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PHYSIOLOGICAL MECHANISMS OF DROUGHT TOLERANCE IN CASSAVA (MANIHOT ESCULENTA CRANTZ)

The University of Arizona PH.D. 1983

PHYSIOLOGICAL MECHANISMS OF DROUGHT TOLERANCE IN CASSAVA (*MANIHOT ESCULENTA* CRANTZ)

by

Marcio Carvalho Marques Porto

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF PLANT SCIENCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Marcio Carvalho Marques Porto entitled Physiological Mechanisms of Drought Tolerance in Cassava (Manihot esculenta Crantz)

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

James W. O'Leary — 10/21/83 — Date

Karen Nastrom — 10/21/83 — Date

Paul G. Bartels — 10/21/83 — Date

James O Anderson — 10/21/83 — Date

_____ — _____ — Date

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Victoria Marcarian — October 21, 1983
Dissertation Director — Date

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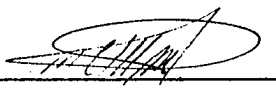
SIGNED: 

DEDICATION

Durante o curso, quantas vezes sentamos, nós os brasileiros longe da Pátria, e quantas vezes "resolvemos" os problemas do Brasil . . .

Hoje, termino um Ph.D. e volto para lá. O país está mal e sera difícil conseguir viver da mesma maneira que viviamos no começo da crise.

Porém, tenho a certeza, a absoluta certeza de que não será difícil trabalhar. A mesma vocação que me fez sair para o exílio voluntário saberá como ajudar-me a contornar os problemas e avançar na busca de uma pesquisa ÚTIL, DINÂMICA E CRIATIVA.

Acredito em milagres. Acredito nos propósitos daqueles que querem soerguer o BRASIL.

Tucson, Arizona, 21 de Outubro de 1983

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ABSTRACT

The response of cassava (Manihot esculenta Crantz) to water stress was evaluated in two experiments conducted in Tucson, Arizona and Santander de Quilichao, Colombia, involving five cultivars (MVen 218, CMC 40, MCol 22, MIta 1158 and MCol 1684). In both experiments stress was imposed in a given stage of the plant cycle. A third experiment, conducted in Palmira, Colombia, evaluated the relationship existing between photosynthesis, relative humidity and yields of cassava.

Cultivar MCol 1684 reduced its transpirating area by either reducing leaf formation (stress given to 3-month-old plants) or increasing leaf fall (6-month-old plants). A reduction in plant growth and leaf expansion rates is attributed to reducing the plant's total leaf area. Water stress imposed in Tucson also showed reductions in plant growth, leaf formation, extension and final leaf size (except for MVen 218). Plants of MCol 1684 in Santander de Quilichao, like MVen 218 in Tucson, did not change their final leaf sizes due to stress.

Dry matter production was more reduced when stress was imposed early in the plant growth cycle. Dry matter partitioning was also altered by stress given to 3-month-old plants of MCol 1684. The stressed plants delayed the allocation of dry matter to the storage roots.

Noon and afternoon values of leaf conductance and transpiration of MCol 1684 were reduced after 40 days of stress. Interestingly, leaf temperatures of non-stressed plants were higher than those of the stressed plants. This can be attributed to an increase in leaf reflectance in the stressed plants by changing the angle of orientation of their leaves in relation to the sun.

Leaf conductances of non-stressed plants were correlated to photosynthesis, leaf temperatures and vapor pressure deficits in measurements taken at 3:00 PM. In the stressed plants conductances were also correlated to photosynthesis leaf temperatures, air moisture and transpiration.

Leaf water potentials were slightly reduced by stress in Tucson, except for MVen 218. Plants of MCol 1684, in Quilichao, did not show significant reduction in $_{L}$ due to stress. In contrast, noon and mid-afternoon values of $_{L}$ were lower in the non-stressed plants after 30-40 days of treatment. This suggests the occurrence of higher daily water stresses in non-stressed plants, because of elevated transpiration rates.

The effect of air humidity on the stomatal functioning of MCol 1684 seems to be strong, as proved by the dependence of transpiration, conductances and photosynthesis on relative humidity.

CHAPTER 1

INTRODUCTION

Water shortage is one of the most crucial problems in the economics of agriculture today. As the world population expands, the need for exploiting marginal areas of the world increases. The arid and semi-arid lands represent approximately 32% of the world's total arable land [25]. Exploitation of those areas is imperative in order to increase the agricultural frontiers for the production of food, oils, fibers, and vegetable fuels.

There are two distinguishing strategies adopted by man to exloit arid and semi-arid lands. The first and perhaps the simplest method is to avoid drought by applying water through irrigation. This, however, is becoming more and more difficult because of high costs and competition with urban and industrial sectors for use of water.

A second strategy is to use drought-tolerant crops which can produce well under conditions of limited amounts of water. This appears much more rational and depends on the existence of drought-tolerant material which can be adapted to arid and semi-arid regions.

The aim of this research was to identify possible mechanisms of drought tolerance in cassava, Manihot esculenta Crantz, a crop which is broadly distributed in the marginal lands of the tropical and semi-tropical areas of the world. This member of the Euphorbiaceae has

the ability to grow and produce relatively well even when the amount of nutrients and water in the soil are limiting for other crops. Research efforts have been increased in the last five years in order to confirm that cassava is a drought-tolerant crop.

Cassava is a tropical plant with its center of origin in America [33, 41]. It is cultivated between 30 degrees north to 30 degrees south in the tropical areas of the world. Brazil is the major cassava-producing country in the world, contributing 21% of a world production of 118 million tons of fresh storage roots [24].

The importance of cassava as a food crop in the third world is very significant, since it represents the basic component of the diet of 500 million people in 24 countries. Cassava is also important as an animal feed and has been used in some counries for feeding pigs, poultry and ruminants.

Additionally, cassava is a good raw material for production of ethyl alcohol, mainly in the areas in which sugar cane cannot be grown. In Brazil, where alcohol is being used as a motor fuel, the perspectives for alcohol production from cassava are almost unlimited, considering the capacity of this plant to grow in marginal, underutilized lands.

Evidence for drought-tolerance in cassava has been reported by several authors [1, 7, 11, 12, 13, 38, 46, 52, 67]. However, the amount of data now available in the literature is not adequate to identify and evaluate the mechanisms adopted by the plant to withstand prolongated drought periods.

1.1 Water Stress in Plants

Water stress affects practicaly every single process that takes place inside the plant [30]. Plants, however, often have mechanisms which reduce or even avoid the deleterious consequences of dehydration. Desert species are good examples of plants adapted to conditions of water scarcity. Adaptations of various kind permit these species to survive well under conditions which are unsuitable for cultivated plants.

Plants have been classified in several ways in relation to their behavior under conditions of limited water [34, 40, 53, 62, 63, 66]. The term "xerophytes," used since 1822 [53], defines those plants adapted to arid zones [40]. Today, the xerophytes are divided into: (1) true xerophytes, which can withstand drought situations; and (2) pseudo xerophytes, which are able to escape drought by accelerating their life cycle and producing drought-resistant seeds [53].

Mechanisms of "drought escape" [34, 40, 53, 62, 66], "drought enduring" [40, 53, 62, 66], and "drought evading" [40, 53, 66] have been proposed to explain the behavior of plants when facing drought. Since the different mechanisms of adaptation are not mutually exclusive in a given species, adaptation should be described as "the sum of traits expressed at several levels" by the plant [28].

The effects of water stress in plants might be also classified on a chronological basis, corresponding to a given leaf water potential. As the water potential becomes more negative, cell expansion is rapidly affected by water stress [30]. Following the sequence of events affected by water stress, the other processes, in the other they

are affected, are: wall synthesis and protein synthesis, formation of photochlorophyll, nitrate reductase level, ABA accumulation, cytokinine levels, stomatal opening, CO_2 assimilation, respiration, proline accumulation, and sugar accumulation [30].

In the field, the sequence of events begins with a restriction in canopy development, an increase in the shoot/root ratio, osmotic adjustment, stomatal closure, and leaf movements such as rolling, wilting, senescence and death by dessication [5]. The effects of water stress in some metabolic and physiological events will be discussed here, but more emphasis will be given to effects of stress on the processes of growth, photosynthesis, transpiration, stomatal mechanism, resistances, and their dependence on leaf potential.

1.1.1 Growth

Growth occurs as a result of cell division and elongation. Assuming that turgor above a critical level is necessary for growth to occur [30, 68], the role of water in plant growth is crucial. Water-stressed plants quickly reduce cell elongation [30, 59, 68] and polyribosome activity [30], with deleterious effects on protein metabolism. Cell division is also reduced in response to water stress, although data on this subject are scarce [30].

Under well controlled laboratory conditions, growth reductions in response to water stress are reported to occur in a matter of seconds [30]. Responses under field conditions can only be detected on a relatively long-term basis, since conditions do not permit the use of highly sensitive equipment. In the field, growth reductions due to

water stress are caused by a pool of factors, including changes in photosynthetic rates [3, 5, 16, 30, 59], leaf area [5, 30, 59], reductions in the uptake of minerals [16, 30, 59], changes in the plant's hormonal balance [30, 48], translocation [16, 30, 59], respiration [5, 30, 59], transpiration [5, 16, 27, 30, 57, 59], and protein breakdown [5, 30].

As a consequence of the physiological, metabolic and morphological changes that occur in plants during drought, a reduction in plant size and dry matter production eventually occur. Mechanisms of adaptation, then, arise and enable the plant to minimize the deleterious effects that will result in death by dessication [5, 30, 59, 63, 66, 68].

Leaves are highly sensitive to drought conditions [8]. Under stress, leaves might become thicker [34], with smaller epidermal and mesophyll cells [18], and thicker outer walls of epidermis and cuticle [53]. Other adaptations include an increase in number and a reduction in the size of leaf hairs [30], abundance of coatings such as cutin, suberin and resins [30], leaf rolling or folding [5, 30], and acceleration of the process of abscission [35, 59]. These mechanisms, together with changes in stomatal mechanism, distribution and size [5, 6, 13, 30], have the ability to reduce the amount of water lost by the plant and the effects of heat caused by excessive absorbed radiation [5, 16, 27, 30, 34, 53, 62, 63].

Growth reductions due to water stress are also found in stems. Stems can act as water storage structures and, by adopting special characteristics, prevent water loss and reduce the resistance to water

conduction [53]. Root growth is also affected by water stress [35, 53, 59], although one of the most apparent consequences of water stress in plants is the growth of roots in search of water in the deeper layers of the soil [35]. Moisture can also be stored in fleshy roots and underground storage organs such as tubers, rhizomes and bulbs [53]. Stress almost invariably increases the root/shoot ratio, as a consequence of a drastic reduction in vegetative growth [5].

When considering the economic aspects of plant cultivation, the effects of water stress on differential growth are important. In short-cycle plants, water shortage during periods of flowering and early grain filling will reduce yield to a greater extent than at earlier or later stages [30]. In contrast, effects of water stress on root crops are more pronounced at the time of root formation or root bulking, since these storage organs represent the economic part of the plant.

1.1.2 Stomatal Mechanism

Stomata control CO_2 uptake and water loss. In the absence of leaf water deficits, stomatal aperture is mainly controlled by CO_2 concentrations, light, relative humidity, K^+ content, and abscisic acid (ABA) [5, 6, 30, 54, 57]. Stomata open as a result of an increase in vacuolar saps, and water moves from the epidermis to the guard cells [54]. As a result, and considering the form of the guard cells (bent by the extremities), a "swelling" of these cells forms a pore through which gases can move in both directions. When stomata open, K^+ content in the guard cells increase as a result of an exchange of this ion for hydrogen ions; when stomata close, there is a reduction in the

concentration of potassium and a concomitant increase in the concentration of ions hydrogen, again by exchange [54].

Stomatal opening is also triggered by a reduction in the concentration of carbon dioxide in the intercellular spaces, caused by the assimilatory activity of the mesophyll cells. Since stomata can open at night by CO_2 depletion [30, 54], this is reported to be independent of the photosynthetic activity of the chloroplasts in the guard cells [30, 54]. Appreciable reductions in leaf water potentials were found to occur in many species before stomata closure begun [5, 6, 35, 54]. These observations led to the idea that leaf water potential has to be lowered to critical or threshold values before closure is initiated [5, 30]. Threshold values of many hebaceous plants are reported to be in the range of -12 to -16 bars, but can reach lower limits, depending on the previous history of stress, as well as the occurrence of osmotic adjustment [29, 30, 68].

The mechanism described above considers that stomata respond to changes in leaf water potential, and ultimately to changes in the turgor balance between guard cells and subsidiary cells. This leads to the concept of a "feed-back" model of stomatal response to water stress [5, 30, 43, 54]. Stomatal closure reduces water loss and allows the plant to recover its original water potential, which may cause a series of partial closures and openings during the day [44].

However, stomatal closure in response to a threshold value of water potential has been noticed only when leaves suffer an abrupt change in their water supply, such as those caused by leaf excission and other artificial methods [58].

Another model of stomatal reaction to water stress is the "feed-forward" model proposed by Cowan [14]. The model assumes that stomatal movements are controlled by differences in humidity between leaves and air, or more specifically, the differences between the vapor pressures of the leaf and the external air. The larger the vapor pressure deficit (VPD), the higher the stomatal resistance to vapor diffusion [14], with a subsequent increase in the water content of the leaf.

The "feed-forward" model admits a direct response to the evaporative condition of the atmosphere and implies that water can be lost by peristomatal transpiration, not under stomatal control, and at a sufficient rate to affect the turgor of the stomatal apparatus [14, 35]. The model is supported by data showing changes in stomatal aperture in response to differences in the air relative humidity [6, 15, 21, 25, 51, 62], despite some discrepancies in the nature of the results. According to O'Leary [51], these discrepancies are caused mainly because a nonstandardization of the parameters used to define the results and treatments, such as the use of relative humidity as an indicator of the atmospheric moisture content, instead of vapor pressure deficits.

1.1.3 Photosynthesis and Transpiration

Decreases in photosynthetic rates caused by water stress are primarily due to a reduction in stomatal aperture [4, 5, 30, 59], which leads to a reduced entry of CO_2 and lowered carboxylation [3]. However, there is some evidence that water stress affects the chloroplast's ability to photosynthesize [3, 30]. It is important to point

out, however, that enzymatic reactions of photosynthesis can be limited by water stress [3].

Reduction in the total plant's photosynthesis is also expected when water stress occurs, as a result of the effects of stress on foliage growth [5], and senescence [30, 34]. This eventually causes a reduction in the plant's photosynthetic surface. Moreover, if water stress reduces growth and translocation of solutes, an imbalance of the sink:source relations must occur due to the dependence of the sink organs in relation to the source and vice versa.

Transpiration is reduced by water stress mainly because of stomatal closure, which causes an increase in the resistance to water loss [5, 16, 30, 58, 59]. Decreases in transpiration cause secondary effects such as a rise in leaf temperature, which can be dangerous for the integrity of the photosynthetic apparatus [20, 27].

The combination of the effects of water stress on photosynthesis and transpiration determines changes in water use efficiency (WUE). The optimization hypothesis proposed by Cowan and Farquhar [15] assumes that stomatal responses to atmospheric humidity and plant water stress may maximize daily water use efficiency [57].

Summarizing, photosynthesis and transpiration are both affected by water stress in a relatively associated way, since the stomatal aperture serves as an entry valve for CO_2 and a release valve for water vapor [3, 5, 6, 14, 15, 30, 54, 59]. The nature of the responses, however, are not the same due to differential effects of environmental factors when the plant is under stress [6, 57], and also to differences existing between the properties of the two gases [50]. As a result of

these differences, water use efficiency is generally increased with the development of a situation of water stress [25, 57].

1.2 Water Stress in Cassava

Cassava can grow and produce under conditions of low water availability [1, 7, 10, 11, 12, 13, 37, 65, 52]. However, studies involving the use of adequate techniques and measurement of parameters which can describe the real water status of the plant were initiated only in 1979, with the work done by Connor and coworkers [11, 12, 13]. In those studies, a 70-day period of water strss imposed on two cassava cultivars 12 weeks after planting substantially reduced biomass production. However, after a recuperation period of 125 days, storage root yields of the most vigorous cultivar (MMex 59) were higher in the stressed plants when compared with the non-stressed controls. In the other cultivar, the low-vigor MCol 22, reductions in storage root yields continued even after the recuperation phase [11]. This difference in the behavior of the two cultivars is explained by differences in leaf area indexes; water stress reduced an excessive LAI in MMex 59, which caused an increase in the sink strength of the storage roots.

Oliveira, Macedo and Porto [52] noticed that water-stress induced reductions in cassava root yields varies considerably with the stage of plant growth. Decreases in storage root yields up to 80% were observed when 60-day periods of stress were imposed from the second to the fifth month of the plant's growth cycle. Water stress periods after five months of age reduced yields in approximately 20%.

Water stress during the growth cycle of cassava appears to reduce yields by reducing leaf formation and expansion but not leaf shedding, as normally occurs when plants are under water stress [11]. This suggests that the plant reduces water loss by transpiration, in an economical way, by reducing growth and not by dropping leaves that have to be formed later, consuming extra energy from the plant. Partially conflicting results were found by Lal [37]. Under controlled conditions, significant reductions in leaf number per plant were observed when stress was imposed on two cassava cultivars. In the same experiment both root and shoot weights were reduced by water shortage.

Unexpectedly, stressed cassava plants were found to show only slight variation in leaf water potentials [13, 23]. This leads Connor and Palta [13] to conclude that leaf water potential cannot be used as an index of water stress in cassava.

Changes in leaf diffusion resistance are, on the other hand, reported to be more drastic in cassava as a result of water stress [13]. Although the estimated values of leaf conductances in cassava suggest that the plant has the potential for high rates (10 mm sec^{-1}), the values measured in field-grown stressed plants reached a maximum of 5 mm sec^{-1}, suggesting the existence of a stomatal- controlled mechanism for avoiding excessive water loss [13].

The same study showed that varietal differences exist, and that afternoon conductances are lower than those measured in the morning. Stomatal patterns of distribution and size were also altered by water stress: leaves of stressed plants had more dense but smaller stomata [13].

Results obtained by El-Sharkawy and Cock [20] show that net photosynthesis and transpiration in cassava are reduced by high leaf-air vapor pressure deficits (above 20 mb) in either stressed and non-stressed plants of two cultivars. In other studies [21], varietal differences were found in relation to the effect of high VPDs on photosynthesis and transpiration, and eventually in water use efficiency of eight cassava clones.

In order to compare the stomatal sensitivity of cassava and other 7 warm-climate species to air humidity, El-Sharkawy, Cock, and Held [23] measured CO_2 and H_2O exchange over a wide range of VPD's Leaf diffusive conductance in al species was decreased by high VPD, with the higher sensitivity being noticed in cassava, associated with reductions in transpiration, but stable leaf water potential. Calculated values of water use efficiency show a higher increase in this parameter in the cassava plants, when compared with the other C_3 species studied in the experiment (beans, rice, eucalyptus, and siratro). Water use efficiency of the C_4 species studied (sorghum, amaranth weed, and andropogum pasture grass) were higher, mainly due to their higher photosynthetic rates than to a lower transpiration [23].

The above data suggest that stomatal control of water loss is very efficient in cassava, due to changes in the anatomical characteristics of the stomatal apparatus [13] and also to a higher sensitivity of cassava stomata to air humidity, and, ultimately, to the vapor pressure difference between the leaf and the bulk air [20, 21, 23]. Connor and Palta [13] also suggested that cassava can control water loss by following the "feed-forward" mechanism proposed by Cowan and

Farkuhar [15], since the results show the presence of correlations between leaf diffusive conductance and leaf-air vapor pressure deficits.

Therefore, based upon the literature cited, cassava is affected by water stress, with the effects on yield being dependent on varietal characteristics [12, 37], and the period of the growth cycle in which the stress treatment is imposed [52]. Under stress, the plant reduces overall growth rates by decreasing the rates of leaf expansion, the rates of leaf formation, and increasing leaf senescence [38].

Changes in leaf potentials caused by water stress in cassava are reported to be minimal [12], and sensitivity of the stomatal apparatus in reducing the effects of stress is also high, with significant effects on photosynthesis, transpiration, and the calculated water use efficiency [13, 20, 21, 22, 23]. It is important to notice that even under severe stress conditions, cassava plants can still maintain growth and, at least in one case, after a short period of recuperation following water stress, storage root yields were benefitted by stress as a result of a change in the patterns of dry matter partitioning and sink: source relations [12].

CHAPTER 2

MATERIALS AND METHODS

The study was conducted between May 18, 1981 and November 23, 1983. Three experimental sites were used to evaluate effects of water stress on growth and physiological parameters of cassava. The trials were conducted in Tucson, Arizona and in the International Center for Tropical Agriculture (CIAT), experimental stations of Palmira and Santander de Quilichao, Colombia.

2.1 Experiment I: Tucson, Arizona

The experiment was planted on May 18, 1981 at the University of Arizona Campbell Avenue Farm. Climatological data are presented in Tables A.1 and A.2, Appendix A. Soil characteristics are presented in Table A.3.

Four cassava cultivars, 'MVen 218,' 'CMC 40,' 'MCol 22,' and 'MIta 1158' were planted in a split-plot experimental design in three treatment blocks [43]. Two levels of water availability were assigned to the main plots: (1) plants stressed for 80 days after two months of growth, and (2) control, with biweekly irrigations during the experimental period. The four cultivars were assigned to the subplots. Before the differential treatments of water availability started, the whole experimental area was irrigated weekly.

Measurements started on July 23, 1981, or one week after irrigation was suspended from the "stressed" plots. Eighteen plants of each cultivar were used per treatment, and measurements were taken only in the four central plants of each subplot in order to minimize possible errors due to interplot competition. Data on plant height, leaf formation, expansion and duration were obtained weekly. The same schedule was used for measuring leaf water and osmotic potentials, but depending on the occurrence of rainfall, these parameters were measured twice a week.

Soil water was monitored with a Neutron Moisture Meter (Campbell Pacific Nuclear, Corvalis, California) at 30, 60, 90 and 120 cm depths. Soil moisture determinations were made two days before and after irrigation until June 23; after that date, measurements were taken weekly.

2.1.1 Growth Parameters

Plant height was measured from the newest formed leaf on the tallest branch to the soil. Growth of the central leaf lobe was measured with a small ruler graduated in mm increments. The size of the central leaf lobe of the smallest leaf in each plant was determined weekly until the third week from the day it appeared. Data on leaf formation were obtained by tagging the newest leaf each week, and counting the number of leaves above the tagged one the next week.

2.1.2 Leaf Water and Osmotic Potentials

Values of leaf water (ψ_L) and osmotic (ψ_π) potentials were obtained by using thermocouple psychrometers (JRD Merril Specialty Equipment, Logan, Utah). Two leaf discs approximately 5 mm in diameter were sampled between 11:00 AM and 1:00 PM from the basal region of the fifth to the tenth leaf counting from the apex of the plant. The discs were placed in psychrometric chambers immediately after collection, stored in an insulated box and later transferred to the laboratory. After an equilibrium period of approximately two hours at room temperature, leaf water potentials were determined with a Wescor Model MJ-55 microvoltmeter (Wescor Inc., Logan, Utah). The psychrometers were then immersed in liquid nitrogen for 15 seconds, allowed to warm, and measured for ψ_π after 1 hour equilibrating.

2.1.3 Weights

Fresh and dry weights of storage roots, stems, leaves, and the originally planted stakes (stem cuttings) were obtained from plants harvested on November 23, 1981. Data on leaf weight include the weights of the leaf blade and petiole, taken together. Plants were dried for 72 hours at 75 C, and after that, dry weights of each organ were obtained.

2.2 Experiment II: Water Relations and Adaptation Mechanisms to Water Stress in Cassava. Santander de Quilichao, 1982/83

Meteorological data, geographical coordinates and soil characteristics of the experimental site are described in Tables A.4, A.5 and A.6.

The experimental design was a two-way factorial with three replications [43]. There were two treatments of water availability:

1. Plants stressed for 100 days, starting 3 months after planting.
2. Plants stressed for 100 days, starting 6 months after planting.

The water treatments were imposed on plants of two different ages:

1. Plants stressed 3 months after planting.
2. Plants stressed 6 months after planting.

The size of the main plot was 75 m^2 (15.0 m x 5.0 m). The dimensions of each subplot were 7.5 m x 5.0 m (37.5 m^2). Large borders were used in order to prevent experimental errors caused by wind and temperature changes in the plants located inside the experimental area.

2.2.1 Construction of Lysimeter

The experiment was installed on a large lysimeter (30 m x 30 m x 2.5 m) surrounded by the borders. The total experimental area, including borders, measured 1786 m^2 (Fig. A.1). The bottom of the lysimeter was filled first with an asphalt layer, followed by layers of gravel, sand, and finally the soil. The soil layers approximated the original profile. A brick wall was built around the lysimeter, which

also divided it in half (15 m x 15 m x 2.5 m); the dividing wall was also revested with plastic. In each side drainage tables were installed below the gravel layer to allow for good drainage. The tubes discharged into a 2 m x 2 m x 1 m reservoir, permitting the measurement of water coming from each side of the lysimeter.

2.2.2 Planting Methods

Planting dates were June 14 and September 14, 1982. The planting system followed was the one normally recommended by CIAT. Twenty-centimeter-long stakes treated with a fungicide-insecticide solution were planted on beds approximately 20 cm high. The stakes were planted in the vertical position with 1.0 m between rows and 0.8 m within the row; this gives a plant population of 12,500 plants per hectare. The soil was maintained free of weeds during the whole experimental period. Chemicals were used to control diseases and pests. Soil fertility was corrected by applying a 100-200-100 kg/ha of NPK prior to the planting.

On December 14, 1982 water was excluded from the "dry" side of the lysimeter, and the whole experimental area was covered with black plastic. The plastic was extended on the soil, and depending on the soil water content the "wet" side was irrigated by furrow irrigation. Irrigations were scheduled by gravimetric determinations of soil moisture at 20 cm, 50 cm, and 80 cm depths in the soil profile.

2.2.3 Soil Water Potential

Measurements of soil water potential were performed using soil psychrometers (Wescor Inc., Logan, Utah) buried 20 cm, 50 cm and 80 cm in the soil in each experimental treatment. A dew-point microvolt-

meter model HR-33T (Wescor Inc., Logan, Utah) was used for field measurements, which followed the irrigation schedule of the non-stressed plants.

2.2.4 Soil Water Content

Soil moisture was controlled by weighing wet and dry soil samples obtained from 20 cm, 50 cm and 80 cm in the soil profile, before and after each irrigation. Soil samples were collected, placed in small double-sheet plastic bags, which were closed with adhesive tape and transferred to the Analytical Laboratory at CIAT, Palmira. Three samples were always taken per treatment/day, giving an average of one sample per each 40 m^2 of planted area in each depth.

2.2.5 Leaf Water Potential

Leaf water potential measurements were performed by using the Pressure Chamber Technique [56], with equipment manufactured by PMS Instrument Co., Corvalis, Oregon. Detached leaf lobes of leaves number 5 to 10 counting from the apex of the plant were used to determine water potentials. Measurements proceeded at 10-day intervals, starting at day zero of differential treatment. Data were obtained at 6:00 AM, 9:00 AM, 12 Noon, 3:00 PM, and 6:00 PM on eleven occasions during the experimental period. In order to avoid significant losses of water from the detached leaves, the time between detachment of the leaf from the plant and the measurement in the pressure chamber did not exceed three minutes. Data were obtained from 12 plants per each sampling date and treatment, using a single leaf per plant. Leaf water potential is expressed in bars.

2.2.6 Leaf Diffusive Resistance

Measurements of leaf diffusive resistances were taken concurrently from the abaxial surface of the same leaves used for determination of leaf water potentials. Resistances were measured by a Precision Automatic Porometer (Delta-T Instruments, Burrel, England). The porometer also provided data on leaf temperature. Values of leaf diffusive resistance are expressed in sec cm^{-1}, and values of leaf temperature are expressed in degrees Celsius. Leaf diffusive conductances were calculated from diffusive resistance.

2.2.7 Photosynthesis

Depending on the light conditions at the experimental site, photosynthesis in the field was measured three to four times a day between 9:00 AM and 3:00 PM. Measurements were obtained three times during the experimental period for those plants stressed after six months of age, and six times for plants stressed three months after planting. The reason for a small number of measurements in the older plants was a lack of adequate plant material which prevented precise measurements. The method used for determining photosynthesis in the field is a modification of the technique described by Clegg et al. [8]. The materials used in the measurement consisted of a 0.75 liter plexiglas chamber, 10 cm^3 plastic syringes, a Multichannel Infrared CO_2 Analyzer Series 225 (Analytical Development Company Ltd., Hoddesdon, England), and a pen recorder (Cole Parmer Instrument Co., Chicago, Illinois). The method can be described in four steps:

1. The central leaf lobe of an attached, young but well developed leaf is introduced in the plexiglas chamber, in which two identical syringes are inserted through rubber taps. An internal fan is always functioning, in order to recirculate the air inside the chamber.
2. Immediately after closing the chamber, an air sample is obtained by pulling out the first syringes, and 30 seconds later another sample is obtained using the second syringe. After sampling, the syringes are placed on individual black rubber bungs in a perforated wood tray for transport.
3. After obtaining a series of samples from different plants, the syringes are transported to the laboratory. Carbon dioxide concentrations of the samples are measured by injecting the air in the CO_2 analyzer flow system, one at a time, and observing the two peaks on the recorder paper. External air was used as reference air in the present experiment, instead of nitrogen used in the absolute measurements described by Clegg et al. [8]. In order to avoid changes in the CO_2 concentration of the reference flow, external air was stored in a large rubber container before each set of measurements. CO_2 concentration of the reference air was monitored by a small infrared gas analyzer (Hitachi Co., Tokyo, Japan).
4. By knowing the graphical difference between the two peaks and the area of the leaf section, net photosynthesis is calculated using the formula:

$$Pn = \frac{D(c \times 0.118 \times 0.76 \times 2)}{A}$$

where

Pn = Net photosynthesis, mg CO_2 dm^{-2} hr^{-1}

c = calibration coefficient

D = difference, in spaces, of the successive injections, in the recorder paper

0.118 = correction factor, derived from Fick's law

2 = time constant

A = leaf area

The calibration coefficient "c" is obtained by plotting the number of spaces on the graph paper between the reference air and sample with known concentrations of CO_2 (410, 330, 290 and 210 ppm). The coefficient is the slope of the resulting straight line. This value changes for each set of measurements, and a new regression line must be calculated for each day of measurement. Leaf area was measured with a photoelectric leaf area meter model AAG-405 (Hayashi Denko, Tokyo, Japan).

2.2.8 Air Temperature and Relative Humidity

Data on atmospheric relative humidity was considered to be important for the analysis of the data, and were measured on days and times of data collection. Relative humidities were also measured in five-hour intervals of each day of measurements, inside and outside the experimental area, with a Psychrometric Chart model Psychro-Dyne (Cole Parmer Instrument Company, Chicago, Ill.). As the instrument shows the

wet and dry bulb temperatures for calculation of relative humidity, the data on air temperature was recorded directly from the dry bulb readings.

2.2.9 Growth and Yield

Plant growth was measured in several ways. At each 10-day interval, growth was measured in the eight central plants of each sub-plot by recording plant height, lengths of central leaf lobes, number of lobes with and without leaves, number of branches per plant, and total number of apices per plant. Measurements were performed on the same plants and leaves during all experimental periods.

Height of individual plants and lengths of central leaf lobes were measured as described in Experiment I. Starting on the first day of water exclusion from the "stressed" plants, the same leaf lobe was measured in order to evaluate the growth rates of leaves formed at each 10-day interval during the stress period. The number of nodes with and without leaves were also counted at the end of each interval, in each individual plant, as well as the number of branches per plant. Those data were used to calculate the total leaf area per plant, the rates of leaf fall and leaf formation per interval of time (after transforming in $\sqrt{x}$).

Biomass production, in terms of fresh and dry weights, was obtained by sampling on five occasions. The first harvest, which included eight plants of the adjacent borders of each plot, was done at the beginning of the water treatment.

At the final harvest, the eight central plants used for data collection were harvested 100 days after the initiation of the stress period. For the other three harvests, four plants located inside the lysimeter area were used. These intermediate samplings were 20, 40 and 70 days after the first one. Fresh and dry weights of storage roots, stems, leaves and the planted stake were recorded. Fallen leaves were also collected in order to obtain an estimate of the total amount of dry matter produced between two successive samplings.

2.2.10 Leaf Area

Leaf areas were estimated at each sampling date by collecting twenty leaves per subplot and measuring their total area with a photoelectric leaf area meter, model AAG-405 (Hayashi Denko, Tokyo, Japan). The leaf area indexes at each sampling were calculated by using the relationship between dry weight and total leaf area of the samples.

2.3 Experiment III: Influence of Relative Humidity on Photosynthesis and Yield of Cassava. CIAT, Palmira, 1982

This field experiment was conducted from May 7, 1982 to September 23, 1982, at CIAT headquarters. Meteorological data and coordinates are given in Tables A.7 and A.8.

Two cultivars were originally planted, one originating from the Amazon Region (MCol 1684), and MCol 22, from the North Colombian coast. Six weeks after planting, the plants were subjected to two treatments of air humidity: (1) normal conditions, and (2) higher than normal relative humidity conditions, obtained by misting the air with small misters connected to a sprinkler irrigation system operating between

9:00 AM and 4:00 PM. To avoid increasing the relative humidity in the control plots, a barrier of elephant grass was planted between the control and the misted plots. Furrow irrigation was used for both treatments in order to avoid soil water stress. Data of MCol 22 are not presented due to the great nonuniformity observed between plots.

A completely randomized experimental design [43] with two treatment blocks and four replications was used for planting 20-cm-long stakes. The spacing adopted was 1.0 x 1.0 between and within rows. During the experimental period, regular applications of insecticides were used in order to control populations of mites (Tetranychus urticae, Oligonycus peruvianum) and thrips (Frankliniella sp.).

2.3.1 Growth and Yield

Plants were harvested four times during the experimental period. The first harvest was at the beginning of the misting treatment, and the other three were at regular intervals of 20 days. Data on dry weights of shoots and roots were obtained after drying the samples at 75 C in an oven for at least 72 hours. The size of the harvested plot was represented by twelve plants in the first and last harvests, and by six plants in the two intermediate harvests.

2.3.2 Photosynthesis

Photosynthesis was measured in the field using the same method described in Experiment II [8]. A total of 116 photosynthesis measurements was obtained during the experimental period. Photosynthetic Active Radiation (PAR) was always higher than 1500 uE m^2 hr^{-1}, measured

with LI-COR 190 Quantum Sensors and a LI-COR Quantum Radiometer/ Photometer (Lambda Instruments Inc., Lincoln, Nebraska).

CHAPTER 3

RESULTS

3.1 Experiment I: Tucson, Arizona

3.1.1 Development of Water Stress

Soil water content in the non-stressed plots was maintained more or less constant below 60 cm during most of the experimental period (Figs. 1, 2, 3 and 4). Moisture in the most superficial layer was more variable than in the other layers in which soil moisture was measured.

Differences in the amount of water in non-irrigated and irrigated plots were first evident on August 8, 1981, or approximately four weeks after irrigation was terminated in the "stressed" plots. After that date only small changes were observed in the amount of water contained in the first layer (0-30 cm deep). The same tendency was seen in the second layer (30-60 cm) later in the experimental period (Figs. 1, 2, 3 and 4). After nine weeks of water exclusion the third soil layer (60-90 cm) was also almost depleted of available soil moisture, as shown by the horizontal patterns of the curves. After approximately 10 weeks of treatment, plants of all four cultivars depleted the deepest layer in which moisture was measured (90-120 cm). At the end of the experimental period the soil profiles of the non-irrigated plots were almost entirely depleted of available moisture (Figs. 1, 2, 3 and 4).

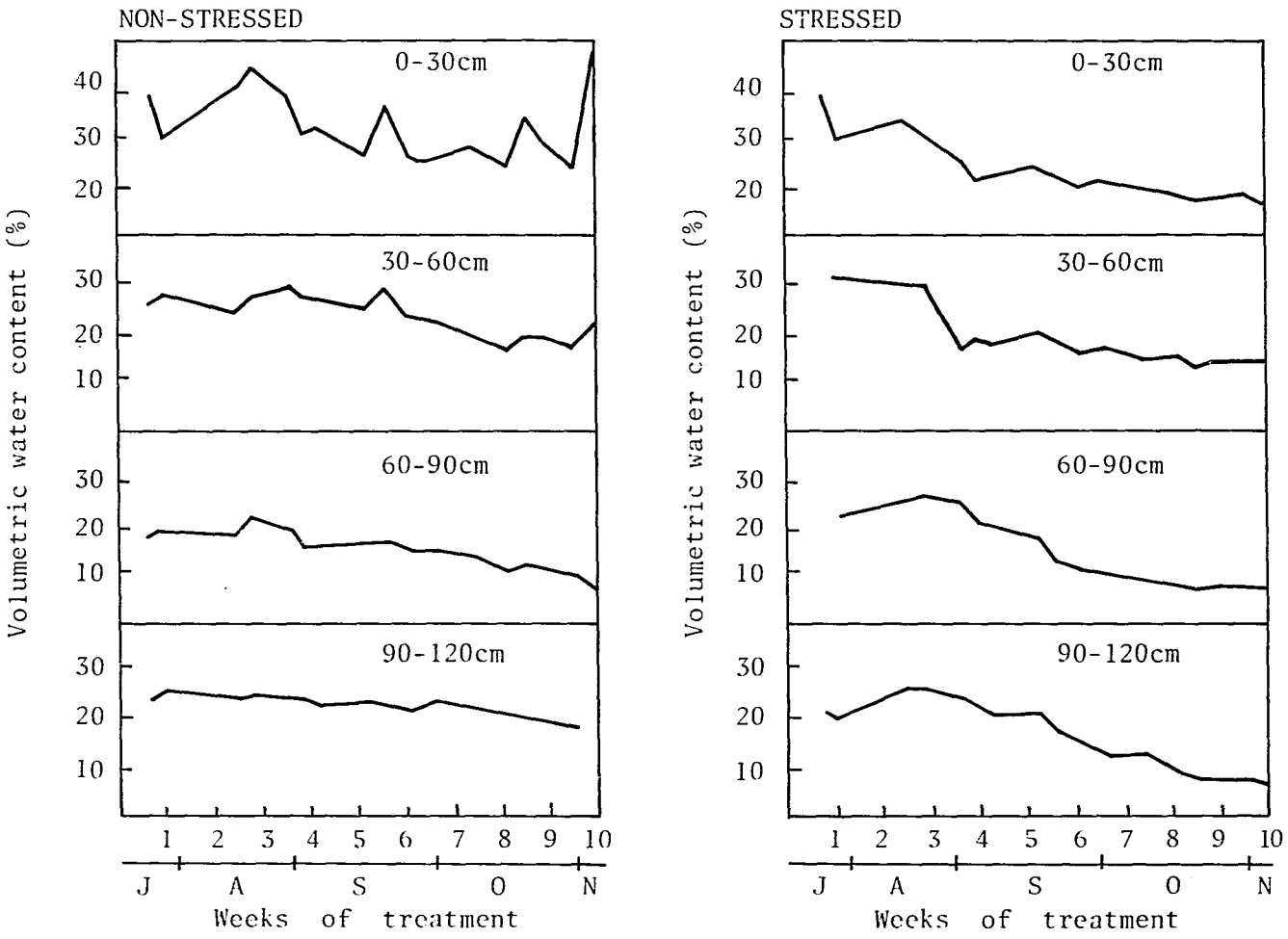

Figure 1. Volumetric soil water content of stressed and non-stressed plots of MVen 218, Tucson, 1981. -- Water stress was imposed two months after planting.

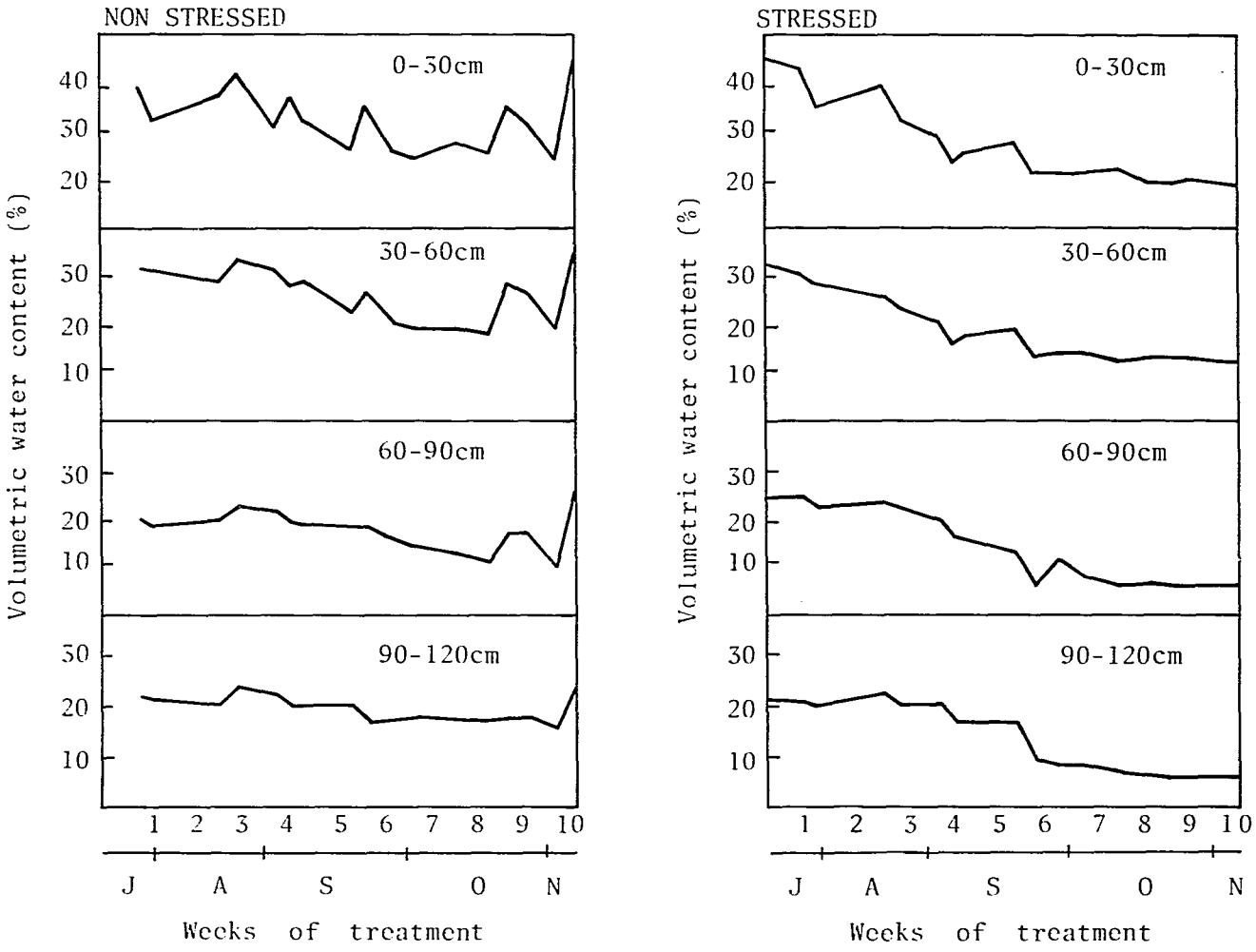

Figure 2. Volumetric water content of stressed and non-stressed plots of CMC-40, Tucson, 1981. -- Water stress was imposed two months after planting.

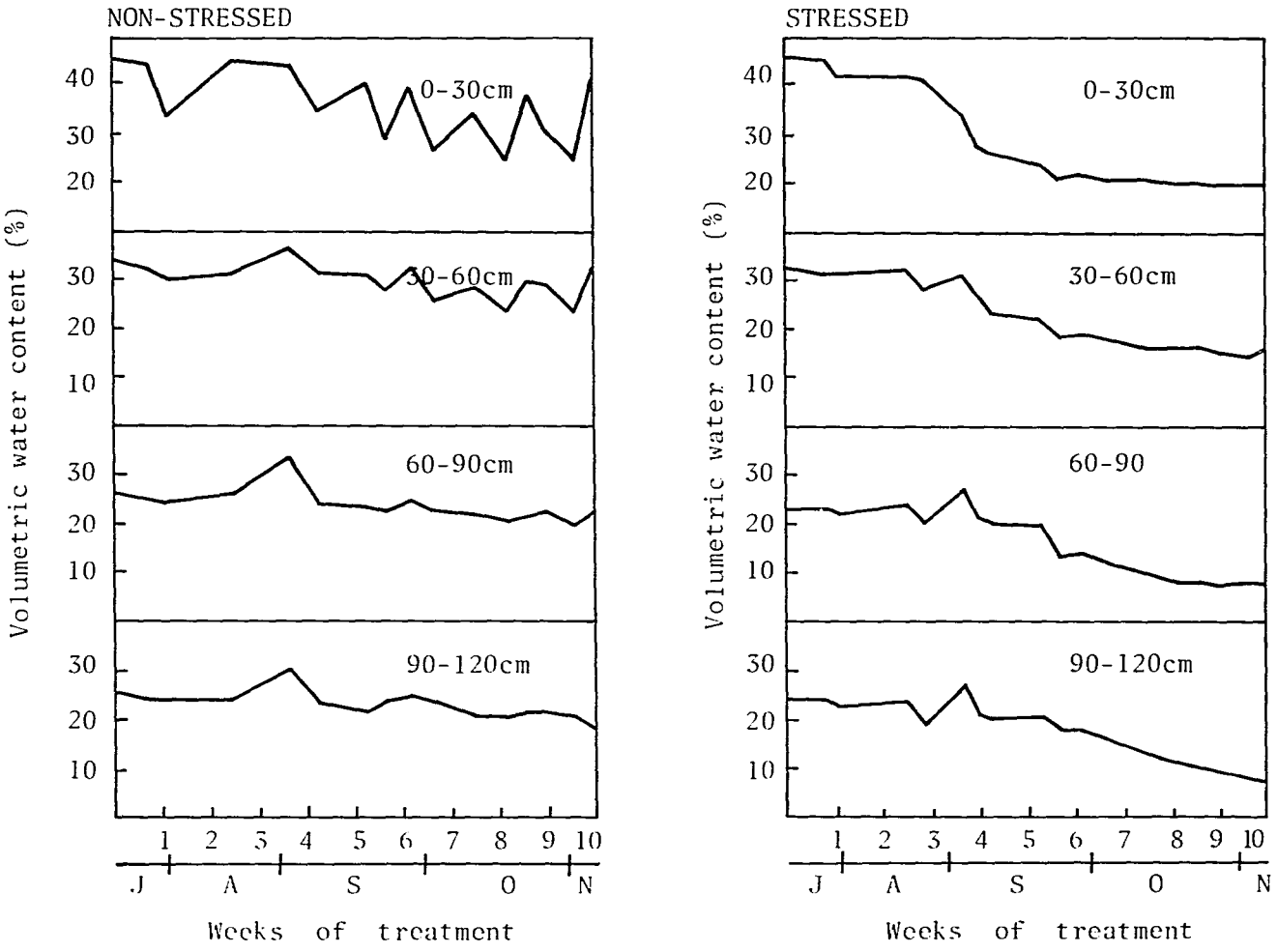

Figure 3. Volumetric soil water content of stressed and non-stressed plots of MCol 22, Tucson, 1981. -- Water stress was imposed two months after planting.

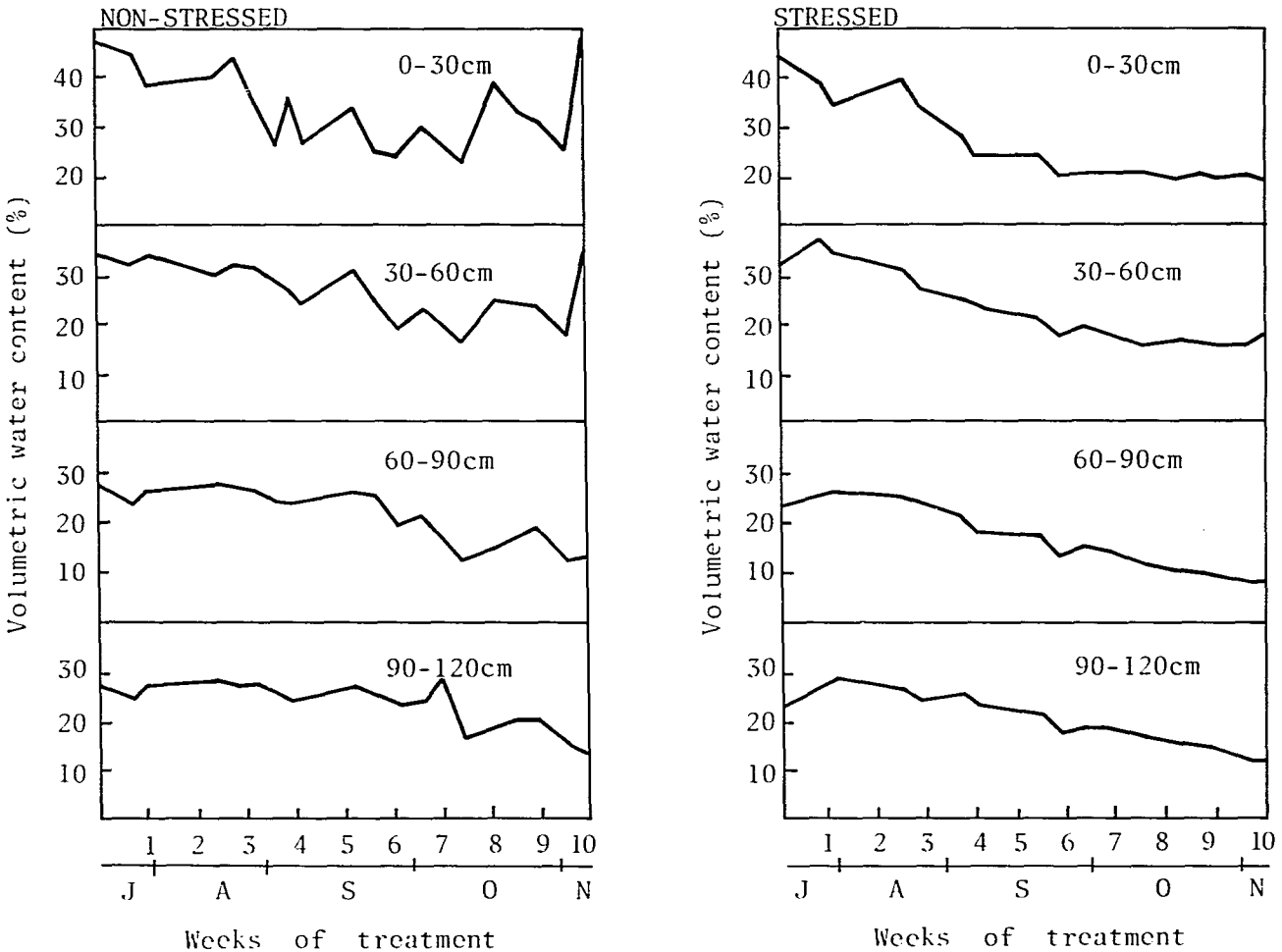

Figure 4. Volumetric soil water content of stressed and non-stressed plots of MIta 1158, Tucson, 1981. -- Water stress was imposed two months after planting.

3.1.2 Growth and Yield

Plant growth, expressed as the increase in plant height with time, was reduced by water stress in all four cultivars (Fig. 5). Although reductions in plant growth in CMC 40 were proportionally greater than in the other cultivars studied, differences among cultivars were not high (Fig. 5).

Changes were also observed in the expansion of leaf lobes formed during the period of stress (Table 1). Except for MVen 218, growth of leaves formed after 5 weeks of water stress was less than those of control. Decreases in leaf expansion of stressed plants of MVen 218 were observed later in the period (Table 1). The final lengths of lobes formed approximately five weeks after initiation of stress were also reduced (Table 2). Reductions up to 50% were observed in leaves of MCol 22 and MIta 1158 formed at nine weeks of water exclusion (Table 2). No differences in leaf size were observed between stressed and non-stressed plants of MVen 218.

Cumulative leaf production per apex was also reduced by water stress, the degree of reduction being dependent of the cultivar studied (Figs. 6 and 7). Leaf production was reduced after one week of treatment in cultivar MCol 22, whereas noticeable reductions in MVen 218, CMC 40 and MIta 1158 occurred after 6, 3 and 3 weeks of stress, respectively.

Water stress caused a significant decrease in dry matter of roots and stems produced by all cultivars (Table 3). Leaf and root dry weights were more affected by water stress in MIta 1158 on a relative

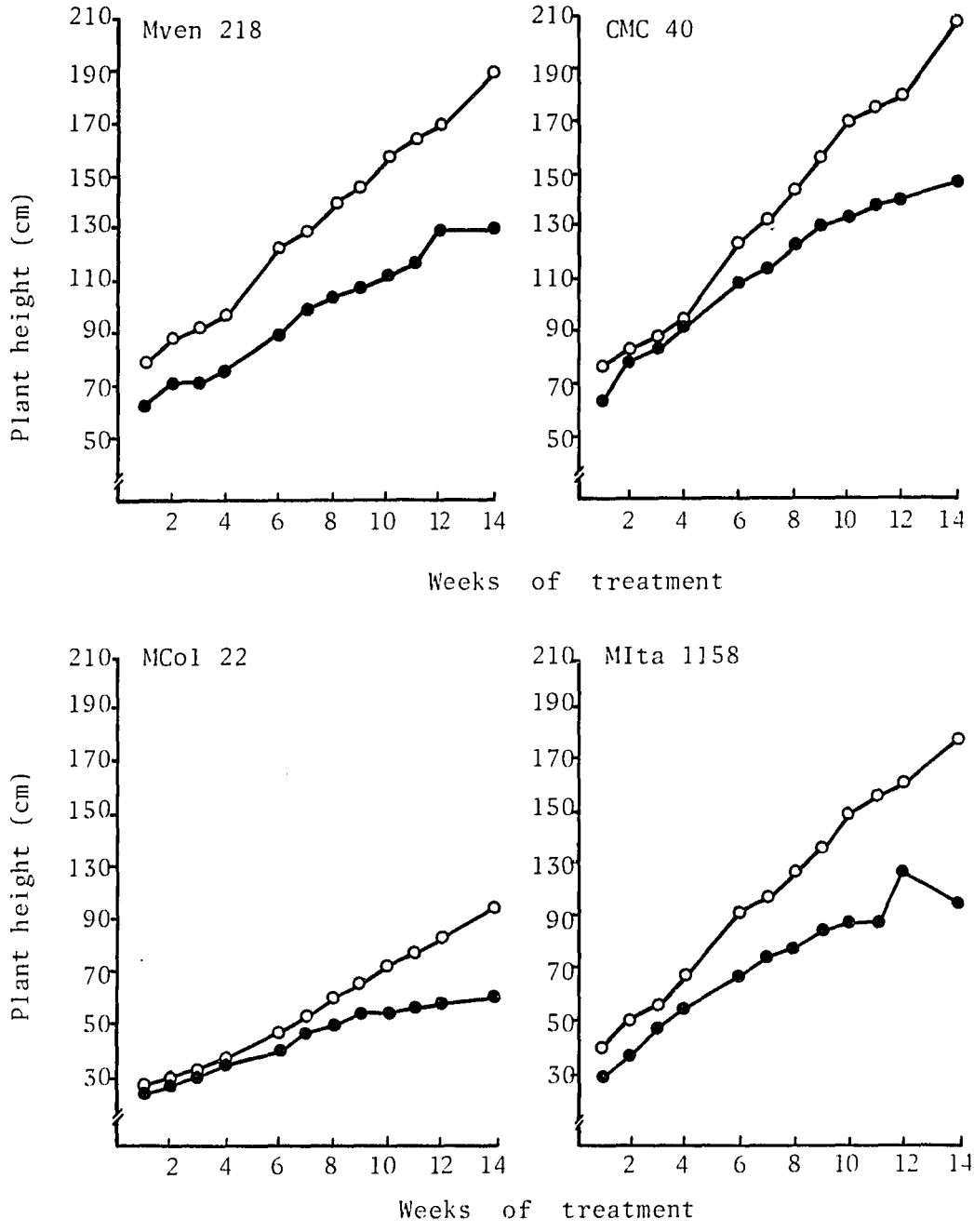

Figure 5. Growth of non-stressed and stressed plants of four cassava cultivars. -- The stressed plants were irrigated after 11 weeks of growth. Plants were watered weekly for 2 months and biweekly irrigations were continued (○) or withheld for 10 weeks (●), Tucson, 1981.

Table 1. Growth rates of central lobes formed at different stages of the growth cycle of non-stressed and stressed plants of four cassava cultivars (cm week^{-1}), Tucson, 1981.

Cultivar	Treatment	Time of Leaf Formation (weeks)					
		1**	3	5	7	9	11
MVen 218	NS*	5.2^{a}	6.1^{a}	8.4^{a}	10.0^{a}	8.2^{a}	7.2^{a}
	S	6.8^{a}	6.8^{a}	7.4^{a}	7.3^{b}	5.1^{a}	5.7^{b}
CMC 40	NS	7.4^{a}	7.8^{a}	13.1^{a}	10.3^{a}	10.9^{a}	8.9^{a}
	S	7.9^{a}	7.4^{a}	7.3^{b}	7.6^{b}	5.1^{b}	3.3^{b}
MCol 22	NS	5.3^{a}	7.7^{a}	10.4	11.1^{a}	11.5^{a}	10.0^{a}
	S	7.1^{a}	9.1^{a}	4.7^{b}	7.7^{b}	4.8^{b}	4.0^{b}
MIta 1158	NS	7.6^{a}	8.4^{a}	13.2^{a}	12.3^{a}	10.1^{a}	11.1^{a}
	S	7.9^{a}	9.0^{a}	5.5^{b}	7.5^{b}	4.6^{b}	4.1^{b}

* NS and S means non-stressed and stressed plants, respectively.

**Leaf formed after one week of treatment.

Each value is the average of four measurements/day.

Means followed by the same letter in the columns and for each cultivar do not differ statistically at the level of 5%, by the t test.

Table 2. Final lengths (cm) of central lobes of non-stressed and stressed plants of four cassava cultivars, Tucson, 1981.

Cultivar	Treatment	Time of Leaf Formation (weeks)				
		1**	3	5	7	9
MVen 218	NS*	12.7[a]	12.9[a]	13.5[a]	15.3[a]	14.1[a]
	S	12.2[a]	13.9[a]	12.2[a]	13.0[a]	10.7[a]
CMC 40	NS	15.4[a]	14.5[a]	16.8[a]	17.0[a]	17.4[a]
	S	13.8[a]	14.0[a]	12.7[b]	14.6[a]	11.9[a]
MCol 22	NS	14.6[a]	16.4[a]	17.3[a]	17.9[a]	19.1[a]
	S	16.0[a]	16.7[a]	10.4[b]	13.0[b]	9.9[b]
MIta 1158	NS	14.3[a]	15.6[a]	18.3[a]	17.9[a]	17.3[a]
	S	14.6[a]	14.4[a]	11.8[b]	11.8[b]	9.1[b]

* NS and S mean non-stressed and stressed plants, respectively.

**Leaf formed after one week of treatment.

Each value is the average of four measurements/day.

Means followed by the same letter in the columns and for each cultivar do not differ statistically at the level of 5%, by the t test.

Table 3. Dry biomass (g/plant) produced by non-stressed and stressed plants of four cassava cultivars, Tucson, 1981.

Cultivar		Leaves	Stems	Roots	Total
MVen 218	NS*	572^{a}	825^{a}	97^{a}	1494^{a}
	S	237^{b}	449^{b}	60^{b}	746^{b}
CMC 40	NS	480^{a}	919^{a}	209^{a}	1608^{a}
	S	202^{b}	409^{b}	72^{b}	683^{b}
MCol 22	NS	431^{a}	755^{a}	151^{a}	1337^{a}
	S	220^{b}	345^{b}	82^{b}	647^{b}
MIta 1158	NS	778^{a}	811^{a}	168^{a}	1757^{a}
	S	228^{b}	501^{b}	42^{b}	771^{b}

* NS and S mean non-stressed and stressed plants, respectively. Means followed by the same letter in each column do not differ statistically at the level of 5% by F test.

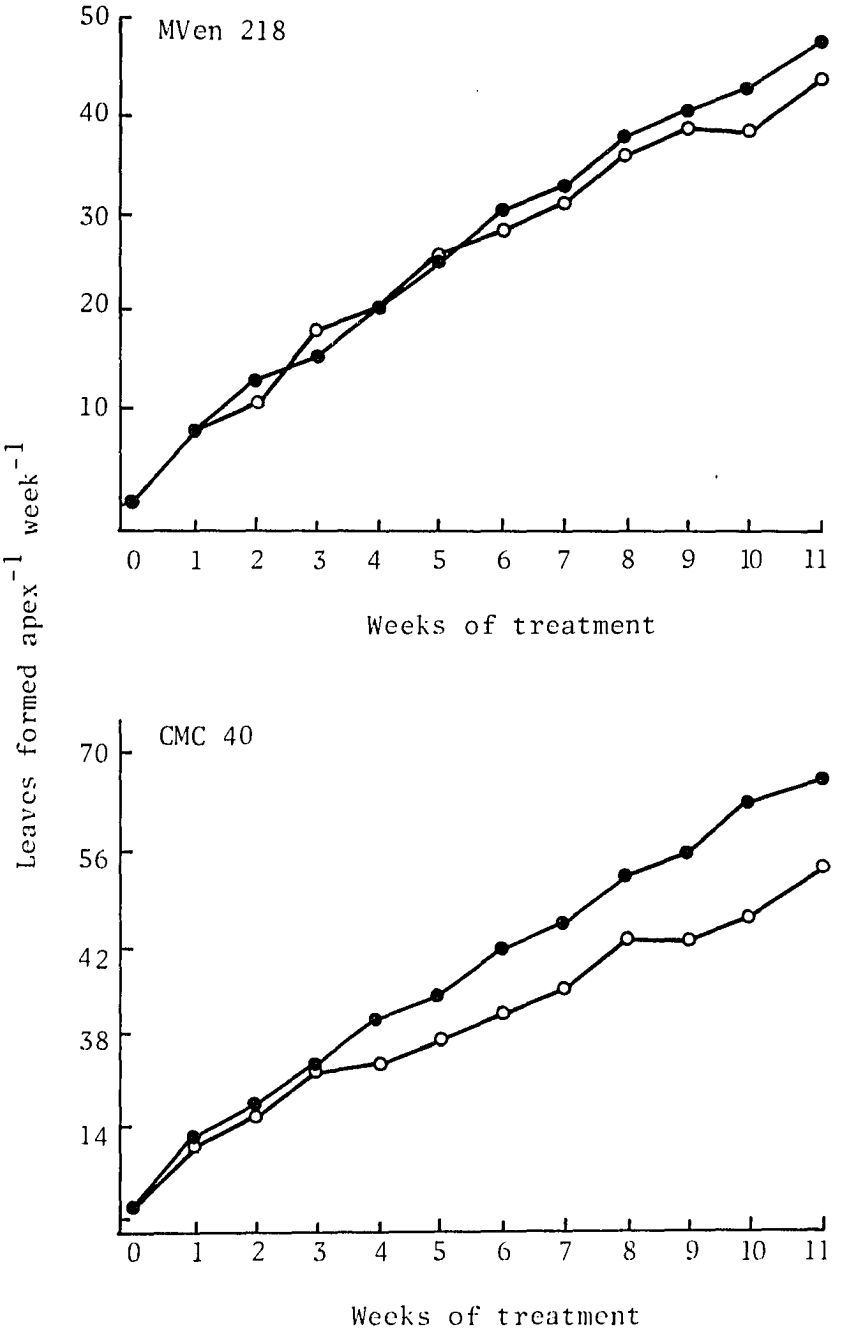

Figure 6. Cumulative patterns of leaf formation in non-stressed (●) and stressed (○) plants of MVen 218 and CMC 40, Tucson, 1981.

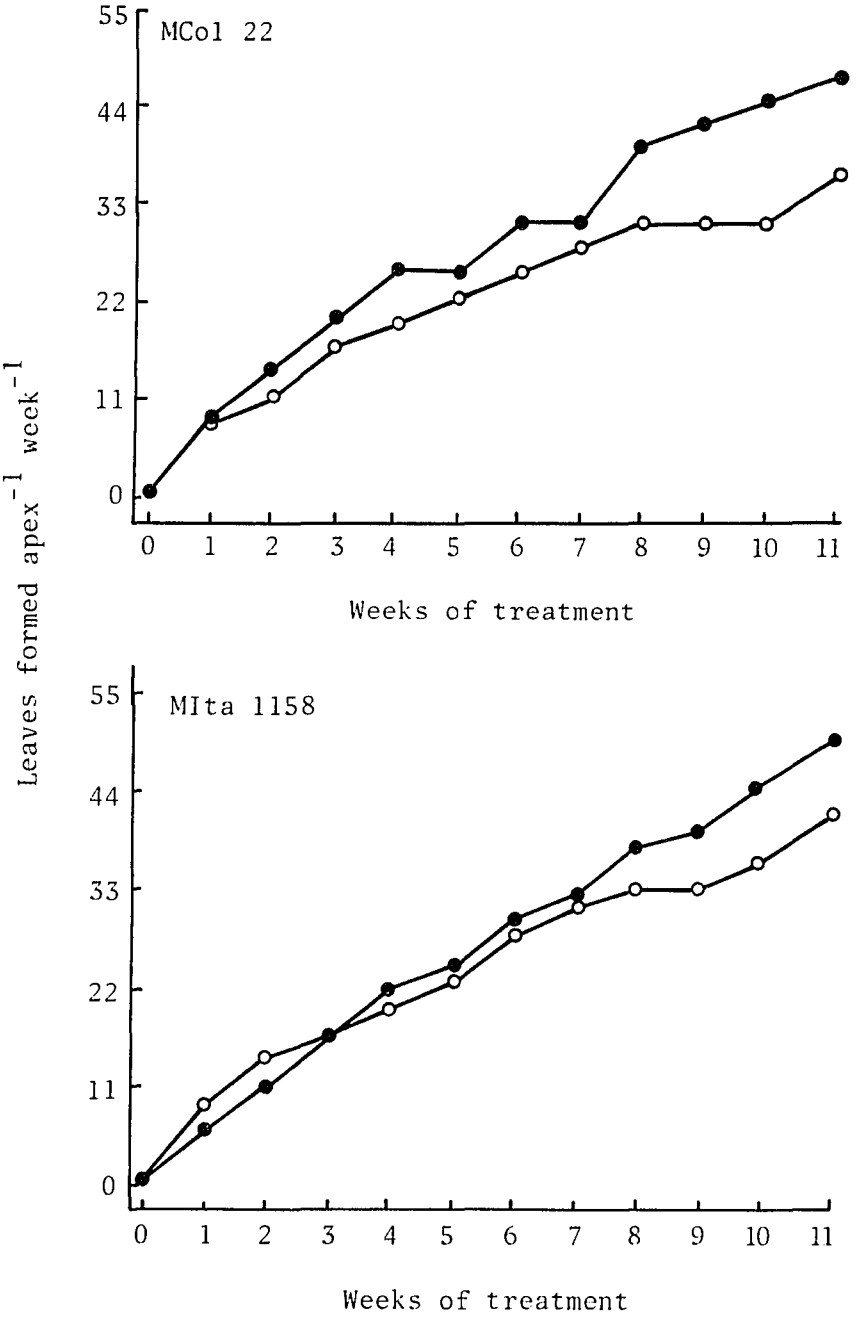

Figure 7. Cumulative patterns of leaf formation in non-stressed (●) and stressed (○) plants of MCol 22 and MIta 1158, Tucson, 1981.

Table 4. Precipitation occurring at the Campbell Avenue Farm during the experimental period, Tucson, 1981.*

Month	Day	Rain (mm)	Total Rainfall Month^{-1} (mm)
May	1	14.7	
	31	2.3	17.0
June	28	5.6	5.6
July	8	2.3	
	10	8.4	
	11	5.0	
	12	1.8	
	14	6.1	
	17	4.1	
	19	9.1	
	22	7.9	
	25	11.2	
	27	6.6	
	29	2.8	
	31	3.8	69.1
August	1	3.8	
	8	8.9	
	10	8.1	
	12	3.0	
	13	1.8	
	14	4.1	29.7
September	6	5.6	
	10	2.0	
	30	1.5	9.1
October	1	0.8	0.8
November	29	19.0	
	30	2.0	21.0
Total			152.3
(from May 18 to November 23)			116.6

* Planting date was May 18, 1981.
Harvest date was November 23, 1981.

basis, although reductions due to stress were high in all stressed plants.

3.1.3 Leaf Water Potential and Its Components

Differences in leaf water potentials at the beginning of the experimental period were attenuated by the occurrence of rainfall (Table 4).

Values of leaf water potential (ψ_L), osmotic potential (ψ_π), and calculated values of turgor pressure (P) are presented in Tables 5, 6, 7 and 8. Changes in ψ_L due to water stress were not the same for all four cultivars studied. This suggests the existence of varietal differences with respect to this parameter. MVen 218 reduced ψ_L to a lower extent under stress, when compared with the other cultivars (Fig. 8a). Cultivar MIta 1158 showed the higher variation in ψ_L due to water stress (Fig. 8d). Cultivars CMC 40 and MCol 22 showed intermediate responses in ψ_L, but almost invariably ψ_L was reduced when water stress was imposed (Figs. 8b, 8c). A general tendency of stressed plants in reducing the differences in leaf water potential in relation to the non-stressed plants was observed with the progress of the stress period until the seventh and eighth weeks of treatment (Fig. 8). This is also true for non-stressed plants and suggests a possible increase in stomatal resistance caused by the stress history and the most unfavorable environmental conditions prevalent after that time (Tables 4 and A.2).

The lack of a sequential, well defined pattern of leaf water potentials with time is certainly dependent on the environmental

Table 5. Leaf water potentials (ψ_L), osmotic potentials (ψ_π) and turgor pressures (P) of non-stressed and stressed plans of MVen 218 during the experimental period, Tucson, 1981.*

Weeks of Treatment	Non-Stressed			Stressed		
	ψ_L ± sd	ψ_π ± sd	P	ψ_L ± sd	ψ_π ± sd	P
2	10.3±1.5	20.0±2.3	9.7	10.0±1.9	16.7	6.7
3	11.6±1.7	18.0±1.8	6.4	11.6±1.4	19.8	8.2
4	11.3±0.5	19.8±1.8	8.5	16.0±2.4	19.8	3.8
5	11.0±1.6	16.8±1.3	5.8	8.5±1.7	14.1	8.5
6	16.5±1.8	16.2±1.4	-0.3	16.5±0.8	22.0	5.5
7	14.7±0.9	20.9±2.1	6.2	14.0±0.8	18.9	4.9
8	16.0±1.2	19.8±2.5	3.8	15.7±0.9	16.8	1.0
9	12.0±1.2	18.9±1.7	6.9	13.2±0.5	17.8	4.6
10	12.1±1.2	18.9±1.7	6.9	13.2±0.5	17.8	4.6

* Each value is the average of four measurements.

Table 6. Leaf water potentials (ψ_L), osmotic potentials (ψ_π) and turgor pressurs (P) of non-stressed and stressed plants of CMC 40 during the experimental period, Tucson, 1981.

Weeks of Treatment	Non-Stressed			Stressed		
	ψ_L ± sd	ψ_π ± sd	P	ψ_L ± sd	ψ_π ± sd	P
2	7.0±1.3	22.1±2.5	15.1	10.2±1.7	24.4±1.8	14.2
3	9.0±0.8	19.0±1.6	10.4	12.0±1.9	25.3±2.4	13.3
4	10.2±1.5	21.0±1.8	10.8	18.4±1.2	14.6±1.8	-0.8
5	11.4±0.7	16.8±1.3	5.4	13.0±1.7	17.6±2.7	4.6
6	15.0±1.2	24.5±2.1	12.5	13.3±1.8	22.0±1.6	8.7
7	13.0±1.0	20.9±2.4	7.9	16.5±0.9	19.0±2.1	2.5
8	13.0±0.7	18.0±2.5	5.0	15.0±1.5	20.0±2.4	5.0
9	12.0±1.0	14.6±1.7	5.6	14.3±1.5	18.0±1.7	4.3
10	13.0±1.4	19.8±2.6	6.8	10.4±1.8	20.7±1.9	10.3

* Each value is the average of four measurements.

Table 7. Leaf water potentials (ψ_L), osmotic potentials (ψ_π), and turgor pressures (P) of non-stressed and stressed plants of MCol 22 during the experimental period, Tucson, 1981.*

Weeks of Treatment	Non-Stressed			Stressed		
	ψ_L ± sd	ψ_π ± sd	P	ψ_L ± sd	ψ_π ± sd	P
2	12.3±2.3	15.0±2.1	2.7	13.8±1.3	14.0±2.1	0.2
3	11.3±1.4	23.0±1.8	11.6	12.5±1.0	24.0±2.2	11.5
4	13.7±1.8	21.0±2.4	8.0	16.0±0.8	19.0±1.3	3.0
5	7.8±0.8	18.9±2.1	11.2	13.6±1.4	21.0±1.2	7.3
6	14.7±1.3	26.4±1.4	11.7	14.0±1.0	24.2±1.8	10.2
7	12.6±0.8	22.0±2.8	9.4	17.6±1.2	18.9±2.4	2.3
8	11.5±1.3	22.0±1.2	10.4	11.4±1.6	21.8±2.5	10.4
9	11.4±1.7	18.9±1.0	7.5	12.6±1.3	17.6±1.8	5.0
10	11.0±1.6	16.0±0.8	3.4	12.0±1.0	18.7±1.0	7.2

* Each value is the average of four measurements.

Table 8. Leaf water potentials (ψ_L), osmotic potentials (ψ_π) and turgor pressures (P) of non-stressed and stressed plants of MJta 1158 during the experimental period, Tucson, 1981.*

Weeks of Treatment	Non-Stressed			Stressed		
	ψ_L ± sd	ψ_π ± sd	P	ψ_L ± sd	ψ_π ± sd	P
2	9.0±0.5	14.1±0.8	5.1	11.8±0.7	20.0±2.7	8.2
3	8.0±0.3	24.2±1.3	16.2	14.8±1.0	14.0±1.3	-0.8
4	11.6±1.2	16.8±1.1	5.0	16.3±2.3	18.9±1.8	2.6
5	6.0±0.3	16.0±1.4	10.0	10.5±1.1	14.4±0.8	3.9
6	14.0±0.8	21.0±2.1	7.0	16.8±0.5	22.0±1.8	5.2
7	13.0±1.2	23.1±2.3	10.1	17.8±0.9	19.0±2.4	1.1
8	12.3±0.9	16.0±2.1	3.6	15.4±1.3	18.0±2.5	2.6
9	10.4±1.4	18.7±1.3	8.3	12.6±1.4	21.0±0.9	8.4
10	12.6±0.6	14.4±0.8	1.8	11.5±1.6	18.9±1.3	7.4

* Each value is the average of four measurements.

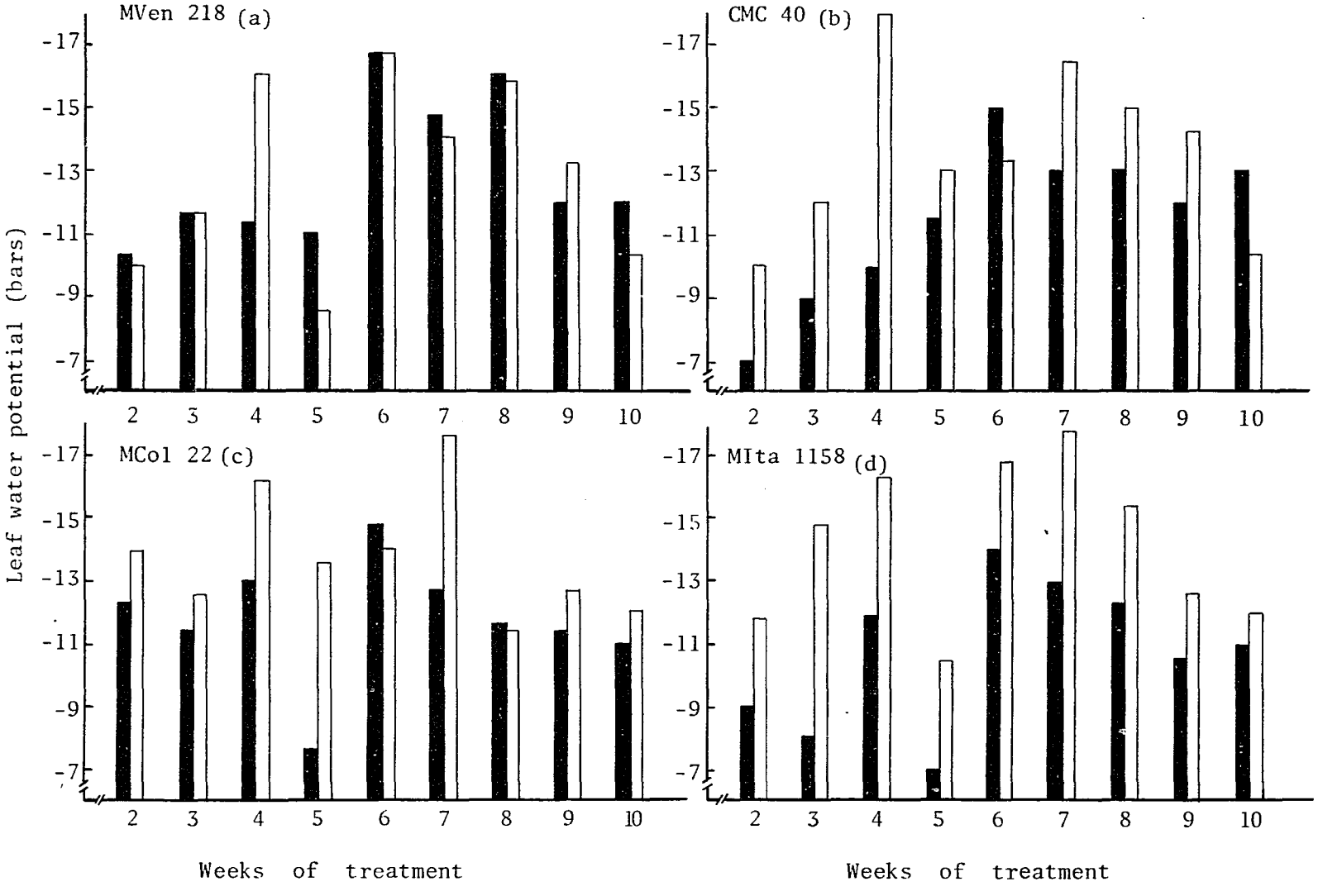

Figure 8. Patterns of leaf water potentials in non-stressed (■) and stressed (□) plants of four cassava cultivars, Tucson, 1981.

conditions pertinent to each day of measurements. For example, the amount of rainfall between the first weeks of treatment probably caused the extreme values on July 30 (4 weeks), and might be a result of a decrease in the stomatal resistance to water vapor. Daily water stresses were probably developed due to the high transpiration rates which probably exceeded the amount of water absorbed by the roots [59].

Except for MVen 218 and for measurements taken at 4 weeks of treatment, differences in leaf water potentials of non-stressed and stressed plants were maintained between 2 and 4 bars during the entire experimental period. For MIta 1158 the values of stressed plants were always lower than those measured in the respective non-stressed plants (Table 8).

Osmotic potentials of both groups of plants were also dependent on the day of measurement, and lack a well defined pattern when plotted against time (Fig. 9). Values were slightly lower in the stressed plants. However, on some occasions of those plants increased and were higher than the values measured in the non-stressed plants in the same day. Changes in osmotic potentials due to water stress were less pronounced in MVen 218 (Fig. 9a). Calculated values of turgor pressures changed during the experimental period for both non-stressed and stressed plants of all four cultivars (Tables 5, 6, 7 and 8). In practically all measurements, values of P were positive and lacked a defined tendency with the development of the stress treatment.

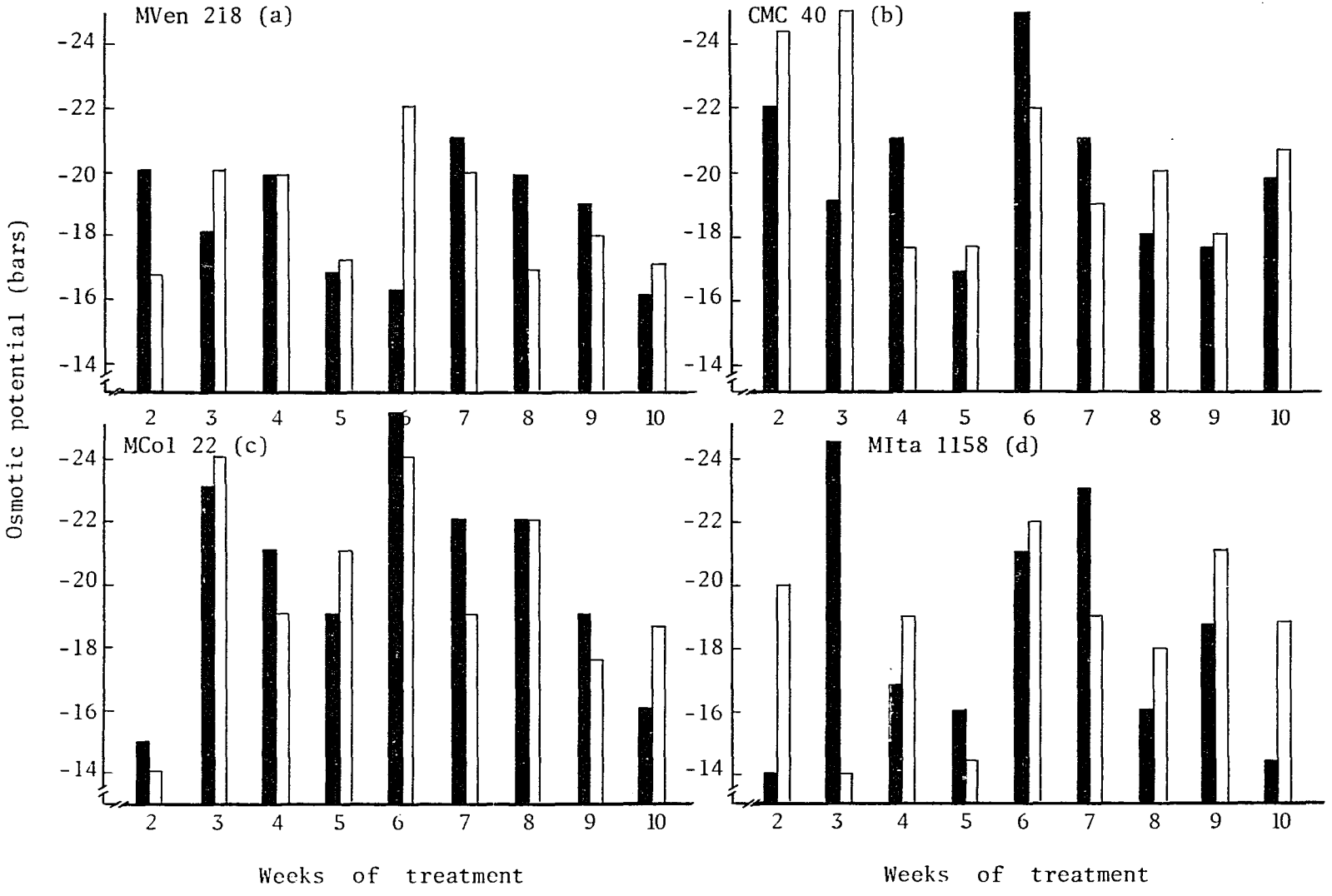

Figure 9. Patterns of osmotic potentials in non-stressed (■) and stressed (□) plants of four cassava cultivars, Tucson, 1981.

3.2 Experiment II: Santander de Quilichao, Colombia

3.2.1 Development of Water Stress

The black plastic soil cover was installed on December 16, 1981. At that time the soil had no excess water since the drainage system instaled in the bottom of the lysimeter was able to remove any accumulated water resulting from rainfall. The soil was not dry, especially in the lower layers of the profile (Fig. 10), due to a total rainfall of 66 mm which occurred from the beginning of September until the date of soil covering (Table A.5).

Changes in the soil's volumetric water content were more pronounced in the top layer of the profile for plants stressed at 3 or 6 months of age (Fig. 10). Changes in moisture contained in deeper layers were evident later in the experimental period, and are more visible in the plots occupied by the older plants (Fig. 10). The possibility exists that older plants with deeper roots were able to exploit deeper layers of the soil profile.

The drying profiles indicate that most of the water used by the plants came from the top layer of the soil (Fig. 10). Twenty days after the initiation of stress the water content in the first 0-70 cm of the stressed plots was lower than in plots of non-stressed plants of 3 months of age. Changes in the water content of non-stressed and stressed plots of 6-month-old plants were noticed later in the period and were also more evident in the top layer (Figure 10).

Changes in soil water potentials of the non-irrigated and irrigated plots reflect differences in soil water status following the

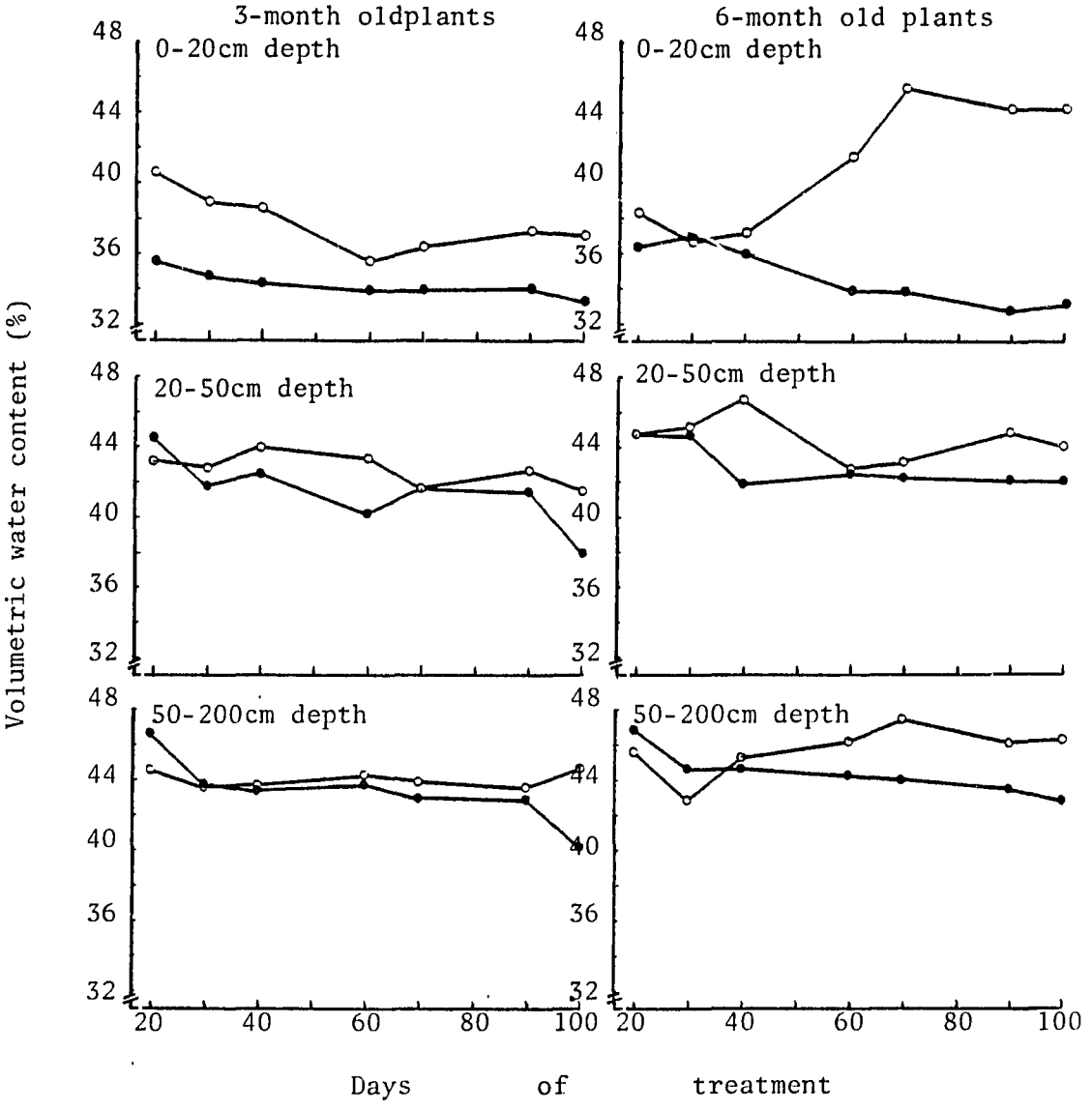

Figure 10. Volumetric soil water content of non-stressed (○) and stressed (●) plots of MCol 1684, at three depths of the soil profile, Santander de Quilichao, 1982/83.

period of water exclusion (Fig. 11). Differences above 8 bars were detected after 40 days of treatment in plots with the 3-month-old plants, and in the three layers of the soil profile. Differences of the same magnitude were noticed (7 bars) in the first layer of the soil profile in plots planted at the same time with the older plants. However, the decrease in soil water potential values measured in the plots having the 3-month-old plants was always more pronounced than in plots having 6-month-old plants (Fig. 11).

Soil water potential values reached a minimum of -9.5 bars during the experimental period, and, at least in the first layer, this value was maintained constant from the fortieth until the hundreth day of water stress (Fig. 11). In another study carried out close to the experimental area and in which black plastic was also used to exclude rainfall, the wilting point of the soil was found to be equivalent to a water potential of -15 bars [12]. The differences between -15 bars and the minimum soil water potentials measured in this experiment are certainly due to modificatons in the physical characteristics of the soil resulting from the construction of the lysimeter.

3.2.2 Growth and Yield

Plant growth, as measured by the increase in plant size, was only significantly reduced in those plants stressed after 3 months of age (Fig. 12). Growth of plants stressed after 6 months was not affected by stress, although differences in plant size existed between the non-stressed and stressed plants. These differences, however, are not due to the stress treatment, because stressed plants were smaller

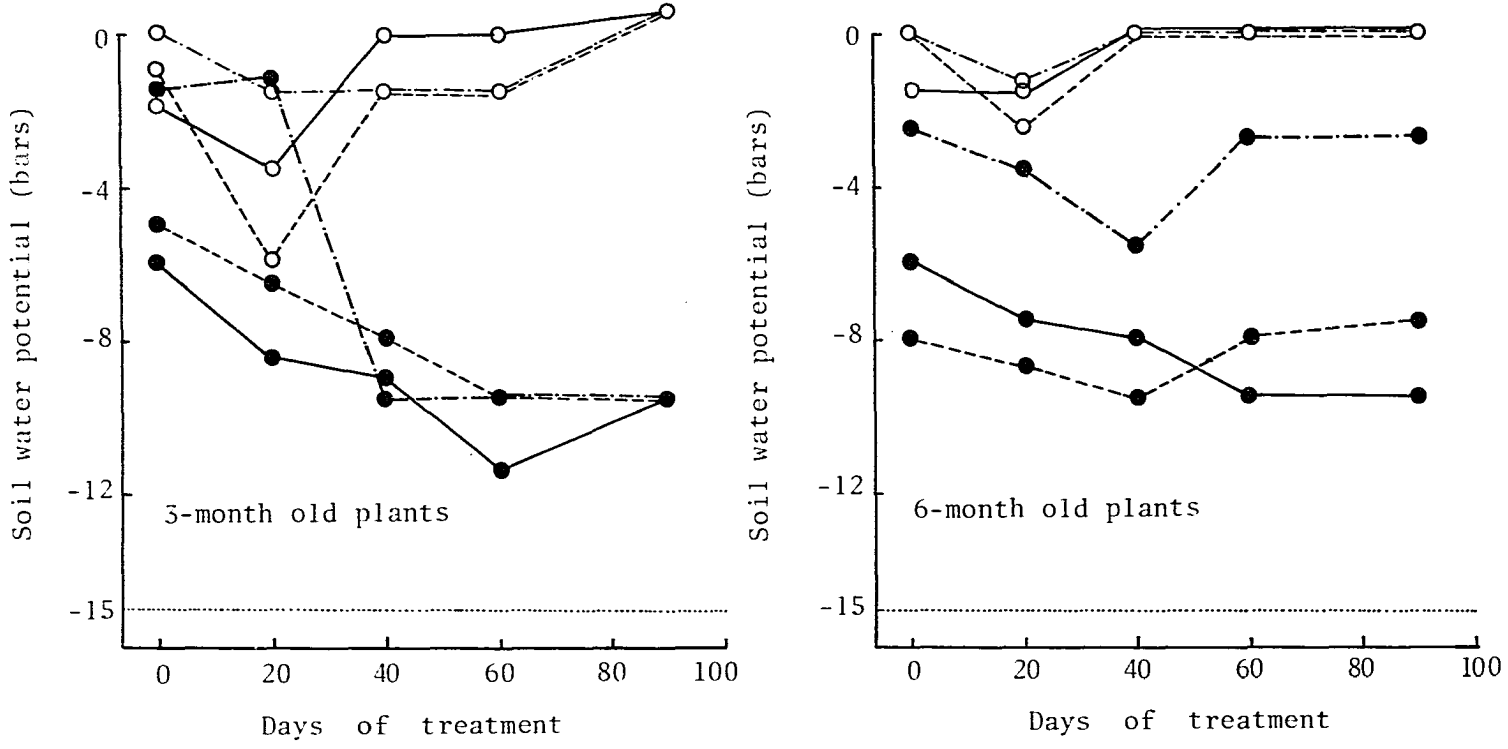

Figure 11. Patterns of soil water potential in plots of non-stressed (○) and stressed (●) plants of MCol 1684, Santander de Quilichao, 1982. -- Measurements were taken at 20 cm (—), 30 cm (--), and 80 cm (-·-) in the soil profile.

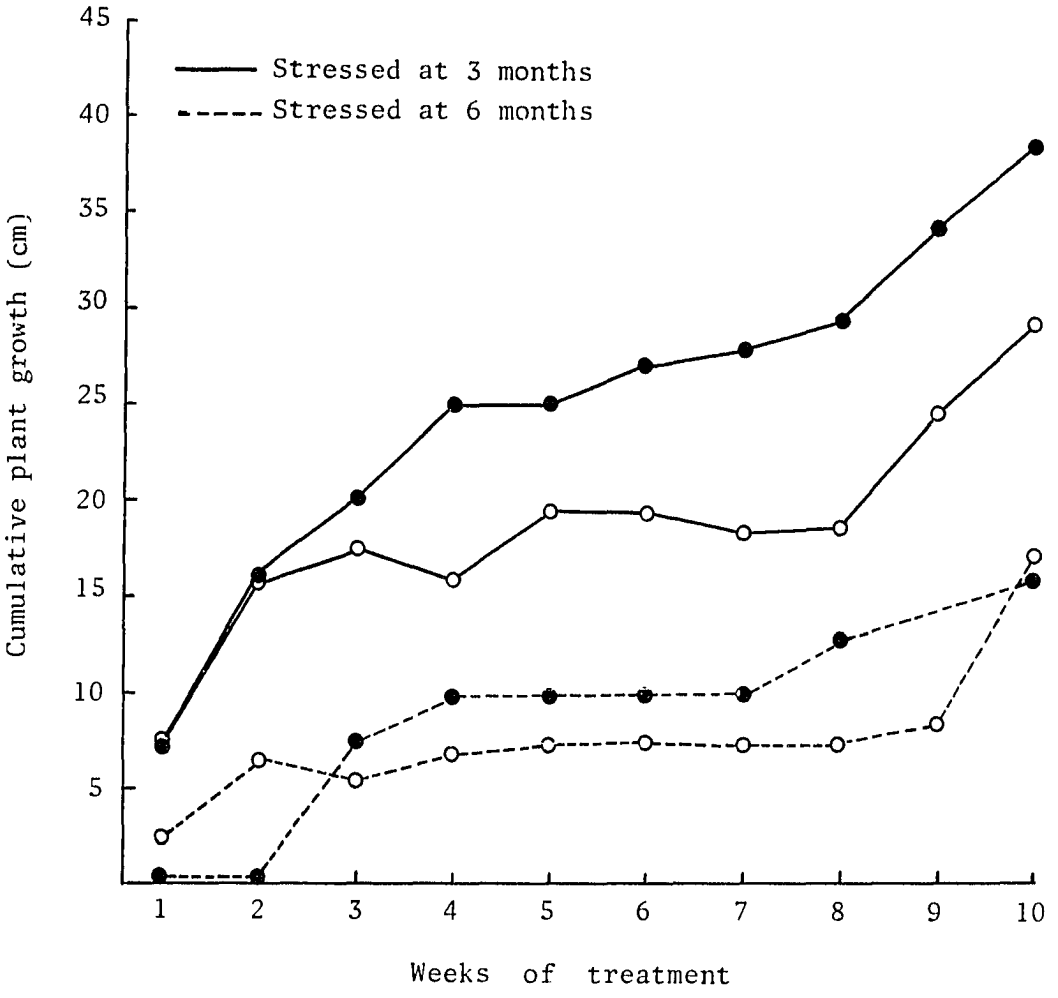

Figure 12. Growth rates of leaves formed by plants non-stressed and stressed after 3 months of growth, Santander de Quilichao, 1982/83. -- Data taken during the period of water exclusion from the stressed plots. Numbers inside the figures mean days of water stress in which leaves were formed.

than the unstressed controls since the first week of measurement. When cumulative plant growth was calculated, the differences in plant growth are clear and indicate that plant growth (increase in size) was reduced by water stress imposed early in the plant cycle (Fig. 12).

Measurements of the central lobes formed during the experimental period indicate that leaf expansion was affected after approximately 30-40 days of water exclusion. Growth rates of leaves formed at 30-40 days of water stress were lower than those of leaves formed at the same time but suffering no stress (Figs. 13 and 14). After 40 days of stress there was no apparent difference between leaf expansion rates of the stressed and non-stressed plants (Figs. 13 and 14). This suggests a resumption of growth at lower rates after the initial reduction noticed at 30-40 days of treatment. A reduction in the final size of leaf lobes was observed as the plants matured (Fig. 15), but the same reduction in lobe size was not observed when non-stressed and stressed plants were compared.

Prolonged stress (greater than 40 days) greatly reduced leaf formation in the 3-month-old plants (Fig. 16). This tendency was not followed by the 6-month-old plants. On the other hand, leaf fall caused by water stress was only evident in those plants stressed after 6 months of age (Fig. 17). This suggests the presence of two different mechanisms for reducing leaf area in cassava.

Production of biomass in plants of both ages was also affected by water stress. Non-stressed plants harvested after 190 and 280 days of growth produced 16.9 and 22.0 tons of total dry matter per hectare,

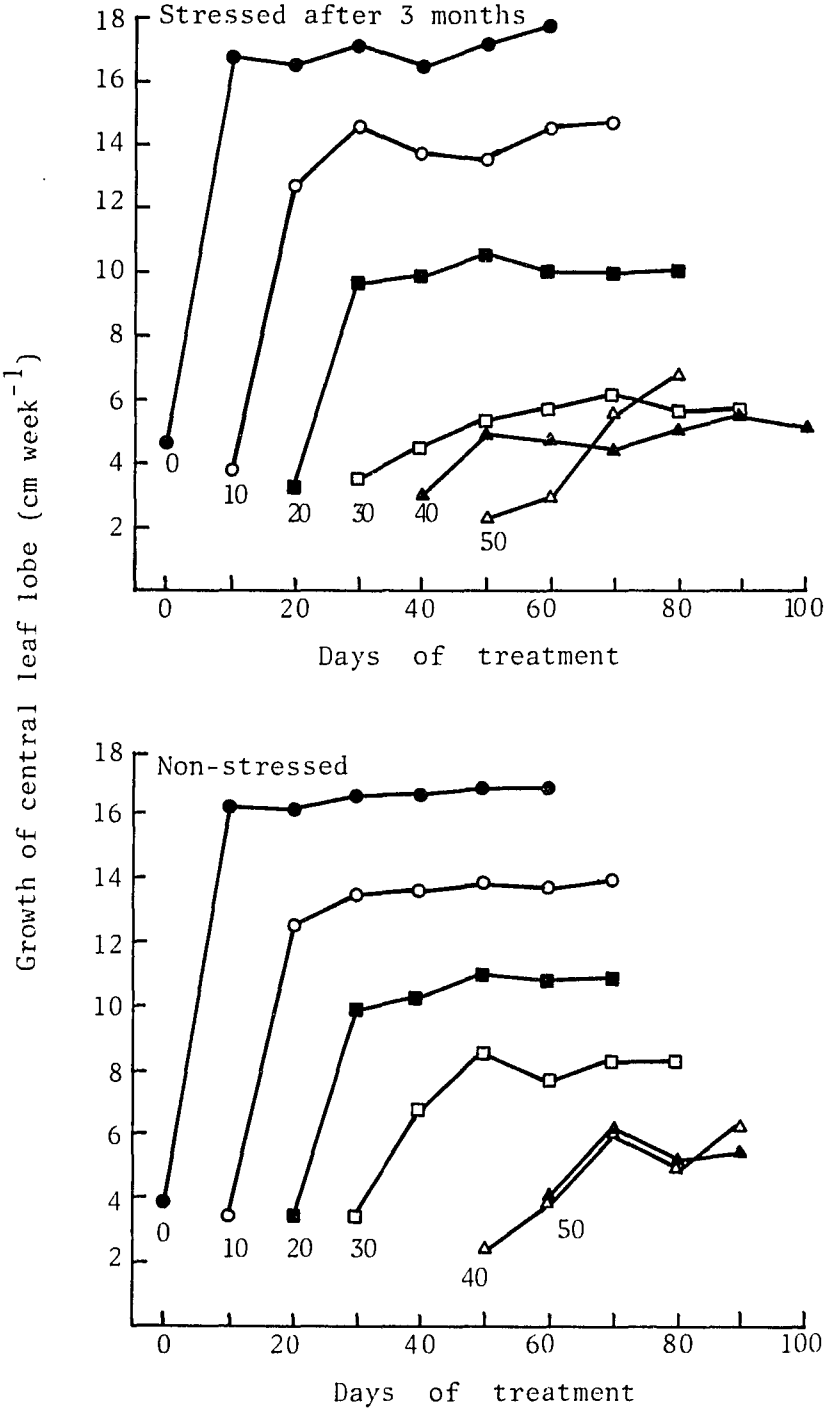

Figure 13. Growth rates of leaves formed by plants non-stressed and stressed after 3 months of growth, Santander de Quilichao, 1982/83. -- Data taken during the period of water exclusion from the stressed plots. Numbers inside the figures mean days of water stress in which leaves were formed.

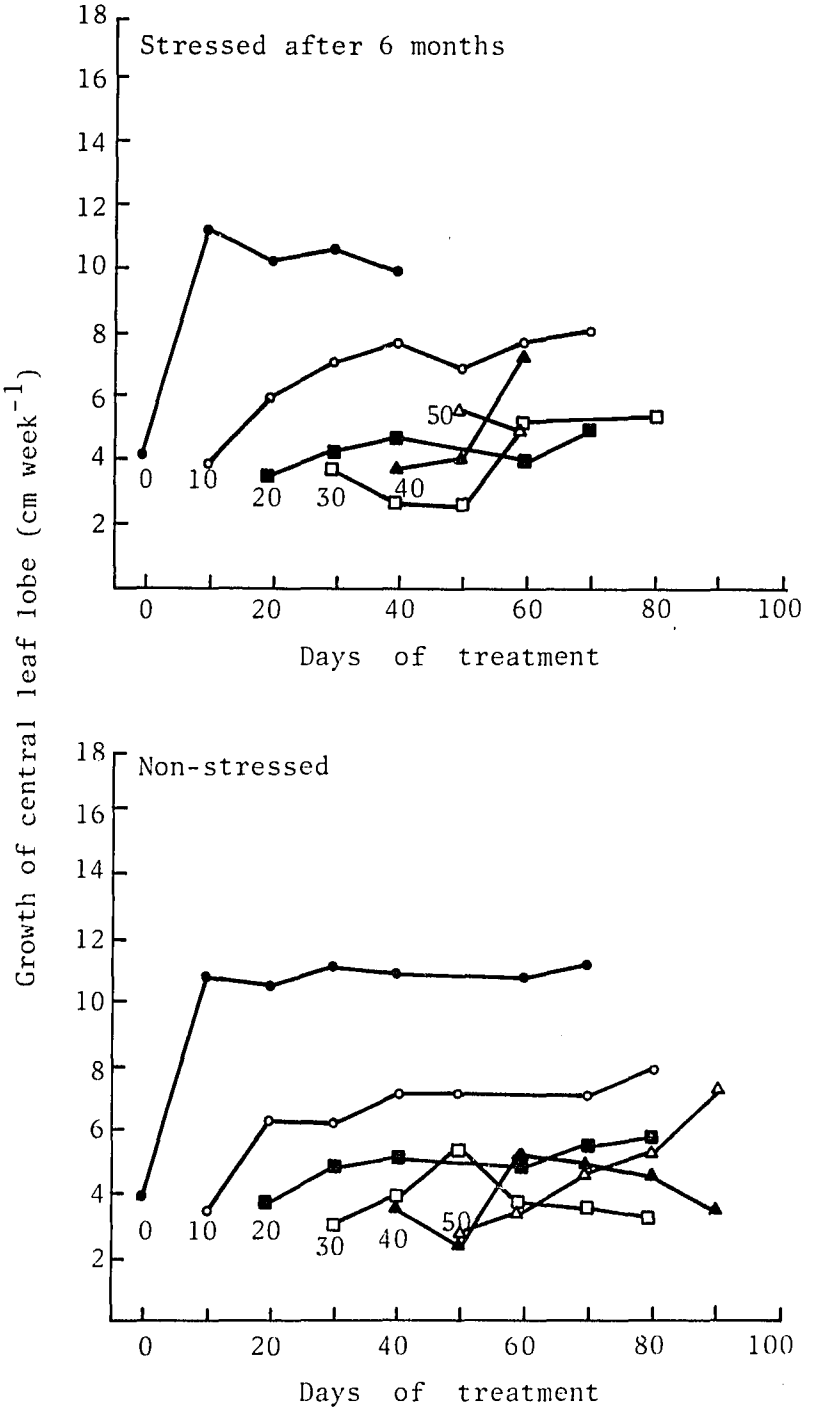

Figure 14. Growth rates of leaves formed by plants non-stressed and stressed after 6 months of growth, Santander de Quilichao, 1982/83. -- Data taken during the period of water exclusion from the stressed plots. Numbers inside the figures mean days of water stress in which leaves were formed.

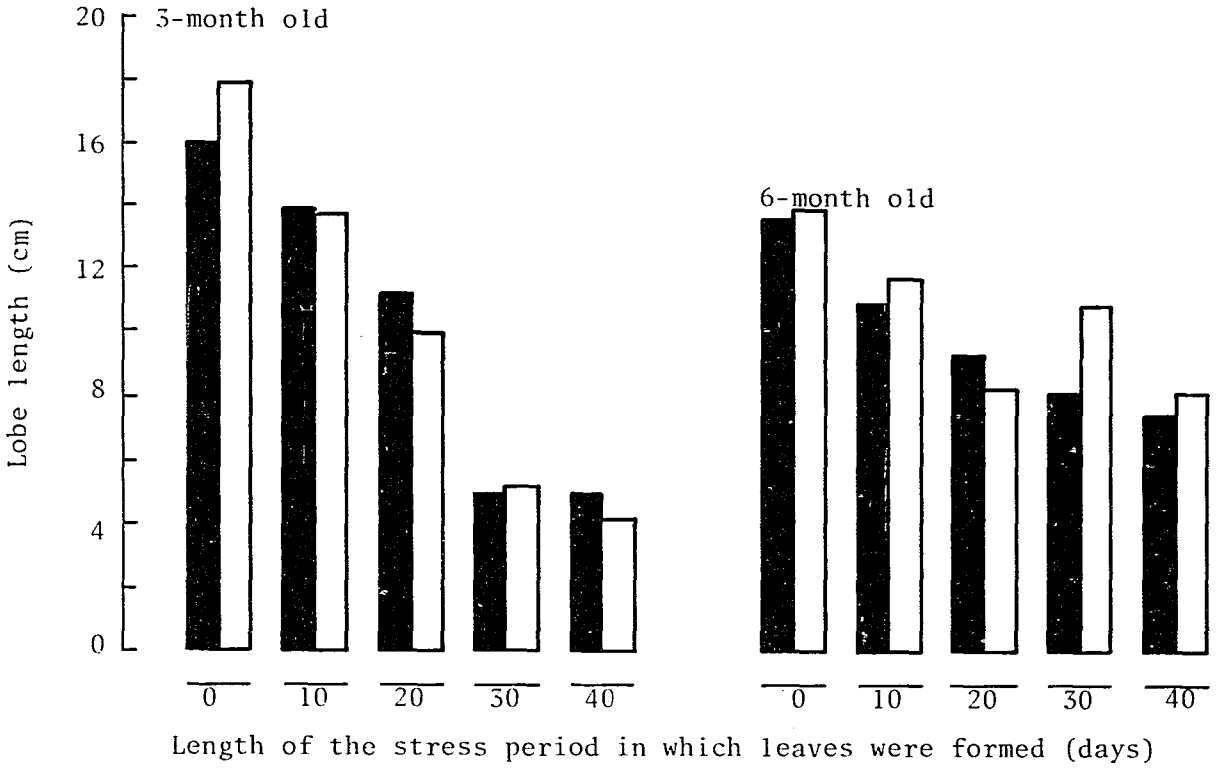

Figure 15. Final lobe lengths of plants non-stressed (□) and stressed (■) after 3 and 6 months of growth, Santander de Quilichao, 1982/83. -- Data were taken from leaves formed during the first forty days of water exclusion from the stressed plots.

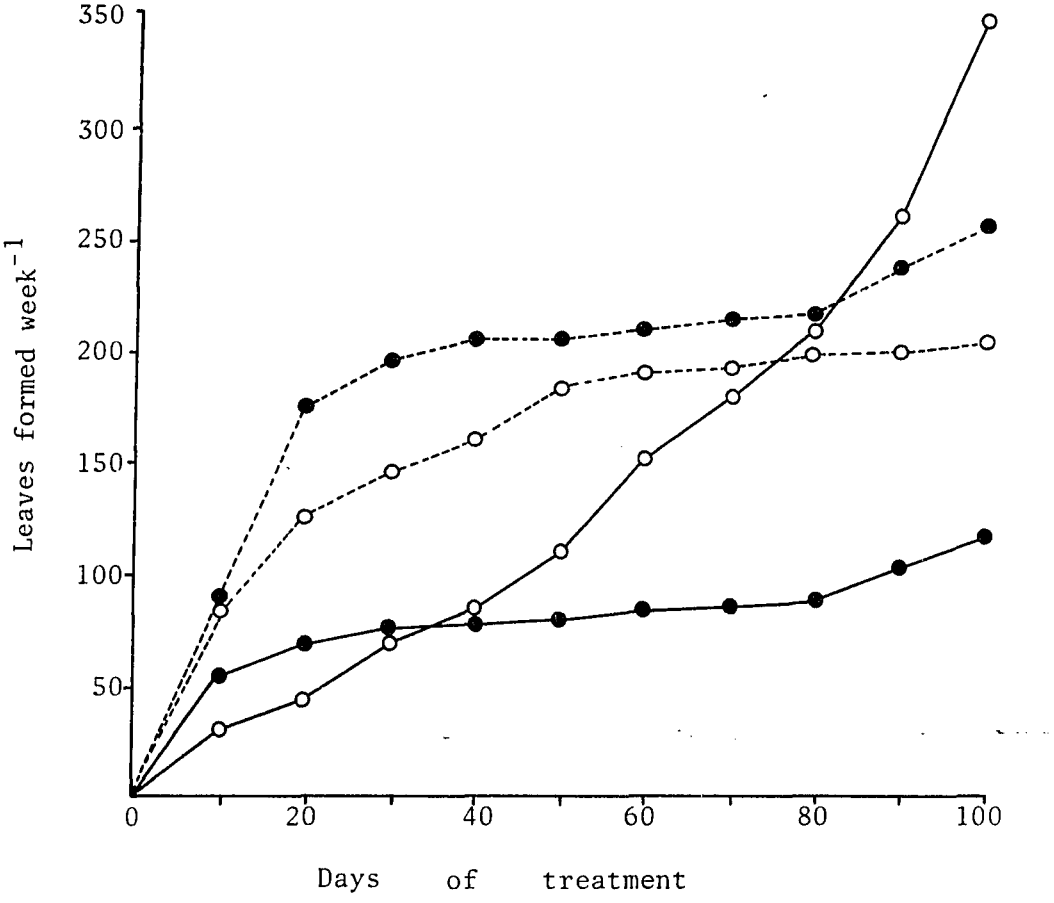

Figure 16. Number of leaves formed by non-stressed (○) and stressed (●) plants of MCol 1684 after 3 (—) and 6 (--) months of age, Santander de Quilichao, 1982/83.

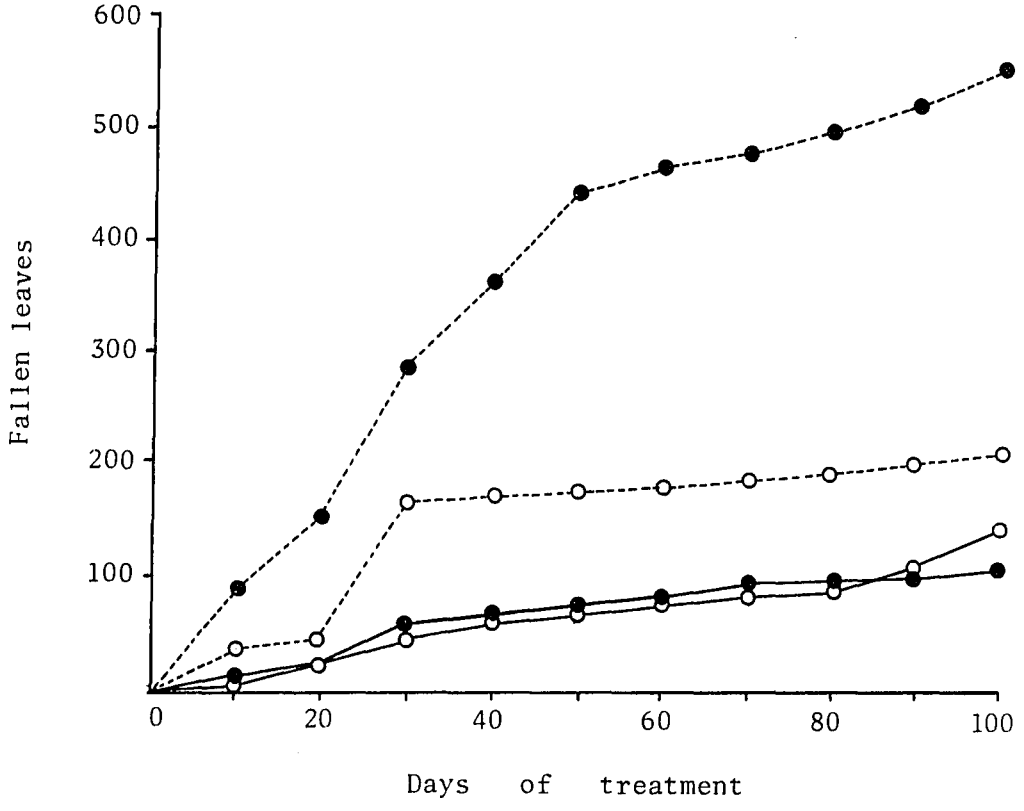

Figure 17. Leaf fall in non-stressed (○) and stressed (●) plants of MCol 1684 after 3 (—) and 6 (--) months of age, Santander de Quilichao, 1982-83.

respectively; stressed plants of the same ages yielded 10.9 and 16.5 tons per hectare, respectively (Figs. 18 and 19).

Significant reductions in storage root yields were noticed after 70 days of treatment, and effects were more pronounced in plants which were stressed after 3 months (36%, Fig. 18) than after 6 months of growth (25%, Fig. 19).

Stress reduced dry matter production in plants stressed after 3 and 6 months of growth (Table 9) and had a pronounced effect in the portion of dry matter found as roots in the younger plants (Fig. 20). At the beginning of the experimental period, 3-month-old plants had 30% of their total dry matter as roots; at the end of the stress period the proportion of dry matter in roots was increased to 48%. Nonstressed plants with the same age showed a change in the percent of dry matter from 30% to 65%, during the experimental period (Fig. 20). Plants which were stressed or not after 6 months of growth practically did not change the proportion of dry matter in storage roots during the experimental period (Fig. 21).

The changes in the pattern of dry matter allocation to the storage roots can be represented by Boerboon-type curves [2], where cumulative root biomass is plotted against the total biomass produced. The calculated lines presented in Fig. 22 indicate that water stress imposed after 3 months of age changed the patterns of dry matter distribution. However, no changes in these patterns occurred when stress was imposed after 6 months.

The percent of the total dry matter represented by the stems increased with time until 40 days of differential treatment in both

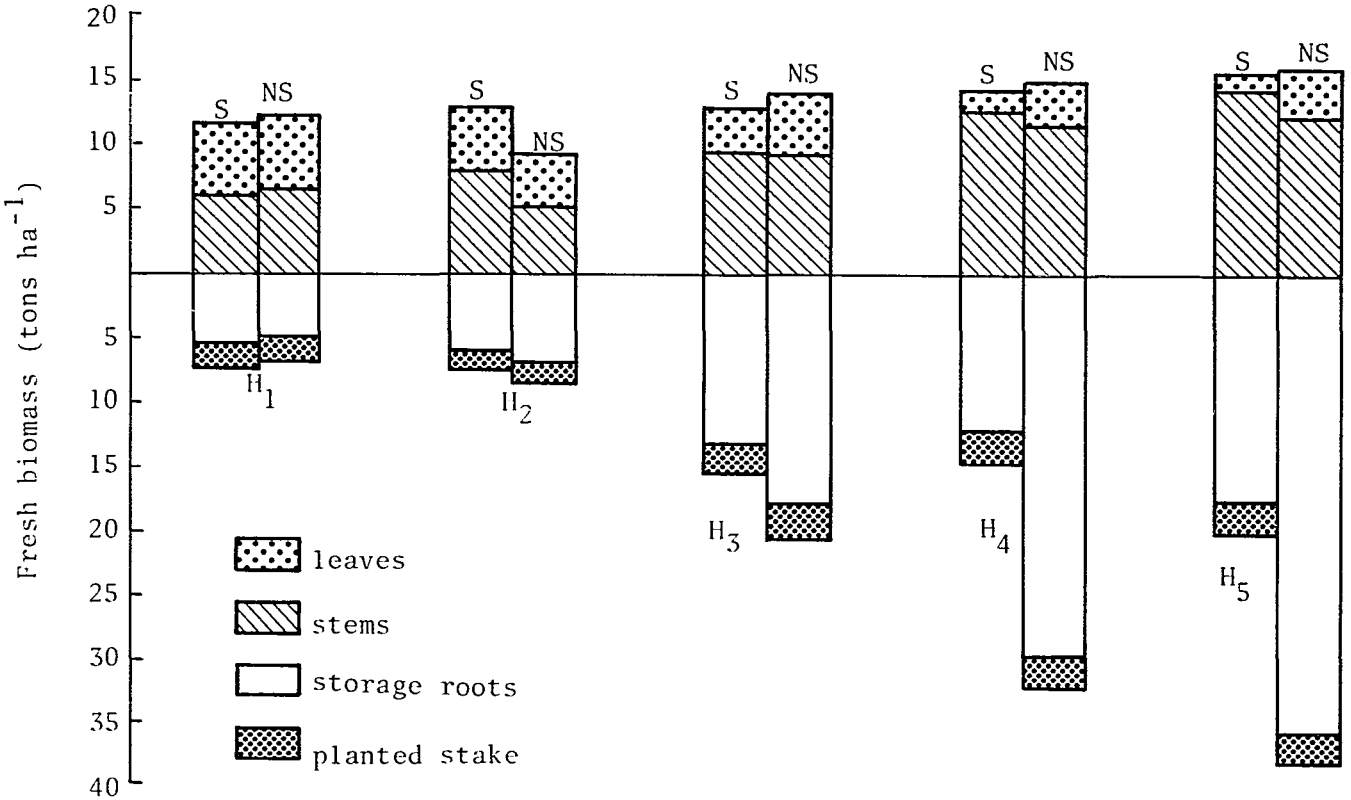

Figure 18. Total biomass produced by 3-month-old non-stressed (NS) and stressed (S) plants of MCol 1684, Santander de Quilichao, 1982/83. -- Harvests after 0, 20, 40, 70 and 100 days of the beginning of the treatments are represented by H_1, H_2, H_3, H_4 and H_5, respectively.

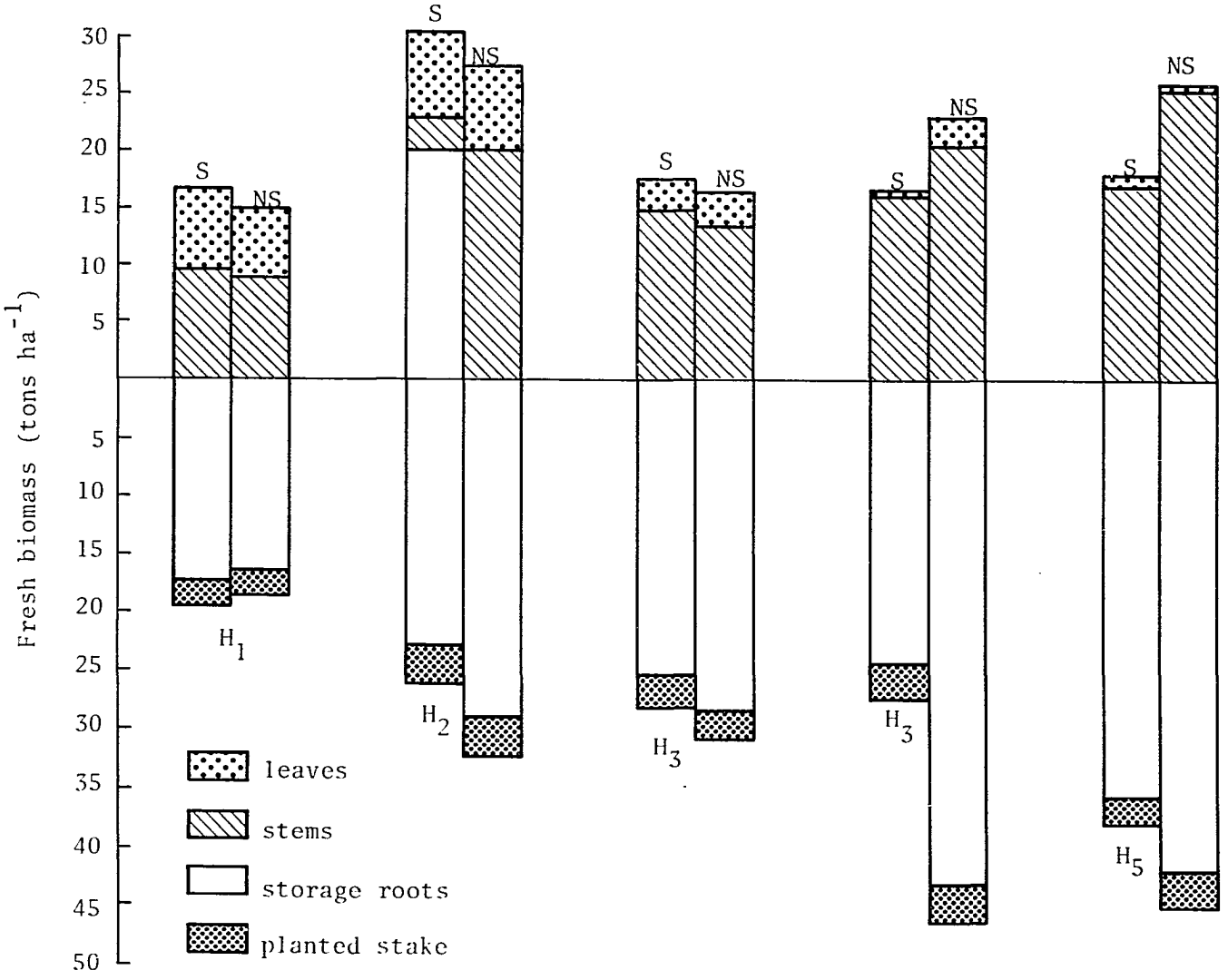

Figure 19. Total biomass produced by 6-month-old non-stressed (NS) and stressed (S) plants of MCol 1684, Santander de Quilichao, 1982/83. -- Harvests after 0, 20, 40, 70 and 100 days of the beginning of the treatments are represented by H_1, H_2, H_3, H_4 and H_5.

Table 9. Dry matter production and distribution in plants of MCol 1684 stressed and non-stressed at 3 and 6 months of age (g/plant), Santander de Quilichao, 1982/83.

Age at Stress Initiation	Days of Stress	Stressed					Non-Stressed				
		Roots	Stems	Leaves*	Stakes	Total	Roots	Stems	Leaves*	Stakes	Total
3	0	97.4	77.4	98.2	35.4	308.8	84.1	86.7	104.9	38.1	313.8
	20	150.6	151.6	280.1	42.4	464.7	165.4	104.7	191.2	44.2	505.5
	40	350.5	223.1	100.6	63.4	737.6	441.5	214.4	127.5	64.3	847.1
	70	345.4	318.9	92.4	77.1	835.6	671.5	274.7	164.0	76.0	1186.2
	100	414.2	328.8	61.4	65.3	869.7	878.3	292.4	109.2	72.6	1352.2
6	0	408.2	178.9	129.1	54.8	771.0	339.6	179.4	118.3	50.9	745.2
	20	619.9	351.0	111.2	83.5	1165.6	788.0	350.3	186.5	84.4	1409.2
	40	746.9	418.1	82.0	79.9	1326.9	767.7	462.5	98.4	67.5	1396.6
	70	695.5	449.1	77.1	75.5	1292.4	1090.4	509.5	137.5	86.7	1824.1
	100	790.5	403.9	49.1	77.8	1321.3	1012.1	597.6	62.1	86.9	1758.7

* Includes fallen leaves.

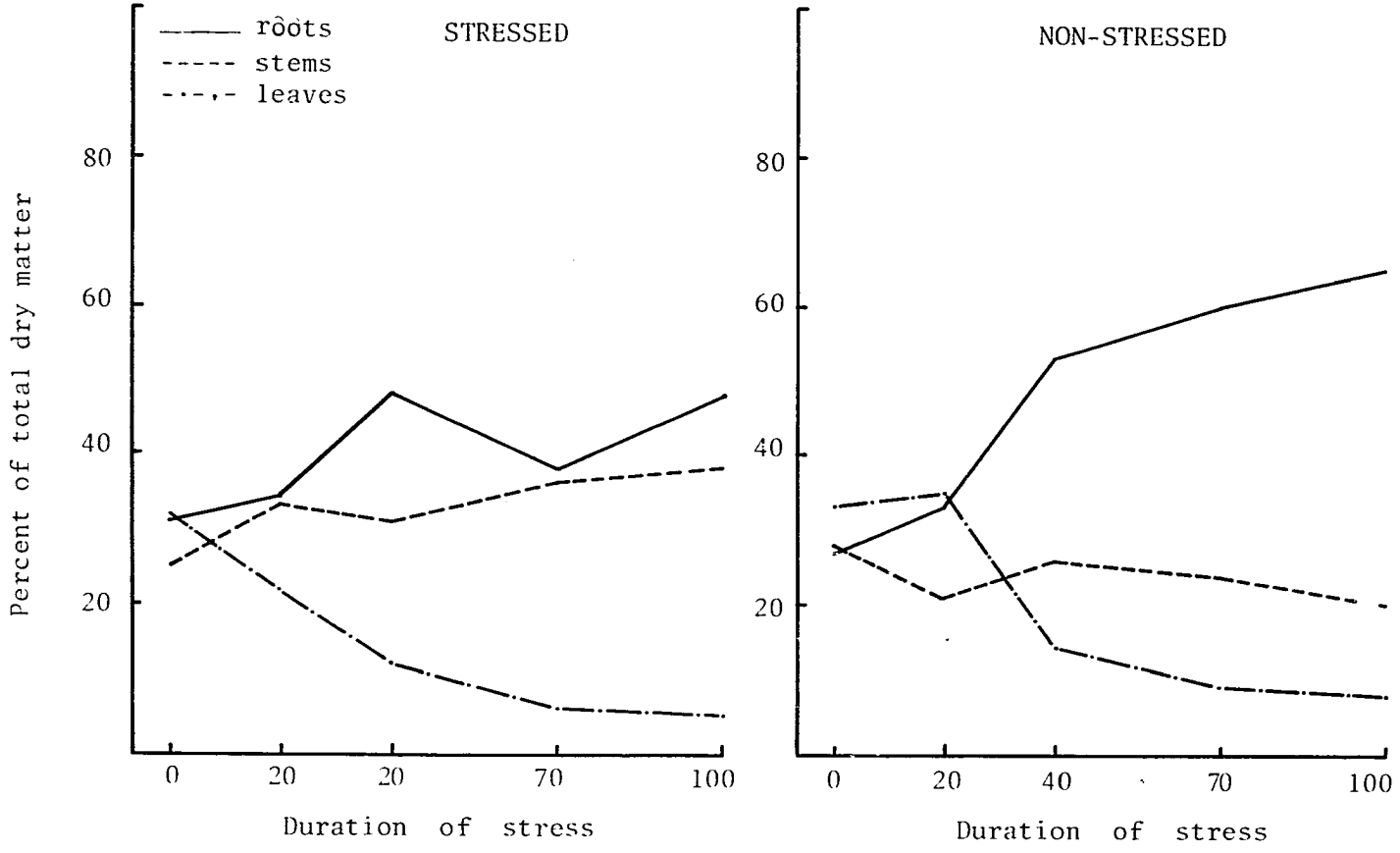

Figure 20. Percent of the total dry matter produced by plants of MCol 1684, stressed and non-stressed at 3 months of age, Santander de Quilichao, 1982/83.

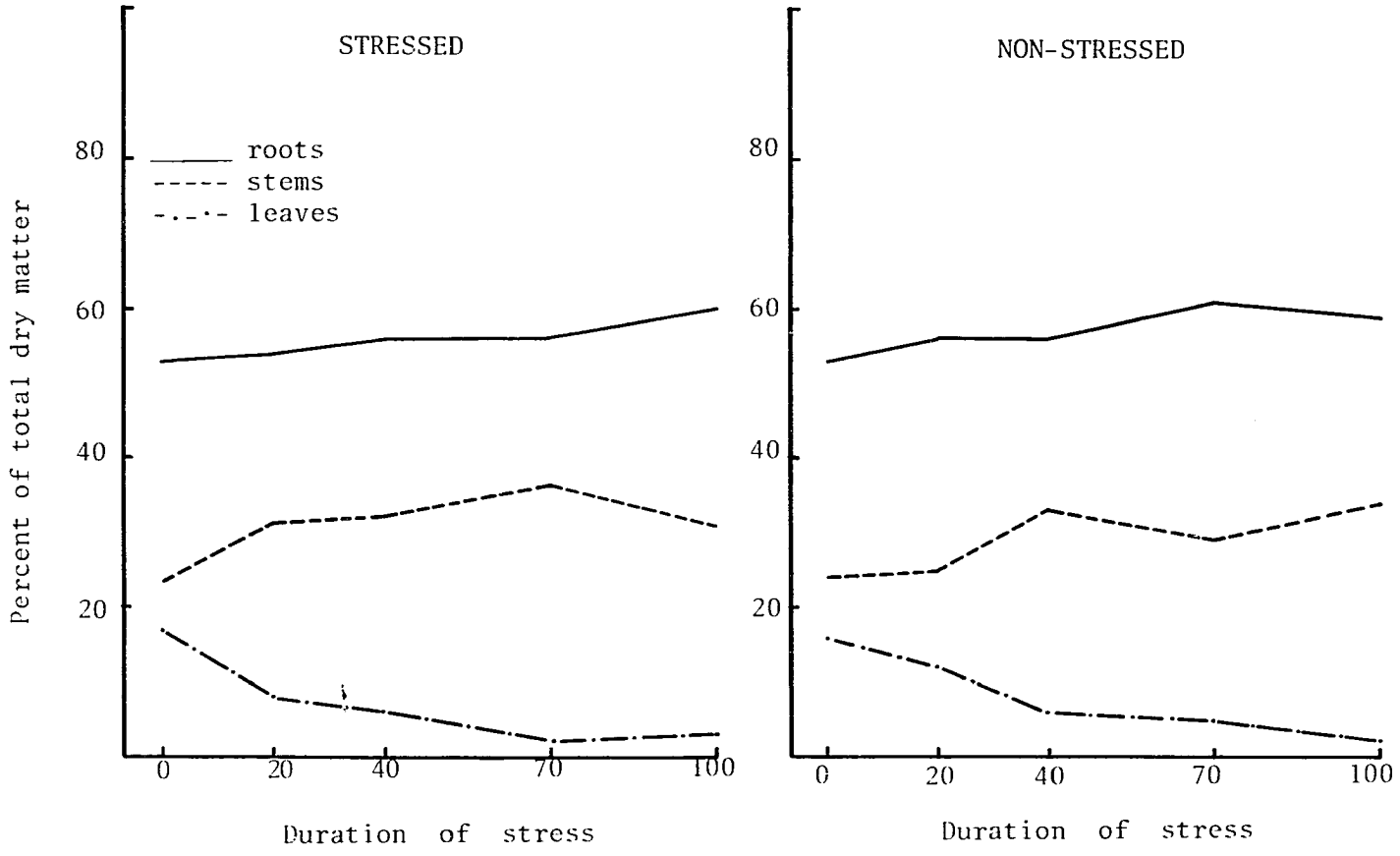

Figure 21. Percent of the total dry matter produced by plants of MCol 1684, stressed and non-stressed at 6 months of age, Santander de Quilichao, 1982/83.

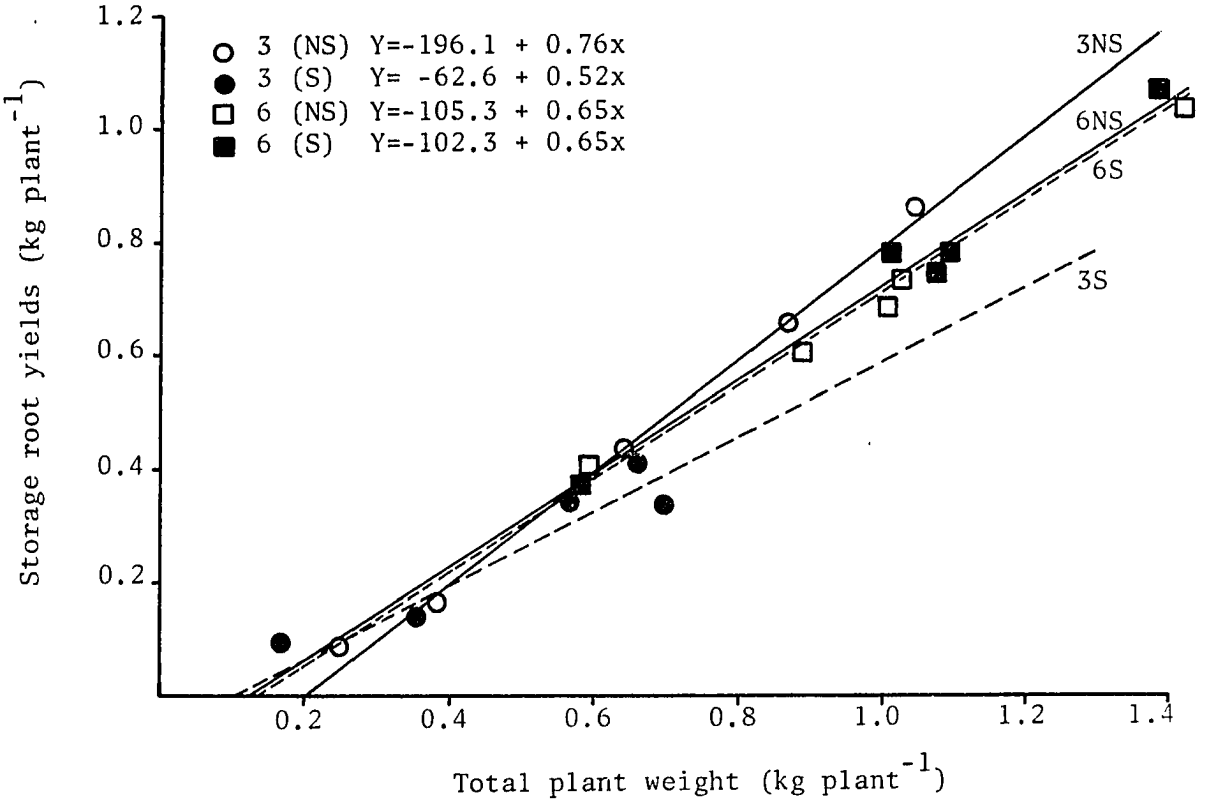

Figure 22. Dry matter allocated to the storage roots of non-stressed (NS) and stressed (S) plants of MCol 1684, at 3 and 6 months of growth, Santander de Quilichao, 1982/83.

non-stressed and stressed plants. However, the proportion was lower in the stressed plants. After 40 days of treatment plants stressed at 3 months accumulated more dry matter in the stems on a daily basis than did those plants stressed after 6 months (Figs. 20 and 21). Accumulation of dry matter in stems of younger plants at higher rates than older ones is in line with the exponential nature of plant growth [39], and with the patterns of growth and development of the cassava plant [9, 61].

Reductions in the proportions of total dry matter represented by leaves were also related to water availability and plant age (Figs. 20 and 21; Table 9). The photosynthetic area, which can be roughtly represented by the leaf area index (LAI) was almost twice as large in the six, as compared with 3-month-old plants at the beginning of the treatments (Table 10). Leaf area indexes were drastically reduced by water stress after 20 days for plants stressed at 3 months and 40 days for those stressed after 6 months. LAI also decreased with plant age in both groups. After 100 days of treatment the plants stressed at 3 months reduced LAI approximately 50% in relation to the non-stressed plants of the same age. The LAI of those plants stressed later in their cycle was practically identical to the index measured in the non-stressed plants (Table 10).

3.2.3 Leaf Water Potential

Leaf water potentials measured in well developed young leaves were higher in early morning and decreased toward midday/midafternoon, increasing again at the end of the day (Table 11). Measurements taken

Table 10. Leaf area indexes (LAI) of MCol 1684 plants, submitted or not to water stress at 3 and 6 months, respectively, Santander de Quilichao, 1982/83.

Days of Stress	Age When Stressed			
	3 Months		6 Months	
	Non-stressed	Stressed	Non-stressed	Stressed
0	1.6	2.1	3.2	3.9
20	1.9	2.4	4.8	5.5
40	1.9	2.6	2.0	1.8
70	1.9	1.2	1.6	0.6
100	2.2	1.0	0.9	0.8

Table 11. Leaf water potentials (-bars) in plants of MCol 1684 submitted or not to water stress after 3 and 6 months of growth, Santander de Quilichao, 1982/83.

Age When Stressed (months)	Treatment (days)	Time of the Day									
		6:00 AM		9:00 AM		12:00 N		3:00 PM		6:00 PM	
		NS	S	NS	S	NS	S	NS	S	NS	S
3	10	4.2	4.2	10.6	10.6	-	-	13.5	13.5	6.0	6.0
	20	4.3	4.3	8.3	9.8	11.2	11.3	11.9	10.4	6.9	7.8
	30	6.1	6.2	10.5	9.9	14.8	10.7	13.7	12.2	8.0	9.1
	40	7.1	6.4	12.3	12.4	12.7	10.2	-	-	10.7	10.9
	50	6.4	7.2	15.0	13.6	16.2	12.2	13.0	11.2	14.2	11.7
	60	6.7	6.8	15.0	14.4	16.3	13.9	17.1	12.5	10.0	11.7
	70	6.4	7.9	13.0	12.6	14.6	13.1	14.6	13.1	12.5	12.1
	80	6.5	6.3	13.6	11.9	15.6	14.7	15.6	14.7	12.7	12.4
	90	-	-	11.0	11.5	14.1	13.9	13.6	14.6	10.9	11.5
	100	8.9	8.2	11.9	11.5	12.6	10.4	16.7	13.8	-	-
6	10	4.9	4.9	11.6	11.6	-	-	13.6	13.6	6.9	6.9
	20	6.0	6.0	14.6	12.9	11.3	11.8	12.0	11.2	6.5	6.4
	30	6.9	6.7	10.8	10.0	14.9	11.8	15.2	12.5	7.0	9.2
	40	8.8	8.7	12.6	12.2	12.1	12.4	-	-	9.5	10.5
	50	9.1	8.9	15.2	13.9	14.3	10.9	15.2	13.2	11.5	11.4
	60	8.1	8.5	15.2	14.5	16.4	13.4	14.6	13.2	8.1	10.4
	70	8.0	8.7	14.7	14.1	15.0	13.3	15.0	13.3	12.3	11.5
	80	7.7	10.0	12.0	14.2	16.0	15.0	16.0	15.0	10.8	11.8
	90	-	-	12.0	13.3	14.1	13.5	12.5	13.5	12.0	13.3
	100	8.2	9.0	11.7	11.4	-	-	14.0	13.3	-	-

* Each mean is the average of 12 measurements taken in leaves of different plants.

at 9:00 AM, Noon and 3:00 PM both in the stressed and in the non-stressed plants showed little differences. Consequently, only those measurements taken at 6:00 AM, Noon and 6:00 PM were used for constructing Fig. 23. The tendency of ψ_L to decrease toward midday is clear, as well as the increase toward late afternoon. However, as water stress progressed those values of leaf water potential measured at 6:00 PM were close to the values obtained at noon.

The effects of water stress on ψ_L were more evident in measurements taken between 9:00 AM and 3:00 PM (Table 11), and especially at midday (Fig. 23). Non-stressed plants started showing lower values of ψ_L after 30-40 days of treatment. This tendency was maintained until the end of the experiment. Leaf water potentials measured at 6:00 AM and 6:00 PM cannot be considered as being consistently affected by stress in a cassava cultivar MCol 1684.

The results indicate that MCol 1684 was able to control decreases in ψ_L under stress, especially when the plants were under stress (Table 11, Fig. 23). Leaf water potentials of both non-stressed and stressed plants decreased with age.

3.2.4 Leaf Diffusive Resistances/Conductances

Leaf diffusive resistances were higher in early morning and late afternoon periods, when light intensities were low (Table 12); and under low light conditions, stressed and non-stressed plants often showed smallest resistance values. Midday or midafternoon diffusive resistances of stressed plants, however, were higher than those of non-stressed plants. Additionally, climatic conditions at the time of meas-

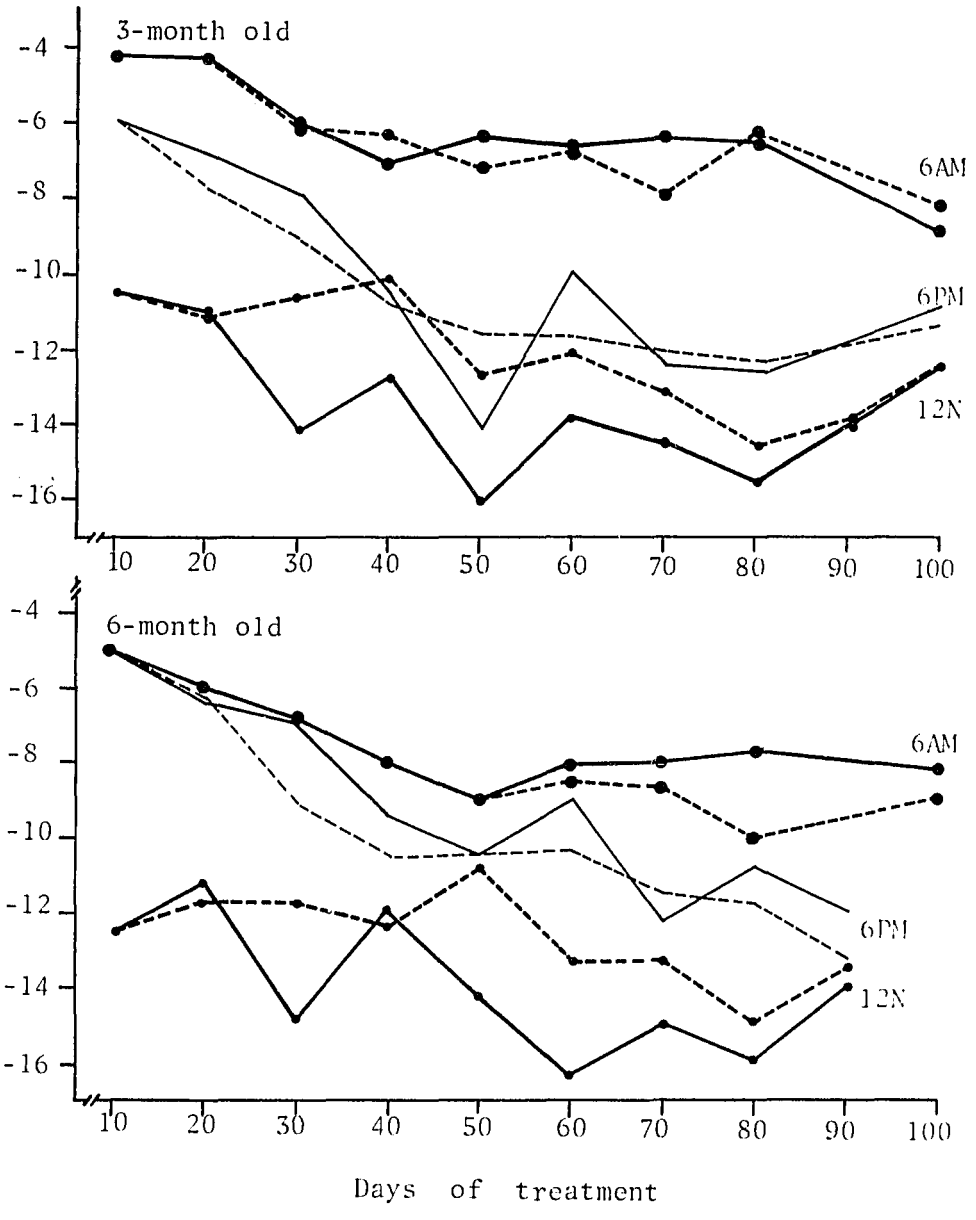

Figure 23. Changes in leaf water potentials measured at 6:00 AM, 12:00 N, and 6:00 PM in plants of MCol 1684 stressed (--) or not (—) at 3 and 6 months of age, Santander de Quilichao, 1982/83.

Table 12. Leaf diffusive resistances (sec cm^{-1}) in plants of MCol 1684 submitted or not to water stress after 3 and 6 months, Santander de Quilichao, 1982/83.

Age When Stressed (months)	Treatment (days)	Time of the Day									
		6:00 AM		9:00 AM		12:00 N		3:00 PM		6:00 PM	
		NS	S	NS	S	NS	S	NS	S	NS	S
3	10	14.7	14.7	9.7	8.2	2.3	2.3	1.8	1.7	9.5	9.5
	20	16.7	13.0	3.9	3.1	14.3	11.4	6.8	7.5	27.1	22.5
	30	-	-	4.3	4.9	1.2	6.5	4.8	11.4	1.6	7.9
	40	19.9	18.2	11.7	15.9	9.9	33.4	4.2	23.3	10.1	11.6
	50	9.1	11.3	5.0	7.6	2.9	5.7	2.9	12.2	5.5	10.2
	60	9.0	22.8	5.5	10.3	2.0	4.0	2.2	8.0	9.8	8.0
	70	7.4	16.4	6.7	8.1	4.9	7.2	4.8	6.8	8.4	9.0
	80	31.5	38.7	-	7.9	2.9	4.2	5.7	6.4	6.6	7.5
	90	26.4	21.7	5.8	8.3	3.8	4.4	3.3	3.6	9.9	7.2
	100	11.1	14.3	3.8	4.7	3.3	5.6	4.4	4.9	-	-
6	10	9.2	9.2	4.1	3.7	2.7	2.7	1.8	2.1	7.3	7.3
	20	12.2	12.9	6.1	5.7	14.6	11.7	9.0	6.6	19.6	18.8
	30	-	-	5.4	5.4	2.2	10.3	1.8	4.0	3.7	9.8
	40	15.6	17.1	14.2	15.7	8.9	29.0	6.9	12.1	14.6	16.7
	50	9.5	14.5	7.8	11.4	2.6	12.2	4.0	10.4	11.2	17.8
	60	7.8	12.2	4.5	6.7	3.1	8.2	2.7	7.1	12.3	12.9
	70	7.8	20.3	9.9	9.5	4.8	7.8	5.1	24.1	14.3	10.4
	80	-	-	-	-	4.4	6.6	6.7	8.8	6.9	8.4
	90	18.0	17.5	6.8	6.1	3.4	3.6	4.8	4.7	6.5	7.1
	100	10.0	11.5	5.4	6.1	2.8	2.9	3.2	4.2	6.5	-

* Each data is the average of 12 measurements taken in leaves of different plants.

urement conributed to alter values of resistance in the plants. In plants stressed from the third month, for example, noon and afternoon diffusive resistance values after 40 days of stress were extremely high. On that day relative humidity was very low (34% at midday) and air temperatures were higher than normal, which also led to reductions in leaf water potentials (Table 11).

Leaf conductance values, calculated from diffusive resistance determinations, were compared with leaf water potential, relative humidity and leaf-air vapor pressure deficits. Considering all measurements, leaf conductance was not significantly correlated to water potential but was correlated to atmospheric humidity measured at 3:00 PM in plants stressed following 3 months of growth ($r = 0.82$). Non-stressed plants of the same age showed no correlation between conductance and relative humidity, but did show a significant negative correlation between conductance and vapor pressure deficits ($r = 0.81$). Correlations were not made between the values obtained in the 6-month-old plants due to the small number of observations available.

3.2.5 Photosynthesis

Photosynthesis was measured at least three times a day (9:00 AM, 12:00 N and 3:00 AM) and on six occasions on unstressed plants and in plants stressed after 3 months of growth. Photosynthetic rates were higher at the beginning of the experimental period. After 40 days of treatment, on January 24, photosynthetic rates, like water potential (Table 11) and leaf diffusive conductance (based on data of Table 12) were greatly reduced in both groups of plants, but non-stressed plants

had higher rates than stressed plants (Table 13). Low relative humidity (34% on January 24) could have reduced stomatal aperture [5, 20, 56, 56].

In plants stressed at 3 months of age, water stress reduced noon and midday photosynthetic rates from the fortieth to the ninetieth days, although differences were higher at midday and 3:00 PM readings.

Correlation analysis suggests that photosynthesis of stressed plants was related to leaf diffusive conductances when measurements were taken at 12:00 N and 3:00 PM (Table 14). Based on simultaneous measurements, photosynthetic rates of non-stressed plants were positively correlated with leaf diffusive conductance at noon. These results suggest that photosynthesis was dependent on leaf conductance, especially at midday in both stressed and non-stressed plants. Correlation between photosynthesis and relative humidity was also significant when the measurements were taken at 3:00 PM, especially in the stressed plants (Table 14).

3.2.6 Leaf Temperature

Leaf temperatures were usually 2-3^{o}C higher than air temperatures in plants of both age groups (Tables 15 and 16), and differences were more pronounced from midday to midafternoon. Interestingly, noon and afternoon leaf temperatures from plants stressed for even up to 100 days were usually lower than comparable unstressed leaves. At 6:00 PM, however, leaf temperatures were slightly higher in the stressed plants (Fig. 24).

Table 13. Photosynthesis (mg CO_2 dm^{-2} hr^{-1}) of non-stressed and stressed plants of MCol 1684, Santander de Quilichao, 1981.

Days of Stress	Treatment	Time of the Day 9:00 AM	12:00 N	3:00 PM	Daily Average
0	NS*	25.4^a	31.5^b	30.9^a	29.3
	S	26.4^a	45.6^a	32.4^a	34.8
10	NS	36.3^a	28.4^a	31.6^a	32.1
	S	32.6^a	33.5^a	33.4^a	33.1
40	NS	23.0^a	11.3^a	9.3^a	14.5
	S	20.7^a	6.5^b	0.7^b	9.3
70	NS	28.7^a	22.4^a	24.1^a	25.1
	S	16.5^b	11.4^b	4.6^b	10.8
90	NS	29.1^a	18.5^a	16.8^a	21.4
	S	23.5^a	9.2^b	7.5^b	13.4
100	NS	34.3^a	27.2^a	19.6^a	27.0
	S	29.6^a	26.4^a	8.7^b	21.5

* NS and S means non-stressed and stressed plants, respectively. Means followed by the same letter in the columns for each date and time of measurement do not differ at the degree of 5% by the t test.

Table 14. Relationships between photosynthesis and transpiration, leaf diffusive conductance, leaf water potential, leaf temperature, vapor pressure deficits, and air relative humidity, Santander de Quilichao, 1982-83.

	Correlation Coefficients for Photosynthesis					
	Stressed			Non-Stressed		
Parameter	9:00 AM	12:00 N	3:00 PM	9:00 AM	12:00 N	3:00 PM
Transpiration (g cm^{-2} sec^{-1})	0.17	0.43	0.86*	0.11	0.57	-0.23
Conductance (cm^{-2} sec^{-1})	0.64	0.86*	0.82*	-0.27	0.93*	0.63
Water Potential (bars)	0.87*	0.38	0.19	0.72	0.02	0.34
Leaf Temperature (°C)	-0.80	-0.65	-0.32	-0.41	-0.55	-0.71
VPD (mbars)	0.30	-0.18	-0.63	-0.20	-0.49	-0.82*
Air R.H. (%)	0.46	0.51	0.80	0.52	0.42	0.97*

* Statistical significance at 5% of probability.

Table 15. Air temperature and leaf temperature in plants of MCol 1684 submitted or not to water strss at 3 months of age, Santander de Quilichao, 1982/83.*

Age When Stressed (months)	Treatment (days)	Time of the Day									
		8:00 AM		9:00 AM		12:00 N		3:00 PM		8:00 PM	
		TA	TL	TA	TL	TA	TL	TA	TL	TA	TL
10	NS	20.7	-	-	32.5	28.4	34.6	29.3	34.5	26.0	-
	S	20.7	26.1	-	30.6	28.4	34.6	29.3	34.2	26.0	33.8
20	NS	20.6	24.3	-	27.8	28.8	37.8	-	31.2	24.7	28.6
	S	20.6	25.5	-	25.6	28.8	33.9	-	33.0	24.7	29.3
30	NS	23.5	-	-	27.7	31.0	34.6	31.5	37.2	26.0	31.8
	S	23.5	-	-	27.9	31.0	32.5	31.5	37.2	26.0	33.0
40	NS	21.0	22.9	28.5	31.6	34.0	40.2	33.0	36.7	27.0	34.4
	S	21.0	23.1	28.5	30.9	34.0	38.5	33.0	37.1	27.0	37.0
50	NS	23.5	27.9	30.0	30.5	31.0	36.5	-	38.2	27.0	33.9
	S	23.5	27.0	30.0	29.0	31.0	34.7	-	37.0	27.0	34.6
60	NS	21.5	25.2	30.0	31.1	32.0	36.1	32.5	38.2	27.0	32.1
	S	21.5	25.7	30.0	29.4	32.0	34.6	32.5	36.8	27.0	33.7
70	NS	23.0	24.2	28.0	30.2	29.0	32.4	30.5	37.1	29.0	34.3
	S	23.0	25.6	28.0	28.6	29.0	31.6	30.5	35.1	29.0	35.5
80	NS	22.5	25.6	26.5	32.3	34.5	36.7	32.3	36.5	28.0	34.5
	S	22.5	24.9	26.5	27.3	34.5	34.7	32.3	36.5	28.0	34.5
90	NS	24.0	26.2	29.0	27.6	33.0	34.8	32.5	36.5	27.0	34.1
	S	24.0	24.8	29.0	27.5	33.0	33.5	32.5	37.2	27.0	34.9
100	NS	26.0	19.5	30.0	31.4	32.5	32.4	31.0	35.8	-	-
	S	26.0	19.5	30.0	26.1	32.5	32.6	31.0	36.3	-	-

* Each value represents the average of 12 measurements in different plants (for TL)
- Data not recorded.
TA = Air temperature.
TL = Leaf temperature.

Table 16. Air temperature and leaf temperature in plants of MCol 1684 submitted or not to water stress at 6 months of age, Santander de Quilichao, 1982/83.*

Age When Stressed (months)	Treatment (days)	Time of the Day									
		8:00 AM		9:00 AM		12:00 N		3:00 PM		8:00 PM	
		TA	TL	TA	TL	TA	TL	TA	TL	TA	TL
10	NS	20.7	25.1	-	33.8	28.4	36.4	29.3	33.7	26.0	-
	S	20.7	-	-	33.6	28.4	36.4	29.3	33.1	26.0	28.6
20	NS	20.6	24.9	-	32.1	28.8	38.0	-	31.2	24.7	27.2
	S	20.6	24.0	-	31.1	28.8	35.2	-	32.4	24.7	27.7
30	NS	23.5	-	-	27.5	31.0	34.4	31.5	35.5	26.0	29.0
	S	23.5	-	-	27.7	31.0	35.6	31.5	36.2	26.0	29.9
40	NS	21.0	22.4	28.5	33.4	34.0	38.4	33.0	36.9	27.0	32.2
	S	21.0	22.4	28.5	30.1	34.0	38.1	33.0	37.0	27.0	32.6
50	NS	23.5	26.1	30.0	33.6	31.0	38.0	-	37.6	27.0	31.2
	S	23.5	26.1	30.0	33.1	31.0	37.3	-	37.1	27.0	31.4
60	NS	21.5	24.7	30.0	34.7	32.0	37.8	32.5	37.0	27.0	30.8
	S	21.5	24.6	30.0	30.6	32.0	36.9	32.5	36.2	27.0	31.4
70	NS	23.0	27.1	28.0	31.8	29.0	33.1	30.5	36.1	29.0	31.3
	S	23.0	25.2	28.0	31.2	29.0	32.3	30.5	37.2	29.0	32.5
80	NS	22.5	-	26.5	-	34.5	36.2	32.3	36.5	28.0	31.5
	S	22.5	-	26.5	-	34.5	36.7	32.3	35.4	28.0	32.3
90	NS	24.0	27.2	29.0	28.4	33.0	33.9	32.5	36.8	27.0	31.5
	S	24.0	26.2	29.0	27.5	33.0	32.6	32.5	37.6	27.0	33.0
100	NS	26.0	19.5	30.0	31.2	32.5	38.4	31.0	34.7	-	-
	S	26.0	19.5	30.0	30.9	32.5	38.4	31.0	34.1	-	-

* Each value represents the average of 12 measurements in different plants (for TL).
- Data not recorded.
TA = Air temperature (°C).
LT = Leaf temperature (°C).

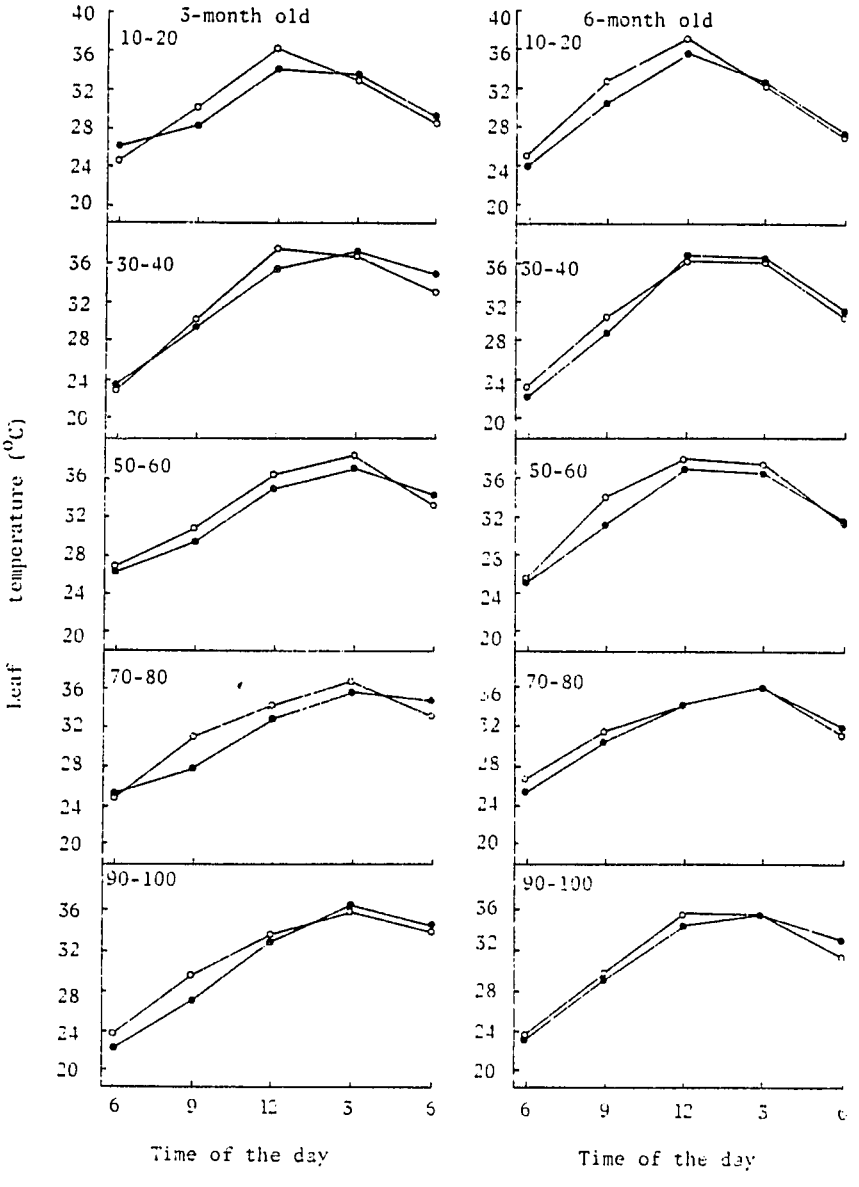

Figure 24. Patterns of leaf temperatures of non-stressed (o) and stressed (●) plants of MCol 1684 after 3 and 6 months of age, Santander de Quilichao, 1982/83. -- Each data point is the average of 48 measurements taken on two occasions. * = Days after stress when measurements were taken.

3.2.7 Transpiration

Measurements of leaf transpiration rates from plants stressed or not after 3 months of growth show that rates were higher in non-stressed plants and also in the stressed plants at the beginning of the experimental period. After 30-40 days of stress, transpiration rates measured at midday and midafternoon were lower than those found in non-stressed plants (5 g M_2O dm^{-2} hr^{-1}), and were reduced to as low as 0.4 g dm^{-2} hr^{-1}.

Substantial increases in transpiration rate in stressed plants occurred after 80 and 100 days of treatment (Fig. 25). The increased transpiration of stressed plants may reflect increased relative humidities (Table A.5).

3.2.8 Water Use Efficiency

Water use efficiency (WUE), the ratio between photosynthesis and transpiration, was always higher when measurements were taken at 9:00 AM for both non-stressed and stressed plants after 3 months of age (Fig. 26). No differences were observed in WUE of non-stressed and stressed plants at noon and 3:00 PM.

The calculated values of water use efficiency are in the range of those obtained by El-Sharkawy, Cock and Held [22]. They found that WUE of six cassava cultivars were usually lower when values of VPD were high. In the present experiment, no correlation was found between water use efficiency and vapor pressure deficits.

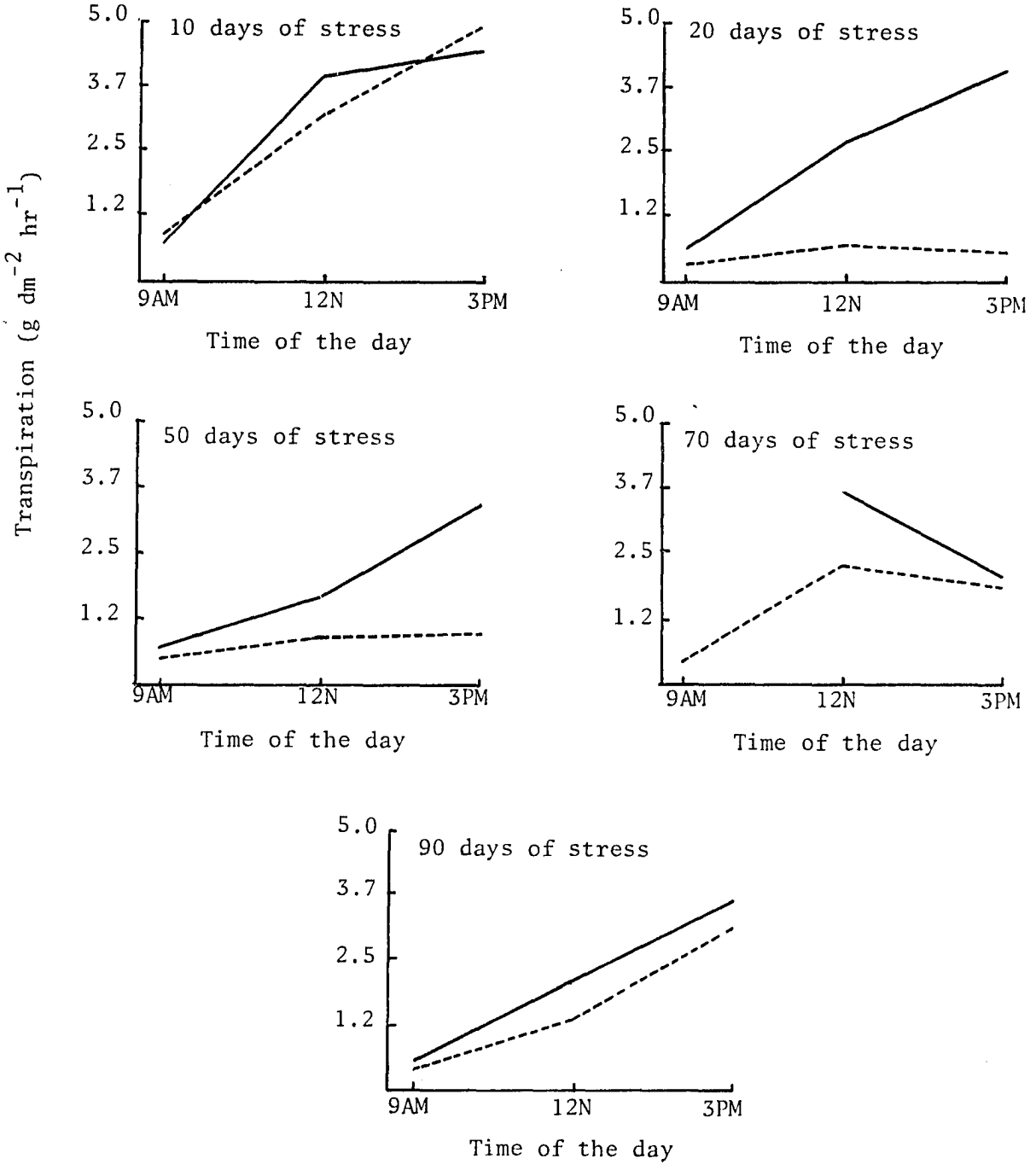

Figure 25. Daily patterns of transpiration in non-stressed (—) and stressed (--) plants of MCol 1684 at 3 and 6 months of age, Santander de Quilichao, 1982/83. -- The data for 9:00 AM after 70 days of stress was not taken.

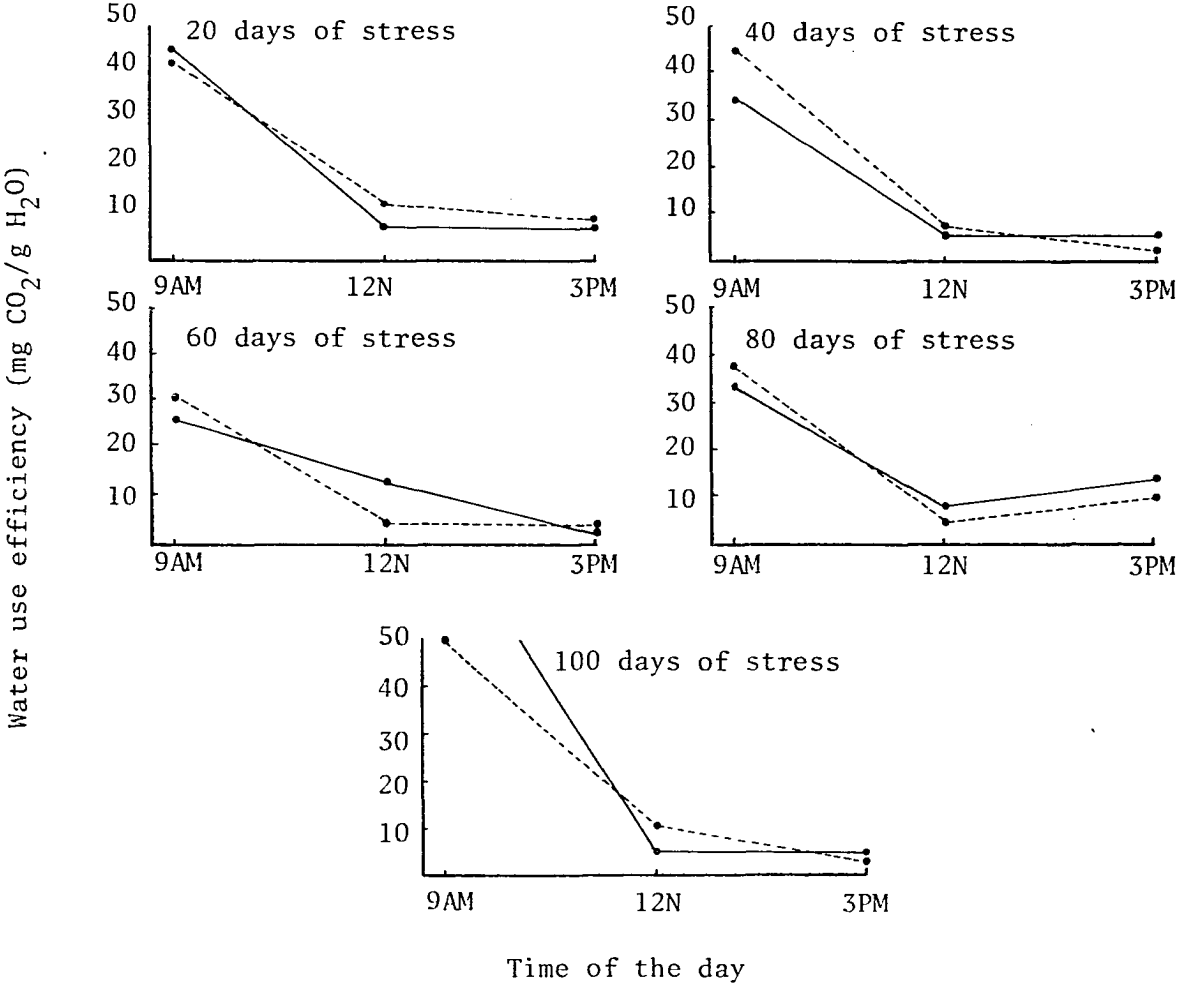

Figure 26. Water use efficiency of 3-month-old non-stressed (—) and stressed (--) plants of MCol 1684, Santander de Quilichao, 1982/83.

3.3 Experiment III: CIAT/Palmira

3.3.1 Growth and Yield

Since atmospheric humidity was effectively increased by misting (Fig. 27), it was possible to detect RM effects on growth of MCol 1684.

Plants examined before 40 days of misting showed no statistical treatment effects on dry weights of storage roots (Table 17), leaf area indexes (Fig. 29), and plant heights (Fig. 28). After 40 days, misted plants produced more biomass than control plants (Table 17). After 60 days of treatment, plants growing under normal conditions partially compensated the previously noted difference in storage root yields. This can only be explained by experimental error, since the coefficients of variation were higher than those calculated in the other three harvests.

The calculated values of Harvest Indexes (percent of the total dry matter represented by the roots) were slightly higher in plants growing under higher atmospheric humidity. This increase in harvest index is a consequence of higher root yields and lower leaf weights produced by the misted plants (Table 7).

Since no significant statistical differences were found between leaf area indexes of the misted and control plots (Fig. 29), dry weights of storage roots, leaves and stems, before 40 days of misting (Table 17), the increases in root yields after that period can be attributed to the beneficial effects of high humidity on photosynthesis.

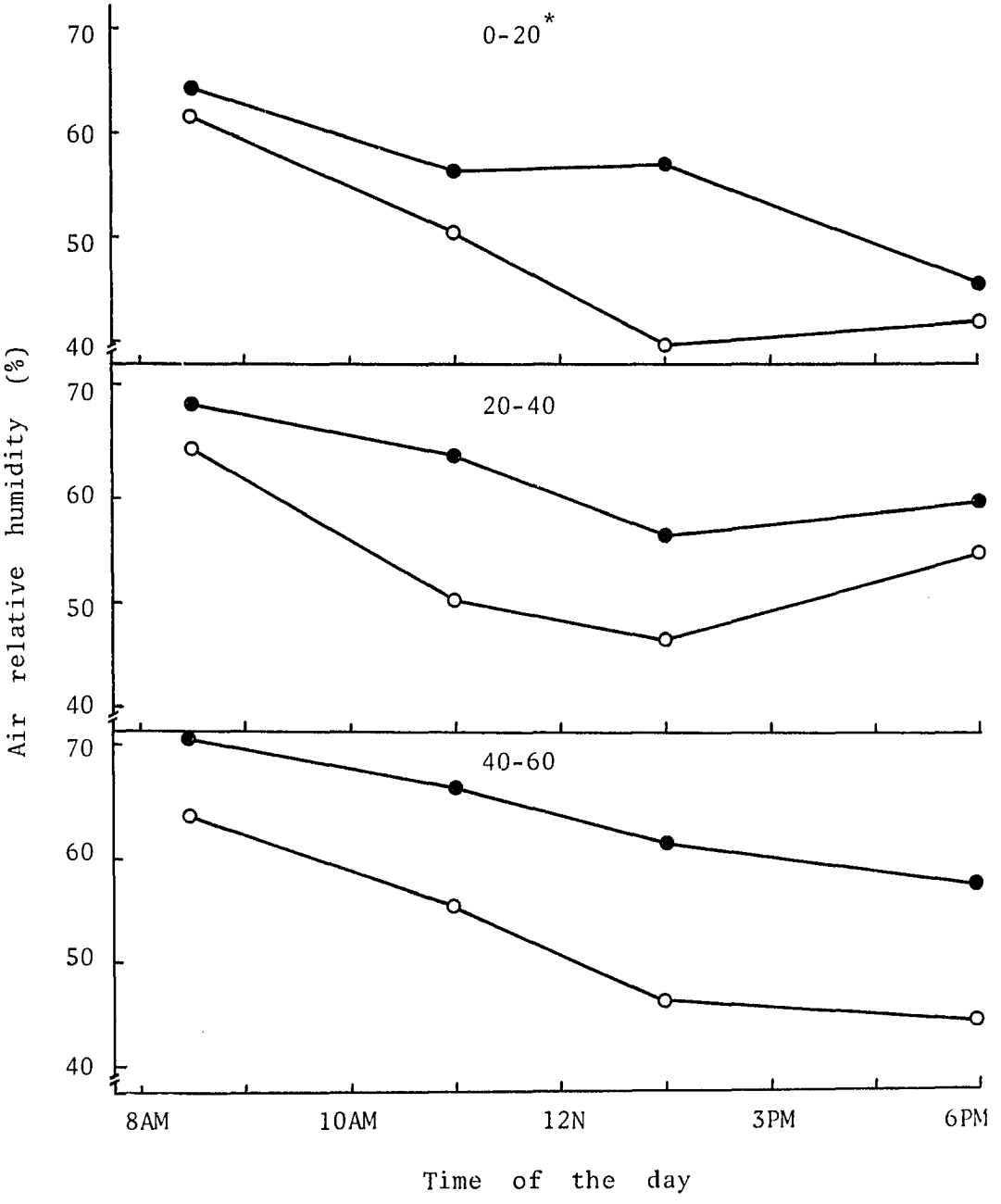

Figure 27. Atmospheric humidity in misted (o) and control (●) plots of MCol 1684, Palmira, 1982. -- Each point represents the average of measurements taken at the same time of the day in the given time intervals. * = Days of treatment.

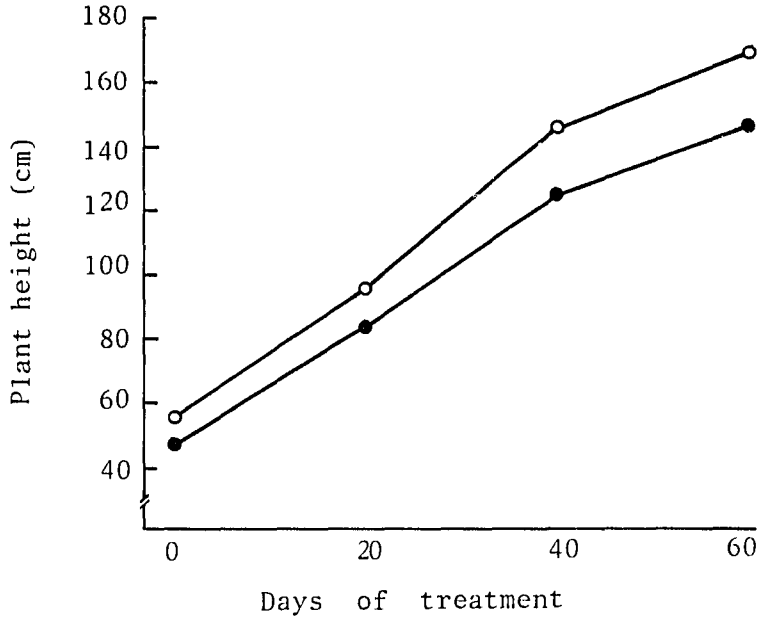

Figure 28. Plant size of misted (○) and control (●) plants of MCol 1684 subjected to two different regimes of air relative humidity, CIAT/Palmira, 1982.

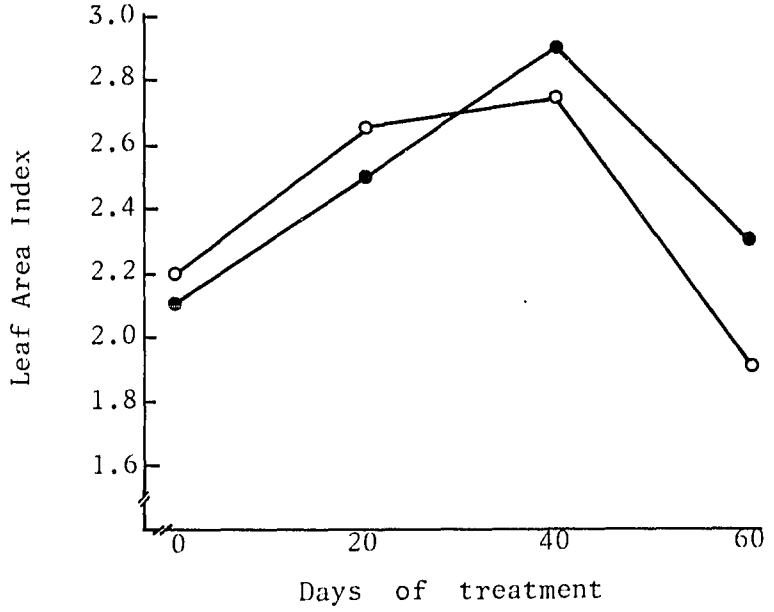

Figure 29. Leaf area indexes (LAI) of misted (○) and control (●) plants of MCol 1684 subjected to two different regimes of air relative humidity, CIAT/Palmira, 1982.

Table 17. Dry matter produced by plants of MCol 1684 growing under two regimes of relative humidity, CIAT/Palmira, 1982. -- Harvests were done after 0, 20, 40, and 60 days of treatment.

Days of Misting	Treatment	Dry Weights (kg/ha)		
		Roots	Tops	Total
0	High RH*	10	90	100
	Control	3	97	100
20	High RH	390	2210	2600
	Control	250	2350	2600
40	High RH	1130	3570	4700
	Control	590	3110	3700
60	High RH	1780	4170	5950
	Control	1010	4500	5510

* RH = Relative humidity.

3.3.2 Photosynthesis

Photosynthetic rates of plants growing under conditions of higher air humidity were higher than in plants growing under natural environmental conditions (Fig. 30). During the first two weeks of treatment the mean daily photosynthesis measured between 9:00 AM and 2:00 PM in the misted and control plots were approximately 28 and 25 mg CO_2 dm^{-2} hr^{-1}, respectively. The differences in photosynthetic rates between misted and control plants increased with time, reaching a maximum after 40 days of treatment. The decrease in photosynthesis observed after the first two weeks of treatment (Fig. 30) was probably due to changes in other environmental factors which were not studied. The important point to be emphasized is that photosynthesis, in plants of MCol 1684, was increased by an increase in atmospheric humidity.

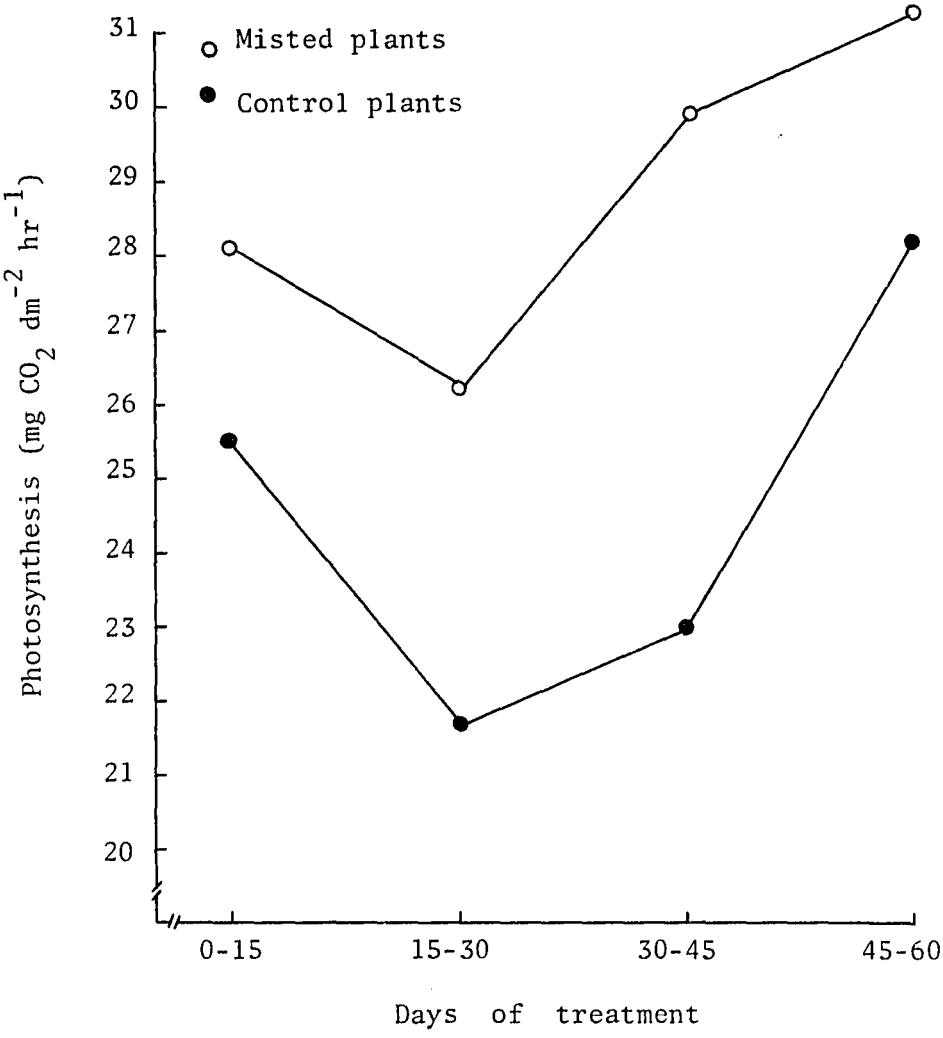

Figure 30. Photosynthesis in plants of MCol 1684 subjected to two different regimes of atmospheric humidity, CIAT/Palmira, 1982.

CHAPTER 4

DISCUSSION

4.1 Growth and Yield

The results obtained in Tucson and Santander de Quilichao support the hypothesis that cassava's growth is reduced [12, 38, 52], but not stopped [12] by water stress. Reductions in growth were more evident in those plants which were stressed earlier in their growth cycle. This agrees with data obtained by Oliveira, Macedo and Porto [52].

If growth is considered to be an irreversible increase in size and/or in weight [39], differences in growth were noticed between non-stressed and stressed plants. All four cultivars studied in Tucson showed reduced plant heights after 80 days of stress which began two months after planting (Fig. 5). When stress was imposed 3 months after planting, reductions in plant growth of MCol 1684 were evident. When stress was given or not after 6 months of development, no differences were found between stressed and non-stressed plants (Fig. 12). This age- dependent response to water stress can be explained by considering the growth patterns of the cassava plant. After six months of growth, cassava plants attain a maximal leaf area index (LAI) [61]. At that stage the storage roots receive most of the carbohydrates produced by the source organs.

In contrast, 3-month-old cassava plants are still undergoing top growth, and a water stress during this period will reduce top growth, leaf area and photosynthesis (Tables 9, 10 and 13).

If the overall growth process of a cassava plant is analyzed considering the aerial and the underground organs as two different sinks, top growth depends on three main components: (1) stem growth, (b) number of leaves per plant, and (3) size of the individual leaves. Stem growth was reduced by water stress initiated after 2 or 3 months of growth, but not when the stress period occurred after 6 months of plant development (Table 9). The number of leaves per plant depends on the rate of leaf formation and the rate of leaf fall. Both factors were affected by water stress in the experiments carried out in Tucson and Santander de Quilichao, the degree of the response being affected by age in which water stress was imposed and cultivar.

The observed changes in leaf formation and fall indicate that water stress imposed early in the growth cycle of MCol 1684 caused a reduction in LAI due to a slowing of stem growth, and a reduction in the number of new leaves formed during the stress period. Reductions in LAI were also evident in the 6-month-old plants. However, in this case it is difficult to remove the effect of plant age on leaf formation and fall, since LAI of non-stressed plants was also reduced with the advancement of the water stress period (Table 10).

The other component reported to play an important role in the adaptation of cassava to water stress is leaf size [11]. The experiment conducted in Tucson shows that leaf growth rates of the four cultivars were reduced by water stress. Eventually, final lengths of leaf

lobes were also reduced in leaves formed during the period of stress, with the exception of leaves of MVen 218 (Tables 1 and 2).

Plants of MCol 1684 stressed after 3 or 6 months of stress also reduced their leaf expansion rates progressively with the onset of a water stress situation (Figs. 13 and 14). However, the same response was not found in relation to the final leaf sizes of non-stressed and stressed plants (Fig. 15). There was no reduction in the final length of lobes formed, regardless of the water stress. This does not agree with the results obtained in Tucson for the three cultivars, and also with those reported by Connnor and Cock [11]. A reduction in leaf size with plant age was clearly evident in all groups of plants, confirming that in cassava, maximum leaf size is attained after four months of development [32, 60].

The behavior of MCol 1684 and MVen 218 might reflect a varietal characteristic. If leaf growth rates were reduced by water stress (Figs. 13 and 14), but not the final lengths of lobes formed (Fig. 15), the existence of a compensatory effect involving the period of active growth of the leaves is suggested. In order to maintan the same final length, even growing at lower rates, leaves of the stressed plants must grow for a longer time. Although leaf growth in cassava is reported to be completed after two weeks of leaf appearance [9, 11, 60], stressed plants of some cultivars may be exceptions.

The effects of water stress on total yields of plants growing in Tucson were evident for the four cultivars studied (Table 9). However, it is important to point out that top growth of the material studied in Tucson was luxuriant as a result of irrigation. This exces-

sive vegetative growth can be responsible for the low root yields obtained in both the irrigated and stressed plants (Table 3).

The effects of water stress on biomass production in MCol 1684 were more pronounced when the stress period occurred earlier in the plant growth cycle (Figs. 18 and 19). These results agree with Oliveira, Macedo and Porto [52], and shows that root yields of cassava are lower when the stress period occurs during the first stages of growth.

Reductions in cassava root yields are also reported by Connor, Cock and Parra [12]. However, a recovery phase with irrigation for 125 days following a 70-day water stress period caused an increase in root yields of MMex 59, which even surpassed yields obtained under conditions of no water stress. This can be be explained on the basis of water stress reducing the usually high LAI of the cultivar. With a lowered LAI the plant was able to divert more reserves to the storage roots.

Patterns of dry matter partitioning were altered by water stress and were dependent on the stage of plant growth in which the stress treatment was imposed (Figs. 20 and 21). When water stress was imposed on the older plants, their "optimal" LAI had been already reached [9]. The same cannot be said for those plants stressed after 3 months. These plants were supposed to be in a stage of high priority shoot growth [9, 60, 61]. As a consequence of the different growth patterns, the younger plants gave priority to top growth and reduced to a greater extent root growth rates (from 8.8 to 4.1 g of dry matter $plant^{-1}$ day^{-1} in non-stressed and stressed plants, respectively).

Plants stressed after 6 months of growth did not strongly reduce root growth rates (10.0 to 7.9 g DM plant^{-1} day^{-1}, for non-stressed and stressed plants, respectively). At that age, the plants had formed the required LAI for maximum growth, and were already directing most of the carbohydrates formed to the storage roots. This is confirmed by the findings that after 40 days of water stress there was practically no net accumulation of dry matter in the stems of the 6-month-old stressed plants, in contrast with those plants stressed after 3 months of the growth cycle (Table 9).

The data on photosynthesis reveal differences between stressed and non-stressed plants. Maximum photosynthetic rates obtained in the field (Table 13) are higher than those obtained by some authors [1, 45, 46, 47], and similar to rates reported by other authors [20, 21, 22, 23].

Photosynthesis in a plant community depends on the photosynthetic rates per unit of leaf area and the total photosynthesizing area represented by the number of functional leaves [59]. In the experiment carried out in Santander de Quilichão both photosynthetic rates and LAI were reduced by water stress in the two groups of plants (Tables 10 and 13). The effect of water stress on photosynthetic rates of the 3-month-old plants was more evident as the stress period progressed. After 70 days of treatment, photosynthetic rates of the non-stressed plants were reduced 50% when compared to rates measured in the non-stressed plants (Fig. 22).

Leaf area indexes of the 6-month-old plants were abruptly reduced from 5 to 2 from the twentieth to the fortieth days of stress

treatment (Table 10). Changes in LAIs of the younger plants were dependent on the stress treatment and were only noticed after 70 days of water stress, being closely associated with the lower rates of leaf formation in the 3-month-old plants, and with an increase in leaf fall in plants stressed later in their growth cycle. The abrupt decrease in LAI of 6-month-old plants after 20 days of stress was due to leaf abscission (Fig. 17).

4.2 Control of Water Loss

The control of water loss by transpiration in MCol 1684 was highly dependent on the environmental conditions. However, the stomatal mechanism seems to play the most important role in the control of water loss and drought tolerance in the cultivars studied. Leaf diffusive conductances decreased with water stress, especially when measured between midday and mid-afternoon. This parameter was increased by relative humidity, and this dependence was stronger in the stressed plants ($r = 0.81$). The negative correlation detected between leaf diffusive conductance and VPD was, on the other hand, more evident in the non-stressed plants ($r = 0.81$).

Data obtained by other workers [11, 20, 21, 22] show that VPD values higher than 20 mbars cause reductions in photosynthesis and transpiration of cassava plants, due to stomatal closure. Their data agree with the "feed-forward" response proposed by Cowan [14], and Cowan and Farquhar [15]. If VPD values are dependent on relative humidity, why, then, the different types of responses observed in those plants which were stressed or not in the present experiment?

The answer for the question asked above can be based on the fact that non-stressed plants are more dependent on VPD, simply because transpiration rates in those plants ae also higher (Table 15). This results in the development of high VPDs during the course of the day. By differences in absolute values, leaf diffusive conductances of the non-stressed plants were closely correlated with VPD. Conductances measured in the stressed plants were closely correlated with atmospheric humidity due to the lower absolute values of conductance.

The data on photosynthesis and transpiration indicate that changes in leaf conductance/resistance to water loss and CO_2 exchange are reflected in photosynthetic rates [3, 4]. Photosynthesis was positively correlated with leaf diffusive conductance, especially when measured at midday/mid-afternoon, and in those plants suffering water stress (Table 13). The same tendency was observed when photosynthesis was correlated with transpiration. This is logical, since photosynthesis and transpiration are both dependent on stomatal aperture [5, 16, 19, 26, 30, 34, 37, 48, 50, 54, 55, 57, 59, 62, 63].

The data obtained in Experiment III (misting experiment) show that photosynthesis in MCol 1684 was increased by high relative humidity (Table 17). This result suggests that an increase in the moisture of the air has the effect of reducing the vapor pressure deficit between the leaf and the bulk air outside [5, 14, 15], what implies in stomatal opening and higher flow of CO_2 from the external air to the photosynthetic site.

More important, however, is that cassava root yields were also increased by the high relative humidity (Table 16). This suggests a

direct effect of photosynthesis on economical yield.

The other measured parameter that is broadly used as an indicator of the plant water status is the leaf water potential [5, 30, 31, 34, 41, 51, 62]. In the experiment conducted in Tucson, in a site characterized by conditions of low relative humidity and high air temperatures, leaf water potentials of stressed plants tended to be more negative than values measured in non-stressed plants (Fig. 8). Cultivar MVen 218 appears to be more efficient in controlling the lowering of $_{L}$ when under water stress, since the differences between non-stressed and stressed plants are minimal.

However, in the experiment conducted in Santander de Quilichao, leaf water potentials of the non-stressed plants were almost invariably lower than those of stressed plants, after aproximately 40 days of the initiation of the water exclusion period (Table 11). This tendency was particularly evident for measurements taken between 9:00 AM and 3:00 PM, when values of relative humidity and air temperatures were higher.

The lack of significant correlations between leaf water potential and leaf diffusive conductance, transpiration and photosynthesis (except for measurements taken at 9:00 AM in 3-month-old stressed plants, in the case of photosynthesis x leaf water potential), suggest that this parameter is not precise enough for describing a situation of water stress in cassava plants. This agrees with the data and comments of Connor and Palta [13].

What appears to occur is that, although conductance, transpiration and photosynthesis are dependent of environmental factors

(especially relative humidity) [5, 57], leaf water potential is not affected by changes in VPD or relative humidity. This is suggested by the work of El-Sharkawy, Cock and Held [22].

The decrease in leaf water potentials of non-stressed cassava plants between midday and mid-afternoon (Fig. 23) was not the key factor in relation to the adaptation of cultivar MCol 1684 to a situation of water stress. The important factor was the lack of a similar decrease in the stressed plants. By closing stomata (as is suggested by the data on leaf resistance/conductance), the plants avoided further water loss and maintained a reasonable water status when growing under conditions of low water. This phenomena can be the "hardening" acquired by a long-term situation of water stress referred to by Cutler and Rains [17], and suggested by Bradford and Hsiao [5]. According to these authors, plants subjected to water stress during development have a lessened sensitivity to water stress.

In the present study, it was evident that the stomatal mechanism plays perhaps the most important role in controlling water loss of stressed cassava plants. This was suggested by the study conducted by Connor and Palta [13], which showed that leaf diffusive conductances were greatly reduced by water stress. Furthermore, increases in the stomatal density and respective decreases in the size of the stomatal pore were reported to occur when the plants were under stress [13].

The effect of water stress on photosynthesis and transpiration (Table 13, Fig. 25) confirms the hypothesis that stomatal mechanism is important in reducing water loss in cassava.

An important parameter in studies of water stress, closely associated with the process of transpiration, is leaf temperature [27]. Leaf temperature depends also on environmental factors such as incident radiation, air humiity and air temperature [19, 27, 42]. The process of transpirational cooling contributes to maintain leaf temperature below a limit which can cause severe damage to the internal structure of the leaf [27].

In the experiment conducted in Santander de Quilichao there was a well defined tendency of leaf temperatures of the stressed plants to be lower than those of the non-stressed ones, especially at mid-day/ mid-afternoon (Fig. 24). These data apparently disagree with the existing reports [5, 19, 27, 42, 57] since in the same experiment transpiration was lower in the stressed plants (Fig. 26).

In the particular case of the stressed plants of MCol 1684, another factor appears to be playing an important role in the control of water loss. As reported by El-Sharkawy and Cock [20], leaf movements in response to light are very drastic in cassava. Stressed plants have the ability to change the orientation of their leaves in relation to the sun in order to avoid excessive values of leaf temperature. The experiment in Santander de Quilichao did not take into consideration measurements of leaf orientation and reflectance, but recent data obtained by Delgado (pers. comm.) show that reflectance is highly increased in stressed cassava plants. An increase in reflectance clearly suggests that leaf temperatures are being controlled [19, 27, 42], even if the rates of transpiration are low.

CHAPTER 5

CONCLUSIONS

Based on the results obtained in the experiments carried out in the three different sites, it is possible to conclude that:

1. Water stress periods of 80-100 days reduced yields of all five cultivars studied. Reductions were higher when the stress treatment was imposed after 2 months of growth in Tucson and in 3-month-old plants of MCol 1684 in Santander de Quilichao. Decreases in yield were lower when stress was imposed in 6-month-old plants of MCol 1684.
2. Dry matter partitioning of plants of MCol 1684 stressed after 3 months of age was altered when compared with the non-stressed plants of the same age. In this case, allocation of carbohydrates to the storage roots was reduced. No significant changes in the pattern of dry matter partitioning were observed when the water stress period started at 6 months of growth.
3. Plants of MCol 1684, when stressed, tended to reduce their total leaf area (LAI). This was achieved by reducing leaf expansion, plant growth and the rate of leaf formation in those plants stressed after 3 months of growth. Plants stressed at 6 months of age reduced LAI by also changing the leaf expansion rates and by increasing the rate of leaf fall.

4. Reductions in yields of MCol 1684 stressed after 3 or 6 months of growth can also be dependent on photosynthesis, since the photosynthetic rates were reduced by water stress. This is suggested since photosynthesis was increased by higher atmospheric humidity in Palmira, with a positive effect on root yields of the same cultivar.
5. Plants started showing modifications in their growth processes after approximately 40 days of water stress in Santander de Quilichao.
6. Stomatal mechanism of cultivar MCol 1684 is sensitive to water stress. This is proved by the fact that leaf diffusive conductances, transpiration and photosynthesis were reduced in the stressed plants of both ages.
7. The air relative humidity plays an important role in the mechanisms of responses to water stress adopted by cultivar MCol 1684. That strong influence was observed in the increases in photosynthetic rates observed by the misting treatment in Palmira, and also by the correlations found between relative humidity, photosynthesis, transpiration and conductance in Santander de Quilichao.
8. A kind of "hardening" seems to occur in cassava, at least in relation to the control of water loss. Stressed plants were capable of limiting severe reductions in leaf water potentials in order to save water. The same phenomenon did not occur in the non-stressed plants. This is the reason for the lower

values of water potential noticed in the non-stressed plants in hours of high evaporative demand.

9. The dependence of leaf temperature on transpiration was altered in stressed plants of MCol 1684. As reported, transpiration exerts a cooling effect and contributes to the reduction of leaf temperatures of most plants. In this study, leaf temperatures of stressed plants were lower than in the non-stressed plants when the measurements were taken between 9:00 AM and 3:00 PM. This phenomenon is explained by changes in leaf orientation in order to avoid the heating effect of direct sunlight and reducing the amount of energy absorbed.

10. Studies involving water stress should be continued in Arizona, in order to analyze the real possibilities of extensively using the crop as a source of carbohydrates and/or protein. These suggested studies must focus the analysis of the growth patterns of the plants when subjected to several regimes of water availability. The next step would be the introduction of a large number of cultivars for selection of drought-resistant plants.

APPENDIX A

Table A-1. Climatological summary for Campbell Avenue Farm, Tucson. -- Means for the period 194911970; Latitude: 32°17'; Longitude: 110°57'; Elevation: 73m.

Month	Temperature (°C)			Precipitation (mm)	Mean Relative Humidity	
	Daily Maximum	Daily Minimum	Daily Average		6:00 AM	6:00 PM
January	19.2	0.2	9.7	22.6	61	41
February	20.8	1.3	11.0	18.3	50	36
March	23.4	3.4	13.4	19.3	47	29
April	28.3	6.9	17.6	11.4	39	22
Mau	33.0	10.7	21.8	2.8	29	16
June	37.7	16.0	26.9	7.4	29	18
July	37.9	21.4	29.7	62.7	46	31
August	36.9	17.4	28.5	52.3	59	36
Setember	35.8	16.6	26.3	25.6	54	32
October	24.2	9.9	20.4	15.5	48	33
November	30.8	3.9	14.0	15.2	48	37
December	19.8	0.5	10.2	2.9	61	47
Year	29.6	9.3	19.2	282.7	48	32

Table A-2. Climatic data during the experimental period, Tucson 1981.

Month	Temperature (°C)			Precipitation (mm)
	Maximum	Minimum	Average	
May	32.5	13.7	23.1	17.5
June	38.8	20.5	29.6	5.6
July	37.4	22.2	29.8	69.0
August	38.1	23.2	30.6	29.7
September	35.9	18.6	27.2	9.1
October	29.0	10.1	19.5	0.7
November	26.4	5.2	15.8	21.1

Table A-3. Soil characteristics and chemical analysis, Tucson, 1981. -- Type: Gila very fine sandy loam; Classification, Soil Conservation Service: 6J.

Depth (cm)	pH	ECE $x10^3$	Soluble Salts (ppm)	Na me/L	K me/L	Esp	N ppm	P ppm
0.30	7.15	2.72	1907	2.57	3.75	-0.05	103.3	93.7
30-60	7.10	9.94	6958	5.94	11.84	0.12	279.0	81.3

Table A-4. Climatological summary for Santander de Quilichao. -- Means for period 1972-1981: Latitude: 3°06'N; Longitude: 76°31'W; Elevation: 990m.

Month	Temperature (°C)			Precipitation (mm)	Relative Humidity (%)	Evaporation (mm)
	Daily Maximum	Daily Minimum	Daily Average			
January	29.8	18.2	23.6	114.0	74	142.1
February	30.2	18.6	24.0	149.9	74	134.4
March	30.0	18.8	23.9	155.0	76	140.1
April	29.4	18.8	24.0	190.0	76	128.8
May	28.9	18.8	23.7	179.9	76	117.8
June	29.0	18.5	23.8	99.0	75	113.5
July	30.2	17.7	24.1	59.3	71	146.6
August	30.5	17.6	24.2	73.3	68	155.4
September	29.9	17.7	23.9	140.1	70	143.3
October	28.9	18.3	23.2	227.7	74	128.1
November	28.3	18.6	23.2	230.9	76	122.2
December	28.6	18.4	23.4	154.8	75	123.3
Year	29.5	18.3	23.8	1773.9	74	1595.4

* Precipitation: 1976-1981.

Table A-5. Climatic data for the experimental period, Santander de Quilichao, 1982/83.

Months	Average Daily Temperature	Relative Humidity	Precipitation (mm)	Evaporation (mm)
June	24.8	70	82.0	129.1
July	24.3	66	56.7	139.6
August	25.4	58	00.0	183.9
September	24.5	65	149.6	147.9
October	23.3	74	250.7	125.8
November	23.5	75	296.5	129.6
December	24.0	74	202.8	126.6
January	25.0	70	59.7	149.8
February	25.4	67	28.4	150.0
March			176.0	

Table A-6. Soil characteristics and chemical composition, Santander de Quilichao, 1982/83. -- (a) Soil characteristics (Classification: Ultisol (Orthoxic Palehumult, clayey, kaolinitic, isohyperthermic); (b) Soil analysis for each treatment.

a.

Horizon (cm)	Clay (%)	Sand (%)	pH (H_2O)	Org. C. (%)	ECEC	Al	Al (satn. %)
0-20	71	4	4.1	4.1	4.2	2.7	64
20-35	77	5	4.0	2.3	3.2	2.7	83
35-62	64	2	4.3	1.1	3.6	3.2	88
62-91	88	1	4.4	0.4	1.4	1.1	77
91-151	90	1	4.4	0.3	2.3	2.0	85

b.

Age at Stress Initiation	Treatment	%							
		N	P	K	Ca	Mg	Mn	Zn	B
3 Months	NS	4.46	0.24	1.66	1.35	0.33	845	39.0	10.3
	S	4.81	0.24	1.45	1.11	0.29	558	54.9	28.3
6 Months	NS	4.17	0.24	1.50	1.41	0.27	731	30.7	7.0
	S	3.64	0.20	1.25	1.32	0.27	744	38.9	5.3

Table A-7. Climatological summary for CIAT/Palmira. -- Means for the period 1931-1980: Latitude: 3°30'N; Longitude: 76°22'W; Elevation: 965m.

Month	Temperature (°C)			Precipitation (mm)	Relative Humidity (%)	Evaporation (mm)	Illumination $Kcal_{-1} cm^{-2}$ mo.
	Maximum	Minimum	Average				
January	30.1	18.1	23.5	69.0	71	143.2	12.6
February	30.4	18.3	23.8	63.0	70	136.4	13.9
March	30.3	18.5	23.8	90.8	71	145.9	15.7
April	29.5	18.6	23.5	140.3	74	126.8	14.6
May	29.1	18.5	23.2	124.1	76	122.1	14.0
June	29.2	18.1	23.1	69.1	74	114.5	13.0
July	30.0	17.6	23.4	28.5	70	135.1	14.4
August	30.4	17.8	23.6	38.6	68	143.8	14.4
September	30.2	17.9	23.5	63.8	69	138.4	14.7
October	29.2	18.1	23.0	148.3	74	135.8	15.0
November	28.9	18.2	22.9	104.4	75	116.6	13.2
December	29.4	18.1	23.2	78.4	74	130.0	13.5
Year	29.7	18.2	23.4	1023.6	72	1588.7	14.3

Table A-8. Climatic data for the experimental period, CIAT/Palmira, 1982.

Month	Average Daily Temperature (°C)	Relative Humidity (%)	Precipitation (mm)	Solar Radiation kcal cm^2 mol
May	23.3	79	137.5	12.6
June	23.5	78	38.9	11.4
July	23.8	71	14.8	14.1
August	23.8	72	45.7	12.9
September	24.1	69	17.2	12.3

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