fifth when the experiment was terminated. In these harvests the emphasis was upon dry matter production and distribution but measurements were also taken of the distribution and density of the fine root system. Samples were also taken for the determination of starch content but these data are not yet available.

b) Soil moisture content to 2 m with a neutron moisture meter at variable intervals but never less frequently than two weekly and each 3 days for one sustained period of 2 months.

c) Non destructive measurements of plant development at two weekly intervals. These include plant height, plant width, apex production, leaf production, leaf expansion, and aspects of leaf senescence.

d) Diurnal measurements of leaf water potential and leaf diffusive conductance on one occasion before the stress period and on three occasions during its gradual development.

In sequence this presentation will describe the overall response of the crops and then seek, through a consideration of the detailed measurements, an explanation of the responses in terms of the component physiological processes. Differential responses between cultivars will be highlighted.

Environmental Conditions.

Two diagrams serve to illustrate this. Fig 1 depicts the weather conditions at Santander de Quilichao during the experimental period, the timing of the harvests and of the period of rainfall exclusion are included. Fig 2 describes the seasonal pattern of soil moisture under the crops and hence the putative cause of the crop response to be analysed subsequently. When the rainfall exclusion period started the soil was below capacity and the entire recuperation phase was characterized by moderately dry soil.

For two reasons these soil moisture data, which accurately define the moisture available to the crops, do not allow the solution of the crop water balance equation and hence the calculation of crop water use. Firstly the water extraction patterns show, and the direct measurements of root distribution confirm, that the crops were using water from below 2 m. Secondly the sloping site that was used to facilitate the shedding of water from the covered plots complicated surface flow and apparently flow at depth also.

Overall Response.

Fig. 3 contains all this information. It shows the loss in leaf area, the reduction in growth and the change in partitioning of dry matter caused by the stress. There was some sort of shared response between tops and roots. During the recuperation phase leaf area increased rapidly and growth of all components was re-established. In one cultivar, M Mex 59, the yield of roots was actually greater following stress reflecting a changed pattern in the allocation of dry matter.

Table 1 defines some of the characteristics of biomass production and the effect of stress. It also includes an analysis of the conversion of solar energy. Responses are clearly seen. The growth rates and the efficiency of conversion are not high by general crop growth standards. They are, however, maintained for a considerable period.

Fig. 4 provides an overview of the partitioning of dry matter between growth of tops and the growth of roots. It is constructed along the lines of the model of cassava growth proposed by Boerboom (1978). It proves to be an adequate descriptor of the overall response and shows that the effect of stress is to change the allocation ratio and hence the harvest index (HI) of the crops, particularily M Mex 59. The remarkable feature of the response of M Mex 59 that this diagram highlights is the fact that in the recuperation phase there is no evidence of reversal to the pre-stress (ie control) allocation pattern.

From the data defining the overall response the following questions (at least) arise:

1) From where do the plants extract water ? How much water can they obtain from the soil ? What are the features of the fine root system ? Are there cultivar differences ?

2) What is the nature of the loss of leaf biomass (area) ? To what extent do the plants discard potentially productive area ? To what extent does leaf loss contribute to reduced water use and hence survival ? How does M Mex 59 maintain a much higher LAI that M Col 22 during the stress period.

3) How does the plant handle water stress internally ? What level of stresses develop ? How do the stomata react ? What is their contribution to water conservation ? The data that follow will contribute at least partial answers to these questions.

Nature of Root System

The decision to install NMM access tubes to 2 m was based upon the published information on cassava root system (Sena and Campo 1973). These data suggested that 1.5 m was probably the extent of penetration but we discovered at Santander that the potential exploration is much greater than this. We essentially followed the roots down the profile and by the fourth harvest (7 months) they had penetrated to below 2.6 m. Fig 5 summarizes the root distribution data of which the most noteworthy feature is its generally low density. The capacity of root systems to extract water is more closely related to surface area, ie length and diamter distribution, than it is to biomass. From

These data we have calculated that root densites are of the order of one tenth of the densities found commonly in other crops. If the mycorrhizal associations discussed by Dr. Howeler in a recent seminar in this series (SE-3-80) effectively replace root surface area in P uptake the important question is what consequence does this have for water relations.

Cassava root systems are able to tap considerable water reserves by virtue of their capacity to extend to great depths. They are, however likely to be able to do this slowly because of their low density. It would seem from these data that cassava is likely to be diurnally limited in water uptake at even relatively high soil water contents.

The data do not define any cultivar differences or large treatment responses. However it should be stressed that the data are highly variable and hence are not definitive. Those who have worked with root systems will appreaciate the difficulties in this work. They should not discourage people from seeking answers for differential cultivar response in the characteristics of the fine root system.

Canopy Dynamics.

The stress had big effects on all the components of leaf area production - apex production, leaf production per apex and leaf expansion (figs 6 and 7). Following release from stress there was some evidence of compensatory growth especially in leaf size. The canopies were quickly re-established following release from stress. We do not yet know the role, if any, of root reserves in this process.

The leaf fall data (fig 8) are perhaps the most interesting because they show, contrary to the conventional wisdom, that leaf area reduction under stress is not caused by increased leaf fall. In fact, leaf life actually increased under stress particularily in the dense canopy of M Mex 59 probably because of improved light levels low in the canopy which result from the restricted activity of the apices.

Plant Water Status

The classical pattern of response which has been shown to occur in many, generally herbaceous, crops is as follows: As the soil dries the plants show at first a greater diurnal range in water potential, at a critical level of water potential the intervention of stomatal control of water use with some level of daytime recovery depending upon stomatal efficiency, and finally incomplete night-time recovery leading to permanent wilting and loss of function.

We have made a sufficiently large number of observations on cassava to be certain that this is not the way it handles stress. Stomatal control occurs rapidly and is so effective that leaf water potentials do not fall below the controls. In fact if anything the plants over-compensate and this can be seen in fig 9 which depicts the response of the plants towards the end of the stress period. Stomatal control of water use in cassava is very effective. M Mex 59 has generally lower leaf conductances than M Col 22 and this must have been an important part of its ability to maintain a higher leaf area at equivalent levels of soil moisture. High leaf conductances do occur but infrequently. This seems to support the proposition that the supply of water by the roots limits the water exchange capacity of the plant. What controls stomatal response is unknown. It certainly is not a simple feed back response to leaf water potential.

The combined effects of the reduction of leaf area and of leaf conductances are shown in fig 10. These are calculations made in a modified Pennan equation to display the importance of these two methods of restricting water use and hence of survival under water shortage.

Conclusions

The objective of the water relations work should be to elaborate the environmental and cultivar response in such a way that what we understand can be used to predict response in the field. In one year we can make some progress in this and I can already begin to make preliminary entries into a model of growth and water relations (fig 11), which extends the earlier crop modeling work carried out here (Cock *et al* 1979). There is, however, a long way to go and there are plenty of obvious experiments to do. Without the basic information on how the plant responds there is a very great danger that a lot of the more applied research will be highly inefficient. After listening to Dr. Howeler's recent seminar on nutrition in cassava I could not help but wonder how the Frijoleros would shape up in their current field experimentation if they had only just realized that those white lumps on the root system had something to do with the N nutrition of the plant. We really are very ignorant about the nature of the cassava plant and should ask ourselves the question. How quickly can we really proceed with the applied research without an improved understanding of the crop ? Workers in most crops have a legacy of many years of scientific research at their disposal. For cassava this is entirely lacking.

References

Boerboom, B.W.J. (1978). A model of dry matter distribution in cassava (*Manihot esculenta* Crantz). Neth. J. Agric. Sci.. *26*: 267-77.

Cock, J.H., Franklin, D., Sandoval G. and P. Juri. (1979). The ideal cassava plant for maximum yield. Crop Science. *19*: 271-9

Sena, Z.F. De and H.Dos R. Campos (1973). Estudo do sistema radicular da mandioca (*Manihot esculenta* Crantz) submetidas a diferentes frecuencias de irrigaçao. Cruz das Almas, Brazil, Universidade Federal da Bahía. Escola de Agronomia, Brascan Nordeste; Serie Pesquisa 1(1): 41-52.

Table 1

Crop Growth Rate and Efficiency of Solar Energy Conversion.

Period	Duration (days)	Mean daily solar Irradiance (MJ m^{-2})	Mean growth rate (Kg/ha/day) and efficiency* of solar capture (%).			
			M Col 22		M Mex 59	
			Control	Stress	Control	Stress
- H1	109	17.3	27 (0.26)	27 (0.26)	39 (0.38)	30 (0.29)
H1 - H2	39	18.2	103 (0.95)	62 (0.57	96 (0.89)	47 (0.43)
H2 - H3	33	19.3	112 (0.97)	14 (0.12)	74 (0.64)	51 (0.44)
H3 - H4	38	19.7	113 (0.96)	40 (0.34)	130 (1.11)	31 (0.26)
H4 - H5	87	20.3	17 (0.14)	35 (0.29)	61 (0.50)	115 (0.95)

* Energy content of biomass taken to be taken 16.8MJ Kg^{-1}

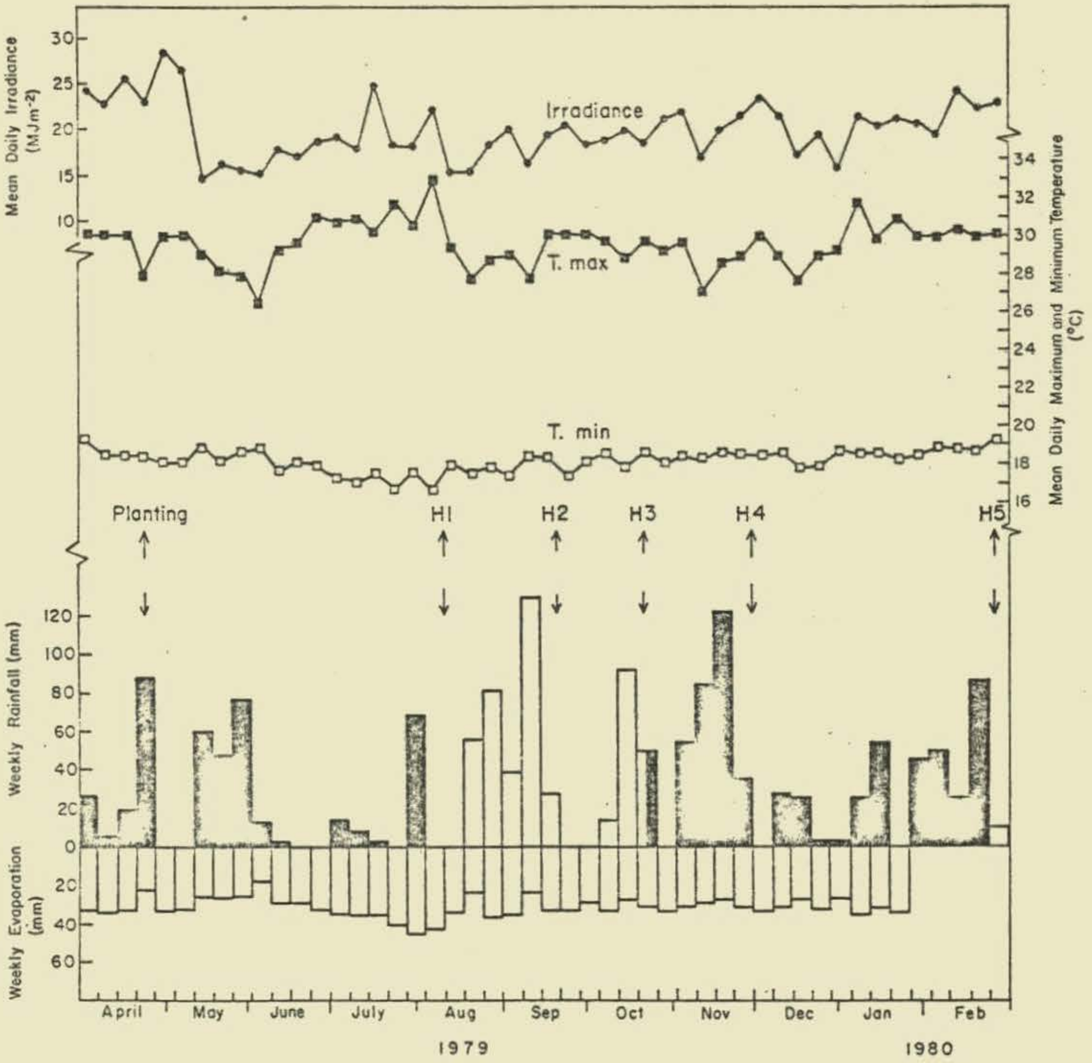


Figure 1. Weather at Santander de Quilichao throughout the experimental sequence. (Timing of five sequential harvests H1-H5 is shown, the period of rainfall exclusion corresponds to the interval H1 - H3).

Figure 2. Soil water content to 2 m under the experimental crops.

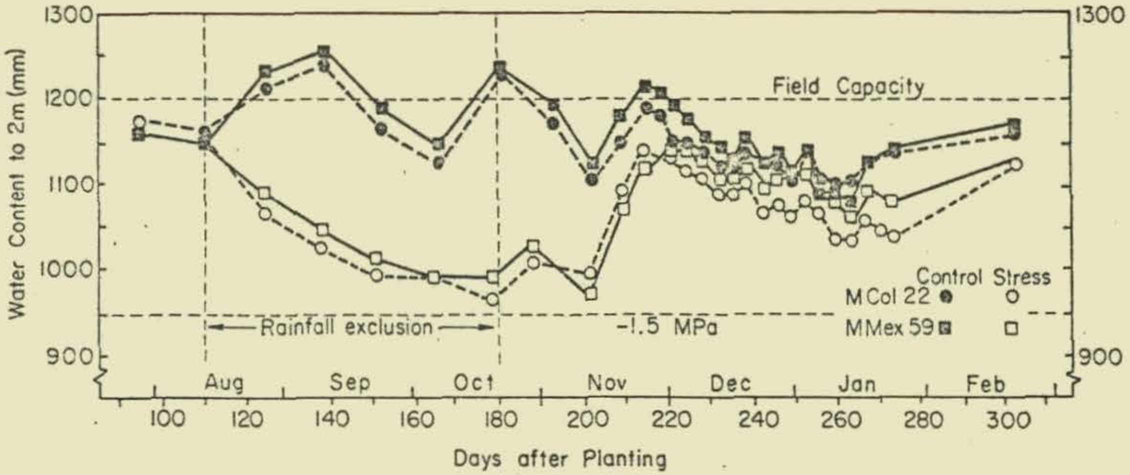


Figure 3. Effect of water shortage on the distribution of biomass in five sequential harvests of two cassava cultivars.

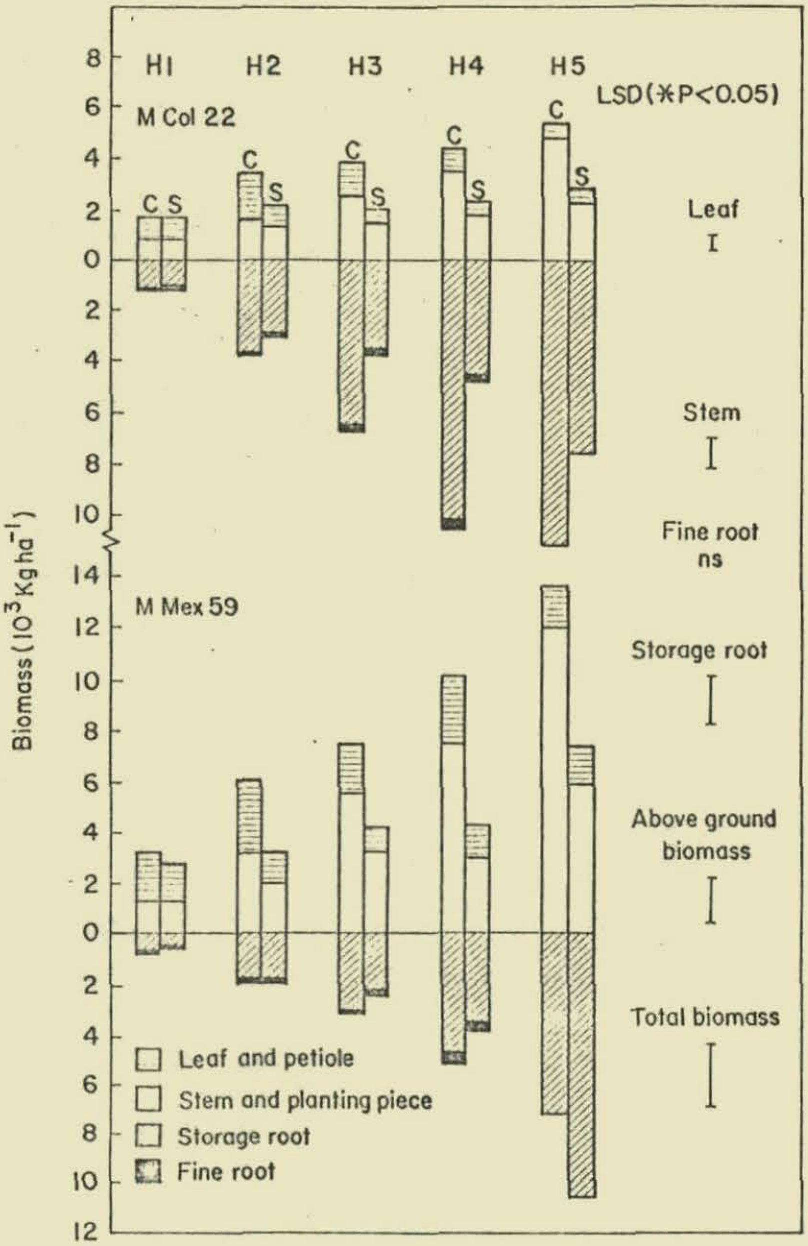
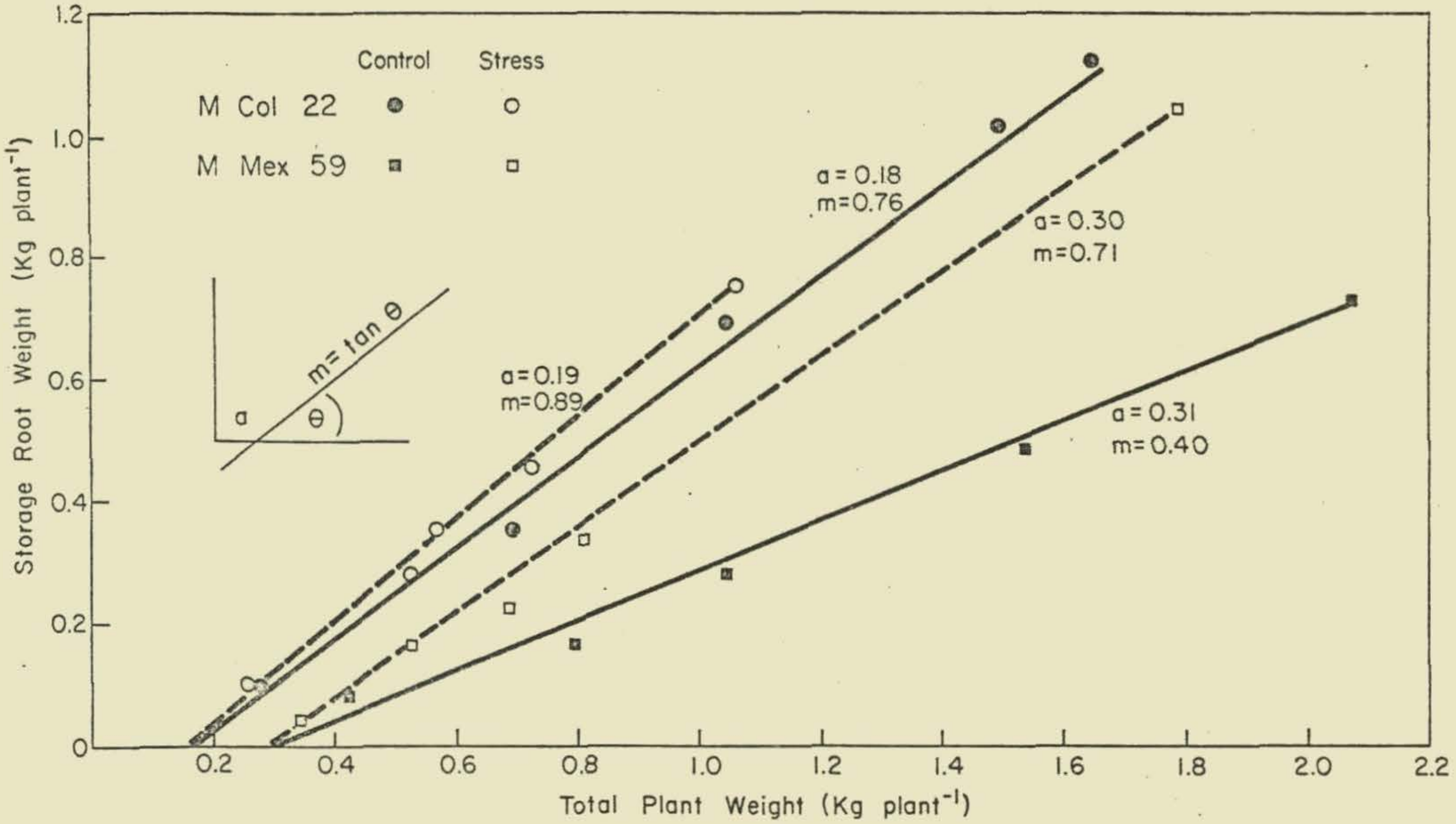


Figure 4. The effect of water shortage and the allocation of biomass to storage root in two cassava cultivars.



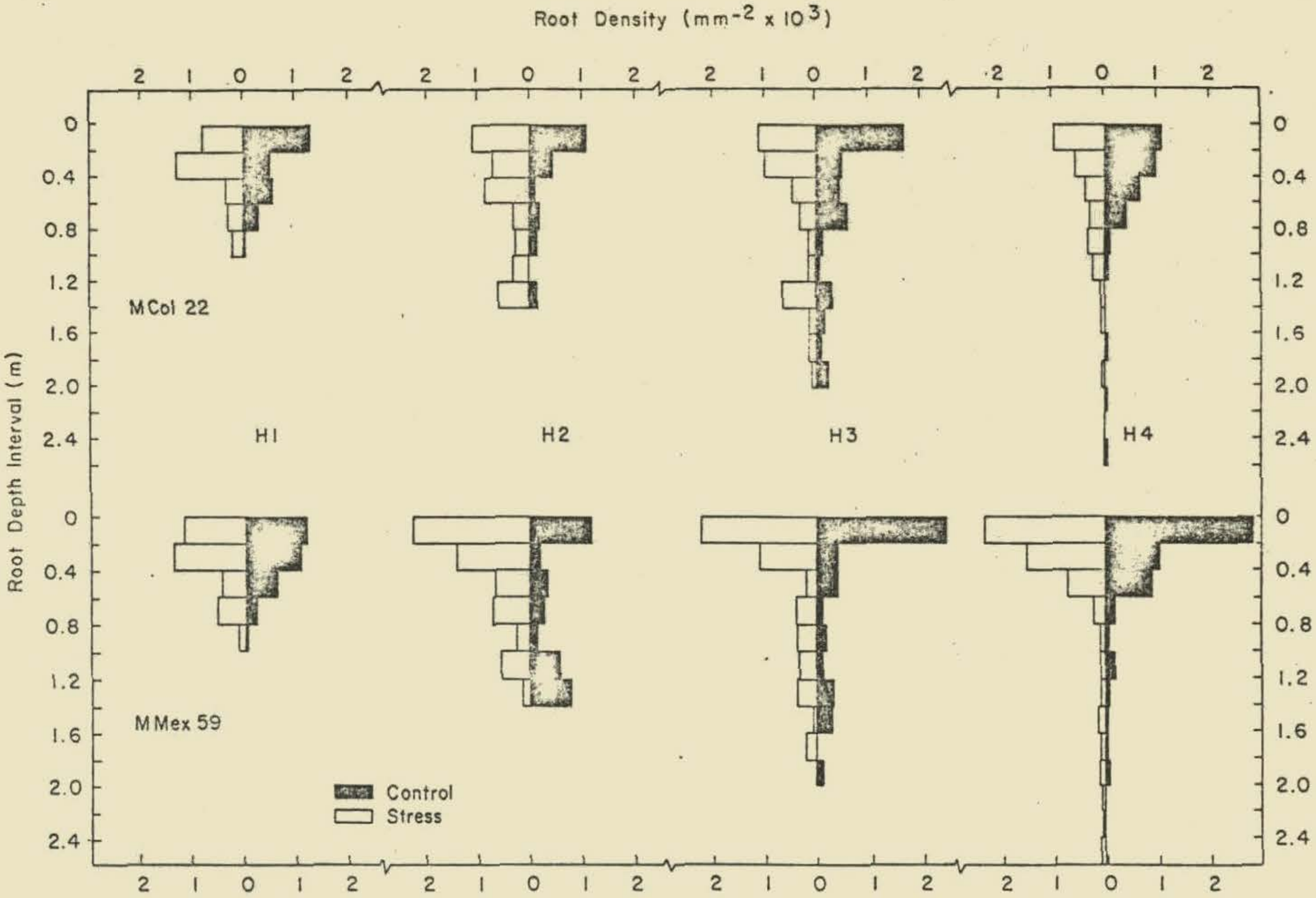


Figure 5. Root density profiles for cassava at four growth stages.

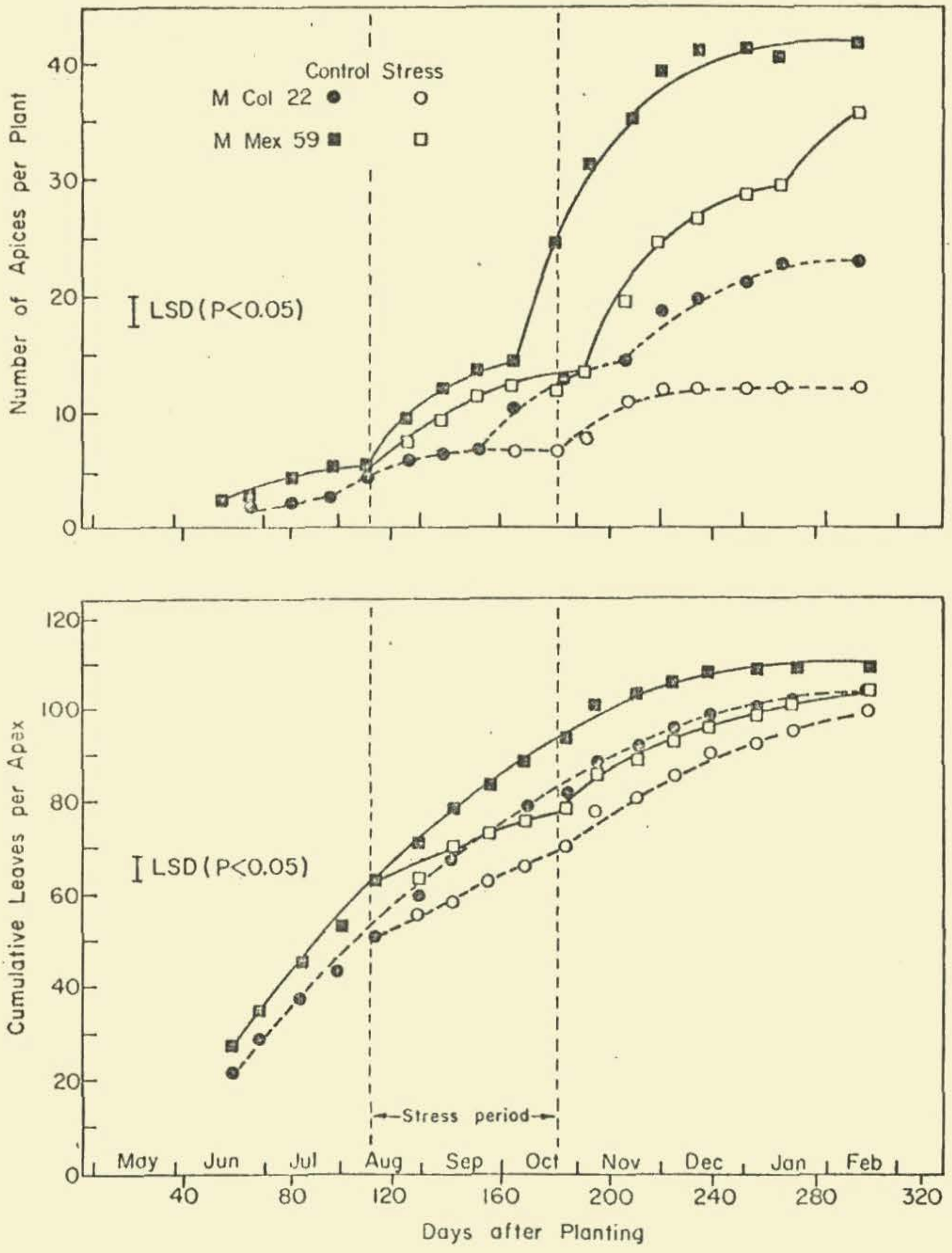


Figure 6. Effect of water shortage on apex production per plant and leaf production per apex in two cassava cultivars.

Figure 7. Effect of water shortage on the area of 2 week-old leaves of two cassava cultivars.

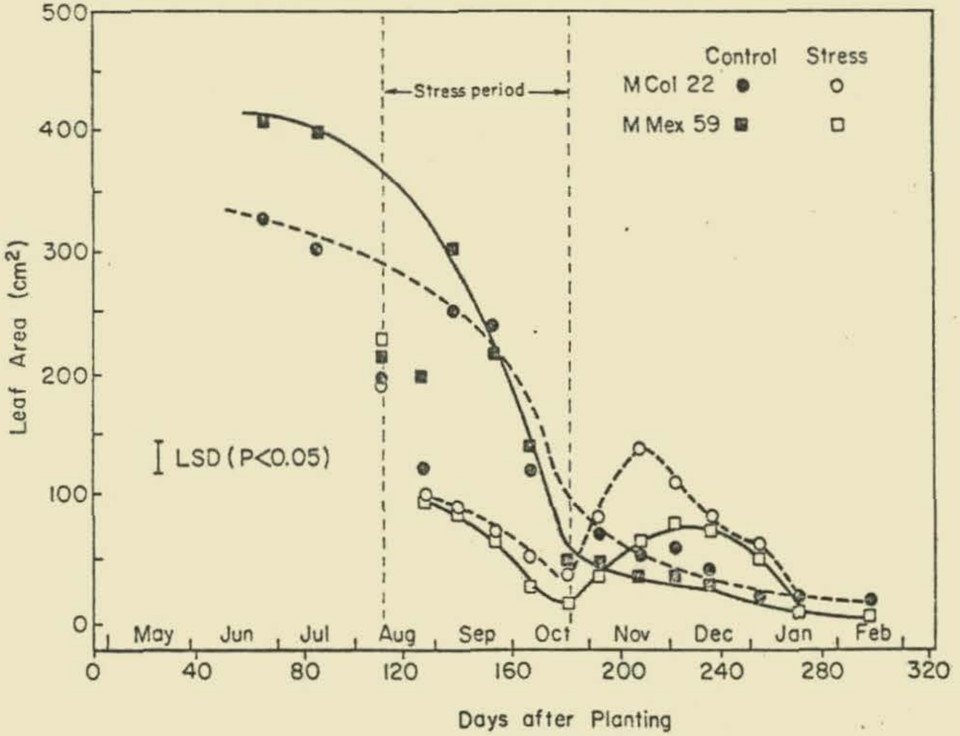
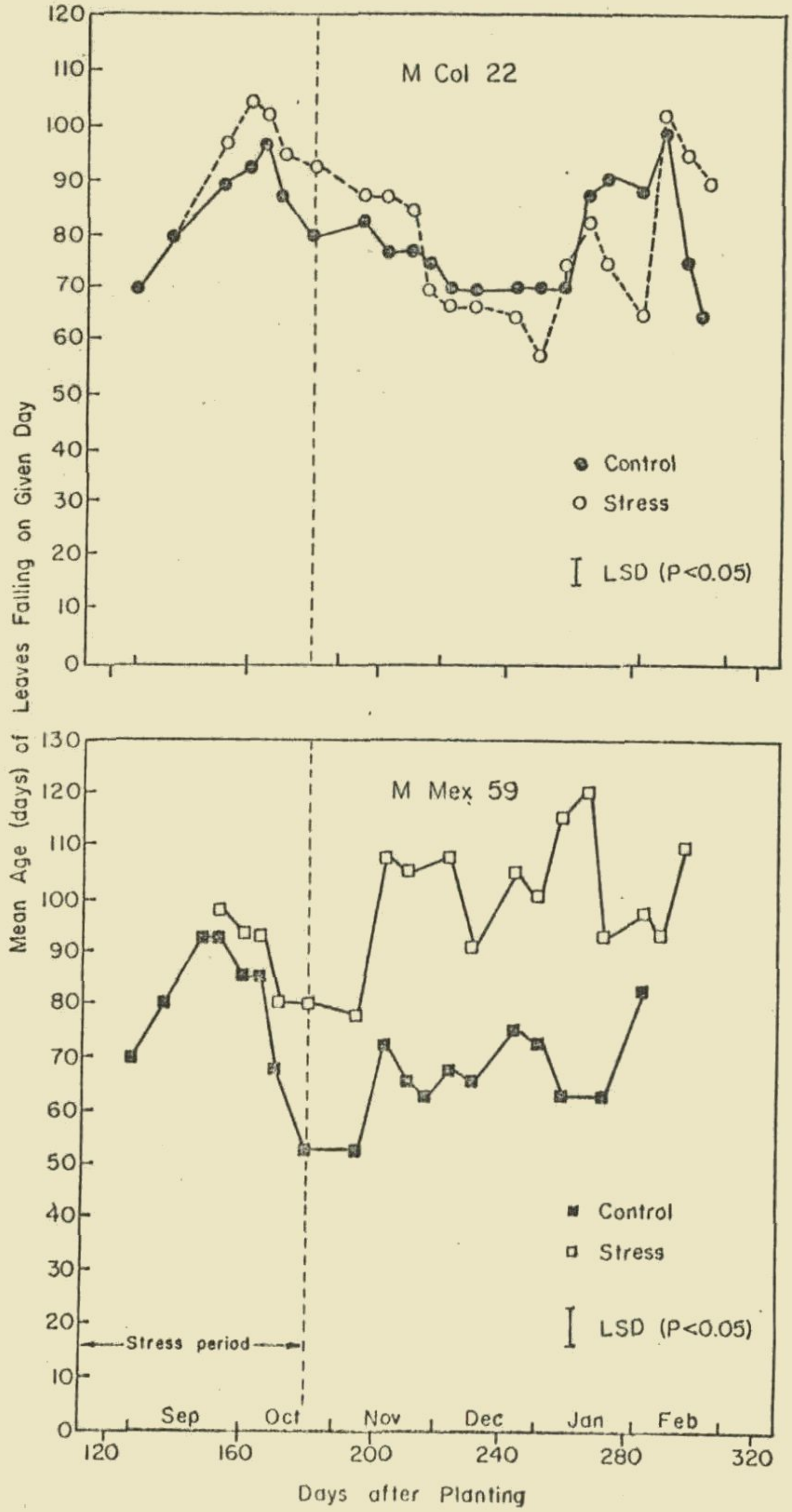


Figure 8. Effect of water shortage on the age of leaves at falling in two cassava cultivars.



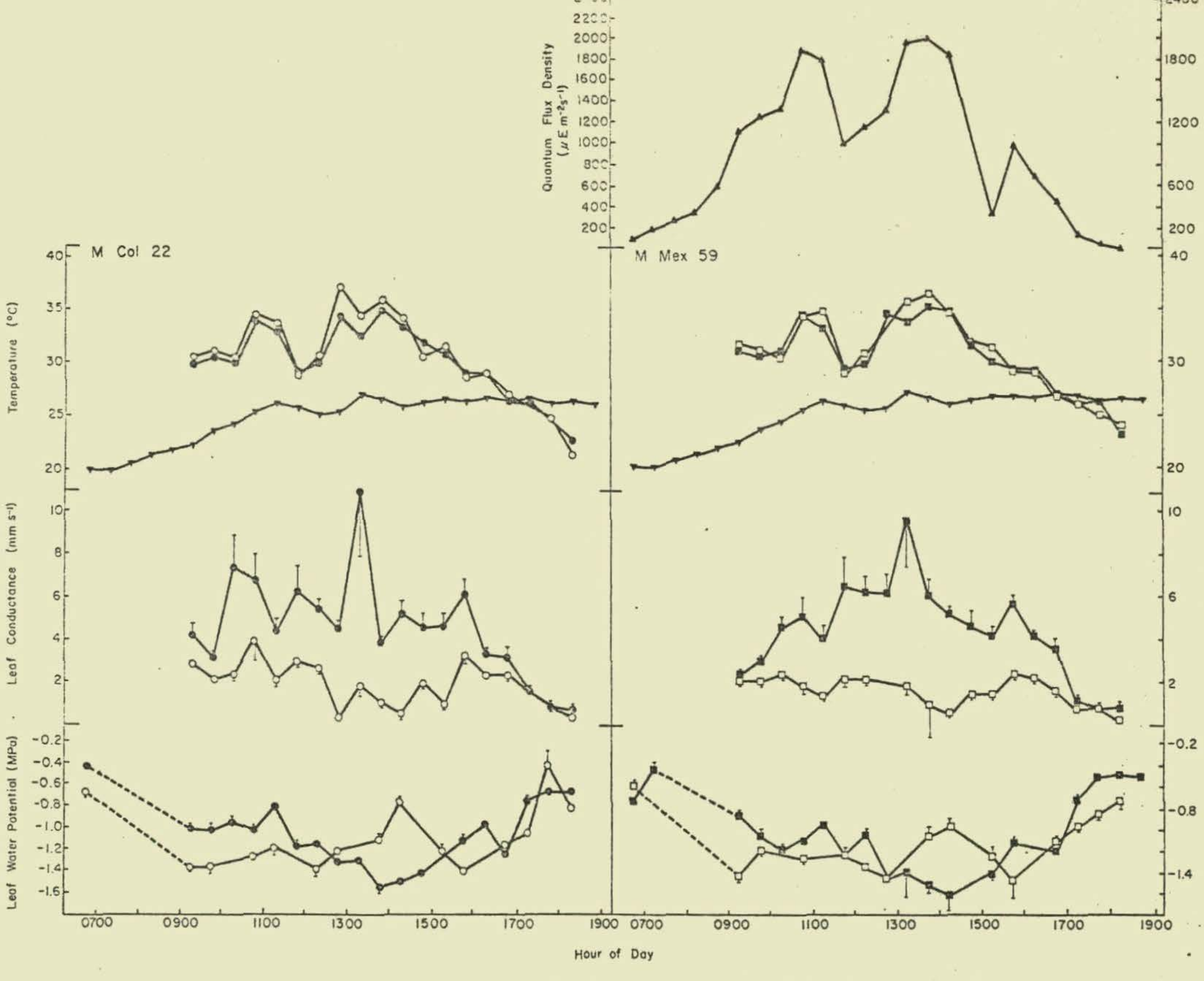


Figure 9. Effect of water shortage on leaf conductance and leaf water potential of two cassava cultivars (the response following 3 weeks of rainfall exclusion).

Figure 10. Combined effect of leaf area and leaf conductance on the transpiration of two cassava cultivars.

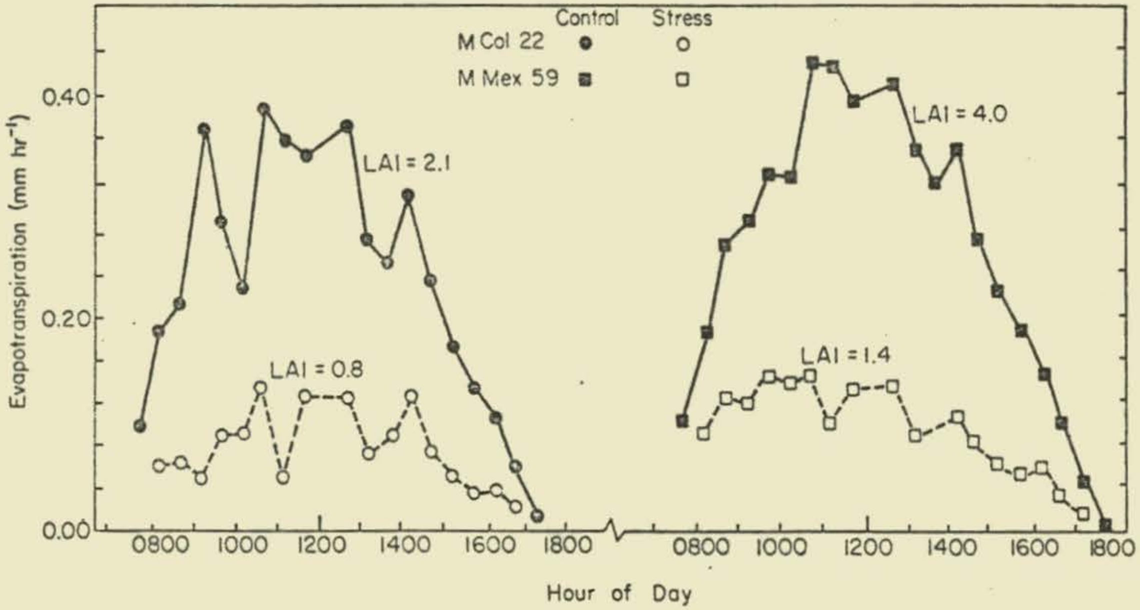


Figure 11.

A SIMPLE GROWTH AND WATER RELATIONS MODEL FOR CASSAVA