EFFECTS OF SOIL WATER DEFICITS ON CARBON PARTITIONING IN SUGARBEET(BETA VULGARIS L.)AND COWPEA(VIGNA UNGUICULATA L.WALP.):EXPERIMENTS AND COMPUTER SIMULATIONS

RICARDO FERRAZ DE OLIVEIRA, TEXAS A. e M. UNIVERSITY
COLLEGE STATION, TEXAS, USA.

ABSTRACT - Partitioning was defined here as the rate of carbon allocation among plant organs, such as leaf, petiole, stem and root. The measurement of partitioning in plants is important because partitioning causes expansion of leaf area, improves canopy light interception, causes expansion of the root system, increases the plant yield and affects the quantity and quality of economic yield. There is a lack of information on carbon partitioning within the plant under controlled environmental conditions. A new approach was used to measure carbon partitioning within the plant. The measurement of carbon partitioning within the plant consisted of a combination of two methods: dry weight and gas exchange.

Sugarbeet(Beta vulgaris L.) and cowpea(Vigna unguiculata L. Walp.) plants were grown in assimilation chambers at $30^{o}C$, a photosynthetic photon flux density of 1000 $\mu E.m^{-2}.s^{-1}$ and a concentration of carbon dioxide of approximately 0.54 g $CO_2.m^{-3}$. The dewpoint temperature was $23^{o}C$, the daylength 12 hours and the windspeed 1.2 $m.s^{-1}$. The daily experimental measurements started when plants reached exactly 0.05 m^2 of leaf area. Water deficit treatments for sugarbeet and cowpea were 0,3,5,8,11 and 0,3,5,8,11 and 17 days, respectively. Two treatments of 3 and 5 days were also carried out under well watered conditions.

On a given day, the carbon partitioning factors for leaves, petioles, stem and roots were calculated as the ratio between the carbon gain in the organ and the photosynthetic input into the whole plant. The carbon gain was calculated from dry weight measurements, by subtracting the mass of carbon obtained in one treatment from the mass of carbon obtained in the previous treatment and dividing by the time interval treatments. The photosynthetic input was calculated from gas exchange measurements. Experimental results were compared with output of a whole plant simulation model(McStress).

Experimental results were variable because of the insufficient number of plants to keep the coefficient of variation below 10%(Figures 1 and 2). The difficulty of measuring very small amounts of carbon in each organ, added to the difficulty in measuring experimentally the carbon allocated to

the storage pool, contributed to a complicated interpretation of the experimental results.

The use of McStress helped to clarify the mechanisms involved in the partitioning of carbon between organs and storage pool. This made an interpretation of the results possible. According to the simulations, during the soil water deficit, sugarbeet invested the majority of the carbon available for root growth into the coarse root(main root axes)biomass. At the beginning of the deficit cycle, 29% of the carbon available for sugarbeet root growth was patitioned to coarse roots in comparison with 65% at the end of the deficit cycle(Figure 3). Cowpea showed an opposite trend(Figure 4). Only 25% of the carbon available for root growth was invested into coarse roots and the remaining invested in the expansion of the fine roots. This indicates that cowpea possess a morphological root development that is better suited to soil water deficit conditions than sugarbeet.

INTRODUCTION - Soil water deficit is probably the most inhinbitory factor of the environment encountered by the plant during its life cycle. Water stress has been major selective force in plant evolution, and the ability to cope with water deficits is an important determinant of plant productivity. Accordingly, an understanding of the mechanisms that confer drought tolerance or avoidance holds much theoretical and practical value.

Whenever the water loss through stomata is greater than the water absorbed by root system of the plant, a water deficit develops in the plant. In order for growth to occur in that situation, a variety of morphological, anatomical, biochemical and physiological mechanisms are brought into play to reduce further water loss. Among these mechanisms are stomatal closure, wax deposition of leaf surfaces, rolling the leaves, reducing transpiration of one surface of the leaf, change in leaf angle(decreasing the amount of radiation received), an increase in water uptake by the development of deeper roots into the wet profile of the soil, early leaf senescence, accumulation of active solutes inside the plant cells, alteration in carbon allocation among plant organs, presence of hairs on the leaf surface(especially around stomata), pubescence leading to increased reflection of light, the storage of water in bulbs or tubers, pattern of carbon patitioning between coarse and fine roots and many others(Levitt 1980).

The primary effect of a soil water deficit is a loss of turgor that affects the rate of cell expansion and ultimate cell size. Loss of turgor pressure inside the cells is the most sensitive response to soil water deficit

because turgor pressure is necessary to force expansion. The result is a decrease of growth rate, stem elongation, leaf expansion, and stomatal aperture(Kramer 1983).

Loss of water from a cell decreases its turgor and its water potential: a decrease in turgor results in wilting; wilting results in decrease interception of photosynthetically active radiation with in turn results in decreased dry matter accumulation and ultimately a reduction in plant productivity. The degree to wich each is affected is difficult to measure because they are for the most part related and the final responce of a plant to a soil water deficit is the result of different combinations of these above responses at various intensities. The interaction of these mechanisms, at various intensities of soil water deficit makes a quantitative analysis difficult.

Classical plant physiology explores the mechanistic bases of plant function by seeking to isolate and to study each of these mechanisms under the influence of the external environment. A quantitative integration of those process into an explanation of the whole system behavior remains a task for integrative physiology.

Mathematical modeling of biological systems is a new approach to obtain improved understanding of complex biological systems. Models consist of a set of mathematical equations that represent a particular physiological mechanism. McCree and Fernandez (1989) have developed a mechanistic model (McStress) to study the contribution of individual mechanisms to the final plant responses and to obtain an integrative understanding of physiological mechanisms involved during a single soil water deficit cycle in a contrelled environment.

Soil water deficits not only reduce dry matter production of plants, but also change the partitioning of carbon among organs. Partitioning of carbohydrates among the various organs of plants affects bth their survival and their economic value. Soil water deficits change to pattern of partitioning of photosynthate at he expense fo the quality and quantity of economic yield. Given the importance of assimimate partitioning among plant parts in determining yield, a pertinent questions is how the distribution of assimilates may be affected by water stress. For example, if soil water deficits inhibit shoot growth more than phosynthesis, this should allow a surplus of carbohydrates to be available for root growth via altered source-sink ralationships for assimilates.

A pattern of carbon partitioning between coarse and fine roots is an example of plant species with different strategy to face soil water deficit. Morphological changes such as decreased root hair initiation and decreased initiation of lateral roots in sugarbeet plants can contribute to the decreased ability of the plant to absorb water. A preferential partitioning of photosynthetic assimilates to fine roots would contribute to an increase ability of the plant to absorb(Krizek et al., 1985). Cowpea plants were found to have a root mophological development that was better suited to dry environments because of a greater allocation of carbon to the expansion offine rrots.

Two plant species were used in this study: sugarbeet(Beta vulgaris L.) and cowpea(Vigna unguiculata L. Walp.). These two plant species are known for having different and well defined responses to soil water deficit(McCree and Richardson 1987).

Sugarbeets have the ability to osmotically adjust by accumulating active solutes inside the cell. This lowers the wather potential of the sugarbeet leaves and keeps their stomata open for a longer period or time and also to a lower soil water content. The leaf water potential in sugarbeet plants continues to fall throughout the soil water deficit cycle, indicating a minimum amount of stomatal closure.

Cowpea are more sensitive to soil water deficit. In this species, earlier stomatal closure is observed. As a result of this early stomatal closure, the water potential inside the leaf cells is kept high, preventing further water loss, but at the same time restricting carbon uptake. For a given leaf water potential, the water loss is much lower in cowpea than in sugarbeet.

Because sugarbeets keep their stomata open at lower leaf water potential, it would be expected that sugarbeets should heve a higher carbon uptake than cowpeas during periods of severe soil water deficit and, if leaf growth is equally inhibited, a higher root: shoot ratio.

Although a great deal of information about gas exchange for these two species is available, very little is known about the partitioning of assimimates during soil water deficits under controlled environmental conditions. Therefore, the objective of this work was to generate data on carbon partitioning for sugarbeet and cowpea plants exposed to soil water deficits. This was done by using a new approach to estimate the carbon partitioning factors plant organs(in this case, leaves, petioles, stem and roots). A second objective was to test the accuracy of McStress in simulating carbon partitioning. This was done by extrapolating the experimental

data collected into an integrative context with the use of the model.

MATERIAL AND METHODS - Summary of Experimental Desing

In carbon balance dtudies, it is essencial that the environmental conditions affecting photosynthesis and respiration be under the control of the investigator, otherwise a precise interpretation of the data would be difficult(McCree 1986 a, Tibbitts and Krizek 1978). Because this study dealt with carbon partitioning within the plant during a single water deficit cycle, a great deal of time was spent to ensure that the environmental conditions during gas exchange measurements were kept constant, so that any changes in carbon partitioning during the deficit cycle could be atributed to changes in the soil water content.

Sugarbeet and cowpea plants were growth room in the Soil and Crop Sciences Departament at Texas A&M University. The growth room was used to assure uniform environmental conditions during plant development over sucessive replications. After a period necessary for both plants species to reach exactly 0.05 m^2 of leaf area, they were moved to assimilation chambers where the environmental conditions were similar to those in the growth room in which the test individuals were grown. Two assimilation chambers built by Fernandez (1977), were used. The assimilation chambers were designed to contain the whole plant including its entire root system. This is a requirement for carbon balance studies because photosynthate that is generated in the leaves is translocated to all the growing parts of the plant and used for the creation of new biomass(McCree 1986 a.).

Water deficit treatments for cowpea and sugarbeet were 0,3,5,8,11 and 17 days, and 0,3,5,8 and 11 days without irrigation, respectively. These treatments were chosen because McCree and Richardson (1987) showed that critical changes related to soil water deficit seemed to occur at these points. Two replicates of each treatment were carried out simultaneously using two assimilation chambers.

Two treatments(treatment 3 and treatment 5) were also carried outunder well watered conditions. It was not possible to grow plants under well watered conditions for a longer period of time because the internal area of the assimilation chamber was not large enough to support further growth. After 5 days under well watered conditions, the plants were larger than any stressed plant. By doing this, it was possible to compare well watered treatments with water deficit treatments and thus to study the effects of water deficit on carbon partitioning throughout the different plant organs.

The best plants and assimilation chambers for each treatment were selected at random. Daily measurements of water exchange rates(WER) and carbon exchange rates(CER) were measured for each treatment.

A new approach consisting of a combination of two different methods was used to calculate the carbon partitioning factors for plant organs of these two species during a single soil water deficit cycle under controlled environmental conditions.

On a given day, the carbon partitioning factors for leaves, petioles, stem and roots were calculated as the ratio between the carbon gain into the organ and the photosynthetic input into the whole plant. The carbon gain was calculated grom dry weight measurements by subtracting the mass of carbon obtained in one treatment from the mass of carbon obtained in the previous treatment and dividing by the time interval between intervals. Experimental results were compared with output of a whole plant simulation model developed by McCree and Fernandez(1989).

In order to measure the carbon partitioning factors under soil water deficit conditions and in controlled environmental conditions, it was necessary to determine the carbon content in each organ every day and the soil water status in the pot every day. Many environmental and plant measurements were taken. This includes the measurement of PPFD, temperature, CO_2 concentration, water vapor concentration, air flow and windspeed in the growing area of the assimilation chambers. For the measurement of carbon content in each organ, the list of measurements includes plant selection, plant establishment, nutrient solution and leaf area measurements. It also includes the determination of carbon in each organ, daily carbon gain, daily photosynthetic input and starch content for storage analysis.

RESULTS AND DISCUSSION

This section is divided into three main parts: sugarbeet results, cowpea results and a comparative interpretation of the experimental data using the simulation model McStress.

Since the objective of this work was to generate data on carbon partitioning for sugarbeet and cowpea under soil water deficit conditions, the following were measured experimentally: the carbon in each organ every day, the daily carbon gain, and the daily photosynthetic input. With estimates of these three variables, it was possible to calculate the carbon partitioning factors for all organs of both species. All the next steps were necessary to obtain the carbon partitioning factors for every plant organ from the dry

weight measurements.

DRY WEIGHT MEASUREMENTS

After the appropriate period of time inside the assimilation chamber, the plants of each treatment were harvested and dried at 75°C for 48 hours.

PERCENTAGE OF TOTAL CARBON CONTENT

Two dry plant samples, a well watered(treatment 0) and stressed (treatment 11), were used to calculate the percentage of total carbon content presented in the dry matter throughout the plant organs. Since no significant difference was found between the well watered plant and the stressed plant, and between the different plant organs within the same plant, an average number of 0.39 gram of C per gram of dry matter was assumed in calculations of carbon partitioning among the plant organs. Therefore, the percentage of total carbon content in the plant tissue was calculated by multiplying the dry weight of each organ by 39, according to the following equation:

$$\%C = \text{Dry Weight(g)} * 0.39(\text{gC/gDry weight}) * 100$$

CARBON GAIN

With the carbon content in each organ measured, the carbon gain in ($mgC.plant\ organ^{-1}.day^{-1}$), was calculated by subtracting the mass of carbon obtained in one treatment from the mass of carbon obtained in the previous treatment and dividing by the time interval according to the following equation:

$$\text{Carbon Gain} = \{C \text{ in organ at day}(n) - C \text{ in organ at day}(n-x)\}/x$$

where x is the time interval between the treatments.

PHOTOSYNTHETIC INPUT

The daily photosynthetic input(ΔS) in($mgC.plant^{-1}.day^{-1}$) was calculated from the carbon exchange method obtained and registered by the computer(Table) and calculated according to the following equation:

$$\text{Photosynthetic Input} = \{\text{Input}(n) + \text{Input}(n-1) + \ldots + \text{Input}(n-x)\}/x$$

CARBON PARTITIONING FACTORS

The carbon partitioning factors were obtained from experimental measurements by dividing the carbon gain by the photosynthetic input. The carbon partitioning factors were variable throughout the soil water deficit (Figures 1 and 2).

MODELING

In this section of modeling a fitting of the simulation model to experimental data is provided to demonstrate how the model simulates plant responses during a single soil water deficit cycle(Figure 5). This was done by varying one parameter at the time. For instance, to match the carbon use efficiency, the synthesis efficiency and maintenance coefficient were varied. To match the water loss and water use efficency, the stomatal sensitivity of stomata to soil water deficits was varied. To match the leaf area, the soil water limits for leaf inhibition were varied. A great deal of time was spent to match the experimental data with the outputs of the model. The exercise of fitting the model to the experimental data in itself is a useful exercise which contribute for a better understanding of the plant behavior.

McStress has three main set of inputs that can be manipulated by the user(Table 1).

TABLE 1 INPUTS OF McSTRESS

USER INPUTS 1	
Air temperature	10 to 40°C
Dewpoint Temperature	10 to 39.9°C
PPFD	0 to 2.0 $mE.s^{-2}.s^{-1}$
Maximum possible photosynthesis	0.1 to 0.6 $mgCO_2.m^{-2}.s^{-1}$
Internal CO_2 at half maximum rate	0.01 to 0.1 $gCO_2.m^{-3}$
PPFD at halg maximum rate	0.1 to 1.0 $mE.m^{-2}.s^{-1}$
Root volume per unit mass of roots	1.0 to 20.0 $liters.gC^{-1}$
Leaf area per unit mass of leaves	0.1 to 20.0 $gC.m^{-2}$
Synthesis efficiency	0.6 to 0.8 $gC.gC^{-1}$
Maintenance coefficient	10 to 100 $mgC.gC^{-1}.day^{-1}$
Number of plants per unit ground area	15 to 25 $plants.m^{-2}$
Number of leaves per plant	1 to 100
USER INPUTS 2: DAILY ALLOCATION OF CARBON(1 - 100%)	
Leaf fraction: new, old	1 to 100%
Petiole fraction: new, old	1 to 100%
Stem fraction	1 to 100%
Root fraction: new, old	1 to 100%
Stored C fraction	1 to 100%
Leaves	1 to 100%
Petioles	1 to 100%
Stem	1 to 100%
Roots	1 to 100%
Storage	1 to 100%
Initial Leaf Area	0.05 m^{-2}
Total gC/plant	1.50 to 2.10 gC.plant

Continuation Table 1

USER INPUTS 3: STRESS FACTORS	
Maximum conductance water vapor	0 to 50%
Soil water limits stomatal closure	10 to 50%
Maximum stomatal inhibition	1.0 to 99%
Soil water limits for leaf inhibition	10 to 50%
Maximum leaf inhibition	1.0 to 99%
Soil water limits for senescence	10 to 50%
Maximum senescence	1.0 to 99%
Biomass senescence factor	0 to 0.5%
Senescence respiration factor	0 to 0.5%
Soil water limits for irrigation	0 to 40%

For sugarbeet, when the match was obtained, the initial carbon partitioning factors for leaves, petioles, stem, roots and storage were 0.50, 0.18, 0.03, 0.28 and 0.01 respectively against 0.42, 0.18, 0.05 and 0.18 measured experimentally. Once again the carbon partitioned to the storage pool was not measured experimentally. For cowpea, they were 0.47, 0.07, 0.12, 0.28 and 0.06 against 0.33, 0.06, 0.04 and 0.19 measured experimentally(Figures 6 and 7).

SUMMARY AND CONCLUSIONS

According to the data reported here, the differences between sugarbeet and cowpea appeared to result from a combination of interacting factors, associated with the process of root morphological development and the pattern of photoassimilate partitioning between coarse and fine roots. The partitioning of photoassimilate between course and fine roots was affected differenlty in the two species by the soil water deficit.

Experimental results of carbon partitioning factor were variable because of the insufficient number of plants to keep the coefficient of variation below 10%, the difficulties of measuring very small amounts of carbon in each organ, the carbon partitioned to the storage pool and the rate of death from harvest data. The use of McStress helped to clarify the mechanisms involved in the partitioning of carbon between organs and storage poll. This made an interpretation of the results possible.

Sugarbeet invested most of the carbon available for root growth in the coarse roots while cowpea invested in the expansion of the fine roots. At the beginning of the deficit cycle, 29% of the carbon available for sugarbbet root growth was partitioned to coarse roots in comparison with 65% at the end of the deficit cycle.

A similar analysis showed that throughout the deficit cycle, cowpea

invested only 25% of the carbon available for root growth into coarse roots and remaining was partitioned into the fine roots. A slight change was observed throughout the deficit cycle with 72% of the carbon located in the fine roots at the end of the deficit cycle. This indicated that cowpea possessed a root morphological development that was better suited to soil water deficit. The greater partitioning of carbon to fine roots would enable more through exploration of soil water reserves and may therefore enhance drought avoidance in cowpea in a manner similar to that reported for wheat (Hurd 1974).

LITERATURE CITED

Fernandez, C.J. 1977. Differences in Carbon Economy among Five grain Sorghum Cultivars. M.S. Thesis, Texas A & M University, College Station.

Hurd, E.A. 1974. Phenotype and drought tolerance in wheat. Agric. Meteorol.14, 39.55.

Kramer, P.J. 1983. Water Relations of Plants. Academic Press, New York, pp 342-374.

Krizek, D.T., A.Carmi, R.M. Mirecki, F.W. Snyder, and J.A. Bunce 1985. Journal of Experimental Botany, vol. 36, nº 162, 25-38.

Levitt, J. 1980. In J. Levitt ed, Responses of Plants To Environmental Stresses, Academic Press, New York, pp 108-117.

McCree, K.J. 1986 a. Measuring the whole-plant daily carbon balance. Photosynthetica 20:82-93

_____ , and S.G. Richardson 1987. Stomatal closure vs. Osmotic adjustment: A comparison of Stress responses. Crop Sci. 27:539-543.

_____ and C.J.Fernandez 1989. A whole plant simulation model for studying physiological water stress responses. Crop sci.(in press).

Tibbitts, T.W., and D.T. Krizek. 1978. Carbon Dioxide. In: A Growth Chamber Manual. Environmental Control for Plants. (R.W. Langhans, ed), pp. 80-100. Cornell Univ. Press, Ithaca, New York.

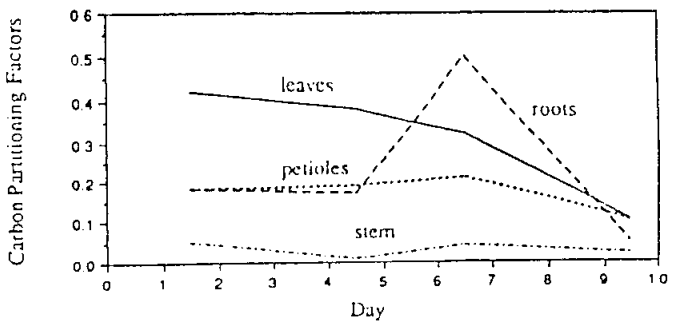

Figure 1 Measured carbon partitioning factors for sugarbeet at different time intervals of soil water deficit cycle.

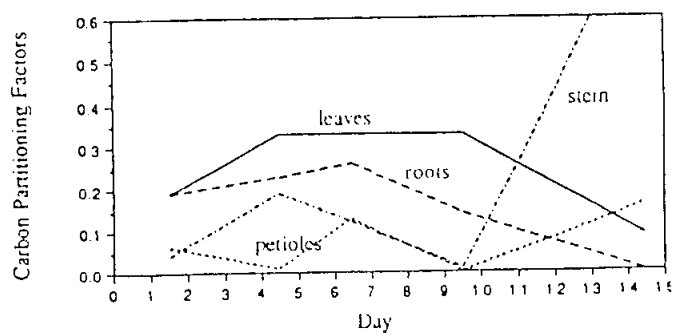

Figure 2 Measured carbon partitioning factors for cowpea at different time intervals of soil water deficit cycle.

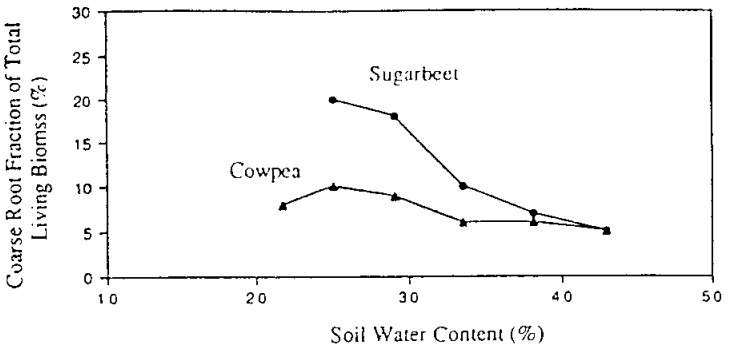

Figure. 3 Coarse root fraction for sugarbeet and cowpea in response to soil water deficits.

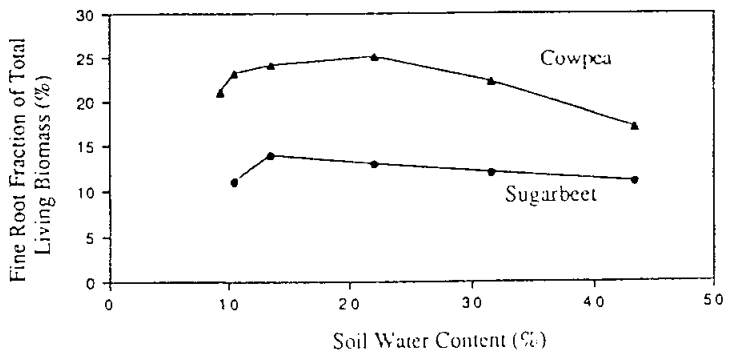

Figure. 4 Fine root fraction for sugarbeet and cowpea in response to soil water deficits.

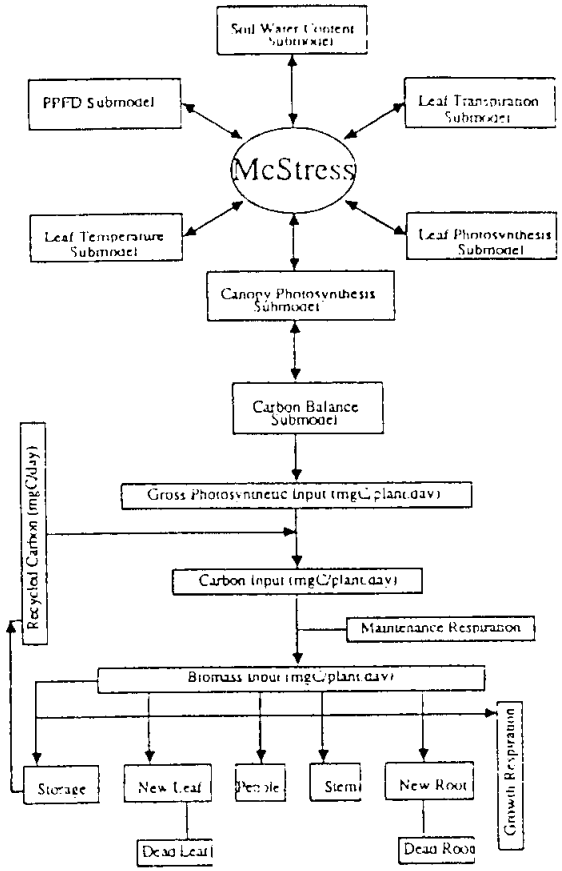

Figure 5 Flow chart of submodels of McStress

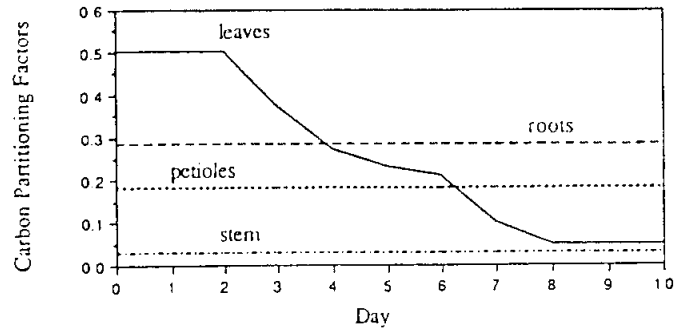

Figure 6 Simulated carbon partitioning factors for sugarbeet in response to soil water deficit.

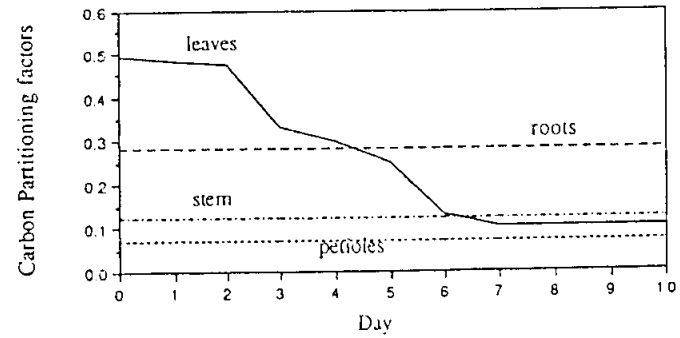

Figure 7 Simulated carbon partitioning factors for cowpea in response to soil water deficit.