Photosynthetic Efficiency of Maize and Bean Leaves in the Canopy of Sole and Intercropping Systems Under Water Stress.

By

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Declaration

I declare that this thesis prepared for Master of Science was submitted by me to the University of the Free State. This is my own work and has not been submitted to any other University or faculty. I agree that the University of the Free State has the right to publication of this thesis.

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List of symbols and abbreviations

ABS	radiant energy absorbed
ABS/CS	radiant energy absorbed per cross section
ABS/RC	amount of photon absorbed per reaction center
ATP	adenosine triphosphate
BIBI/R	irrigated/rainfed intercrop bean bottom leaf
BSBI/R	irrigated/rainfed sole bean bottom leaf
Chl a	chlorophyll a
CR	cross ratio
CS	cross section
CWSI	crop water stress index
D	saturation vapour pressure deficit
DAP/S	days after planting or sowing
D.F.	driving force
DIo/RC	dissipated flux per reaction center
DMRUE	dry matter radiation efficiency
ET = ETt	electron transfer
ETo/TRo $\equiv \psi$o	efficiency that a trapped exciton can move an electron can
move an	
	electron into the transport chain
ETo/ABS	probability that an absorbed photon will move an electron into the transport chain
ETo/RC	energy flux for electron transport
ETo/CS	electron transfer per cross section
f	fraction of active photosynthesis
Fo	minimal (initial) fluorescence in dark-adapted tissue; fluorescence intensity with all PSII reaction centers open while the photosynthetic membrane is in the non-energized state
F_p	fluorescence intensity at the level in Kausky nomenclature

F_M	maximal fluorescence in dark-adapted tissue; fluorescence intensity with all PSII reaction centers closed, all non-photochemical quenching processes are at a minimum
Fo/Fm	initial ratio of maximum Chl *a* fluorescence
F_S	steady state of fluorescence
Fv	variable fluorescence in dark-adapted tissue; maximum variable fluorescence in the state when all non-photochemical processes are at a minimum, i.e. Fm-Fo
Fv/Fm	exciton transfer efficiency in dark-adapted tissue; (Fm-Fo)/Fm
Fv/Fo	maximum variable fluorescence ratio per initial fluorescence
F*	unquenched fluorescence level
H	fraction of dry matter produced
hv	photons
I	fraction of intercepted radiation
IPAR	intercepted radiation
LHC	light harvesting chlorophyll proteins
LWP	leaf water potential
JIP-test	various stages for the rise of fluorescent signal following illumination
MIBI/R	irrigated/rainfed intercrop bean middle leaf
MSBI/R	irrigated/rainfed sole bean middle leaf
$NADP^+$ & NADPH	reduction and oxidation of water, membrane proton transport
NWM	neutron water meter
PEA	plant efficiency analyzer
PSI	photosystem I
PSII	photosystem II
PHI(Do)	dissipated flux
PI(abs)	fitness index
q	water use efficiency
Q	total quantity of incident solar radiation
Q_A	primary bound plastoquinone
R	root
RC	reaction center

RC/CS	reaction center per cross section
RUE	radiation use efficiency
SWC	soil water content
Ta	air temperature
Tc	leaf temperature
TR/RC	expresses the rate by which an exciton is trapped by the RC resulting in the reduction of Q_A to Q_A^-.
TRo/RC	trapping flux at time zero per reaction center
TRo/CS	trapping flux per cross section
TR = TRt	trapping flux
TMB	top, middle and bottom leaves
TIBI/R	irrigated/rainfed intercrop bean top leaf
TSBI/R	irrigated/rainfed sole bean top leaf
TRo/ABS $\equiv \varphi_{Po}$	the maximum quantum yield of primary photochemistry
T_{Fmax}	time to reach F_M
U	uptake
wc	water content
ψ_w	total water potential
ψ_g	gravitational potential
ψ_m	matrix potential
ψ_o	osmotic potential
ψ_p	pressure potential
φ_{Eo}	photosynthetic efficiency

Photosynthetic Efficiency of Maize and Bean Leaves in the Canopy of Sole and Intercropping Systems under Water Stress

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Abstract

In this study the leaf water potential and the photosynthetic efficiency at different leaf levels (top, middle and the lower leaves) for dry bean (*Phaseolus vulgaris*) and maize (*Zea mays*) were measured using intercrop and sole cropping systems under rainfed and irrigated conditions. The specific ecotope in which the study was conducted is Agrometeorological experimental site at West Campus in Bloemfontein, South Africa where the annual rainfall average of 600 mm. The field experiment was only conducted for one season. The expected results are that the rainfed treatments will experience more stress than irrigated treatments, and the rate of photosynthesis would be higher under irrigated than rainfed conditions. A randomised complete block design was used, with three treatments intercrop, sole maize and sole bean (IMB, SM and SB) and three replicates. The experiment determined the most stressed plants throughout the season. Chlorophyll fluorescence kinetics provides considerable information on the organisation and function of the photosynthetic efficiency. Chlorophyll fluorescence is used to study the different functional levels of photosynthesis. Photosynthetic efficiency (φ_{Eo}) changes with leaf water potential, irrigated sole maize (SMI) and irrigated sole bean (SBI) performed better than rainfed treatments since φEo was higher when the leaf water potential was lower negative. Irrigated sole bean (SBI) plants improved considerable over the experimental period as rainfed sole bean (SBR) plants became severely stressed. The whole plant bean leaf water potential indicated that the irrigated plants performed better than the rainfed plants and the sole plants did better than intercrop rainfed maize, the rainfed sole maize performed the best. Photosynthesis can be a good indicator of the overall fitness of the plants, as unfavorable environments and competition decrease the rate of photosynthesis.

Key words: Leaf water potential, photosynthetic efficiency, intercrop and sole crop system, rainfed, irrigated.

FOTOSINTETIESE DOELTREFFENDHEID VAN MIELIE EN BOONTJIE BLARE IN DIE BLAARDAK VAN ENKEL- EN TUSSENGEWASSISTEME ONDERWORPE AAN WATERSTRES

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UITTREKSEL

In hierdie studie is die blaarwaterpotensiaal en fotosintetiese doeltreffendheid van droë boontjies (*Phaseolus vulgaris*) en mielies (*Zea mays*) by verskillende blaarvlakke (boonste, middelste en onderste blare) onder droëland en besproeiingstoestande by enkel- en tussengewassisteme gemeet. Die spesifieke ekotoop waarin die studie uitgevoer is, is die Landbouweerkundige proefterrein te Weskampus, Universiteit van die Vrystaat, Bloemfontein, Suid Afrika, waar 'n jaarlikse gemiddelde reënval van 600 mm voorkom. Die veldproef is slegs vir een seisoen uitgevoer. Die verwagte resultate is meer stres by droëland behandelings as by die besproeiingsbehandelings en dat die fotosintetiese tempo hoër onder besproeiingstoestande sal wees. Ewekansige volledige blok ontwerp is gebruik met drie behandelings, naamlik tussengewas, enkelmielies en enkelboontjies (IMB, SM en SB) en drie herhalings. Clorofil fluoressensie kinetika voorsien heelwat inligting oor die organisasie en funksie van die fotosintetiese doeltreffendheid. Chlorofil fluoressensie word gebruik om die verskillende funksionele vlakke van fotosintese te bestudeer. Fotosintetiese doeltreffendheid (φEo) verander met blaarwaterpotensiaal. Enkelmielies (SMI) en enkelboontjies, beide onder besproeiing (SBI), het beter as droëland behandelings gevaar aangesien φEo hoër was by laer negatiewe blaarwaterpotensiaalwaardes. SBI plante het heelwat verbeter oor eksperimentele tydperk terwyl droëland enkelboontjies (SBR) erg gestrem is. Die hele plant-boontjie-blaarwaterpotensiaal dui aan dat besproeide plante beter gevaar het as droëland plante en enkelplante beter as tussengewas droëland mielies. Die droëland enkelmielies het die beste gevaar. Fotosintese kan 'n goeie aanduiding van die algehele gesteldheid van die plante wees, omdat ongunstige omgewing en kompetisie die tempo van fotosintese verminder.

Sleutelwoorde: *Blaarwaterpotensiaal, fotosintetiese doeltreffendheid, tussengewas en enkelgewassisteem, droëland, besproeide.*

Chapter 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

The immediate source of the energy supply that is needed continuously by all living organisms, both plant and animal, is food. This food is manufactured from simple inorganic substances by the green plant with the aid of radiation capture. Food represents a supply of energy stored by the plant through radiation. All life on earth thus depends upon radiation through the intervention of a green plant. The green plant is thus the sole agent that has the power to transform the kinetic energy as it comes from the sun into this potential energy form (Miller, 1931).

Photosynthesis is the process by which plants, algae, cyanobacteria and photosynthetic bacteria convert radiant energy into a chemically stable form. The process is initiated when the antenna molecules within the photosynthetic membrane absorb solar radiation. The absorbed energy is transferred as excitation energy and is either trapped at a reaction centre or utilised to perform chemically useful work or dissipated mainly as heat, with less being emitted as radiation, called fluorescence. The features of the emitted fluorescence are basically determined by the absorbing pigments, the excitation energy transfer and the nature and orientation of the fluorescing pigments (Strasser, *et al.* 1999).

The rate of photosynthesis is dependent on over 50 individual biochemical reactions, each of which potentially has a unique response to an environmental variable. The ability of plants to compensate for environmental effects on photosynthesis is critical to their performance and survival in growth and development. In an agricultural context, ineffective response of the photosynthetic apparatus depresses yield, with substantial economic cost. Understanding mechanisms controlling photosynthetic responses to environmental change is therefore important in understanding control of plant productivity, species distribution and the responses to climate change (Sage and Reid, 1994).

Fluorescence, affected by the redox state of the reaction centres and of the donors and acceptors of PSII, is moreover sensitive to a wide variety of photosynthetic events, e.g., proton translocation, thylakoid stacking and unstacking, and ionic strength (Strasser *et al.* 1999). Chlorophyll *a* fluorescence is capable of being used to collect a large amount of accurate data without injury to the plant and does not require a large amount of expertise. As such, it has the potential to be a useful tool in the screening of plant health (Clark *et al.* 1996).

Chlorophyll is the green photosynthetic pigment present in chloroplasts, which provides the centre necessary for photosynthesis. The intense green colour of chlorophyll is due to its strong absorbencies in the red and blue regions of the electromagnetic spectrum, and because of these absorbencies the radiation it reflects and transmits appears green. It is capable of channeling the energy of sunlight into chemical energy through the process of photosynthesis. In this process the energy absorbed by chlorophyll transforms carbon dioxide and water into carbohydrates and oxygen (Wikipedia Encyclopedia 2001).

These primary sugars form the raw material from which more complex sugars, starches, cellulose and other plant constituents are subsequently synthesized. Photosynthesis provides the material for plant growth and development of synthesizing and storage organs such as leaves, stems, tubers, and fruits. Radiant energy is captured through photosynthesis and is stored for shorter or longer periods in such diverse materials as easily convertable sugars and the fossil fuels that must be mined and purposefully combusted to release energy. The processes of growth and the synthesis of more complex compounds require the input of energy (Rosenberg *et al.*, 1983). The carbohydrates are the most abundant compounds in the plant and make up the greatest portion of its dry weight. Photosynthesis is the manufacture of some simple carbohydrate (sugar) from carbon dioxide and water by the chloroplasts in the presence of photosynthetical active radiation. In this process the oxygen always appears as a by-product. The process of photosynthesis resides exclusively in the chloroplasts. Nedbal *et al.* (2000) found that high biomass and chlorophyll concentration contribute to increased oxygen content in the water column in the plant through photosynthesis.

The materials that enter the green plant from its environment are inorganic compounds of the most simple character. Thus, for example, the plant obtains CO_2 from the atmosphere, water, and nitrates, sulphates, and phosphates of K, Na, Mg, Fe, Ca, among others, from the soil. From these simple compounds the plant is able to synthesize a large variety of substances of varying degrees of complexity, the most important and abundant of which are the carbohydrates, fats and oils, amino acids, proteins, glucosides, chlorophyll, and various other pigments and numerous organic acids (Miller, 1931).

The Republic of South Africa (RSA) is relatively dry, with an average rainfall of 475 mm y^{-1} (SAWS, 1991) with 60% of the area receiving less than 500 mm. y^{-1} (Scotney *et al.,* 1990). The climate of the study area (Bloemfontein, Free State, South Africa) is arid cold and dry, with mean annual temperature below 18°C, categorized as a semi-arid warm climate (Schulze, 1947; Schulze and McGee, 1978). The annual rainfall is 559 mm and the mean annual global solar radiation is 244 W m^{-2} (Tsubo, 2000).

Irrigation is the main tool of artificial application of water to soil for the purpose of growing crops. Irrigation represents a highly complex practice involving the all-important soil-plant-water-atmosphere continuum. Irrigation relies on sound engineering and economic principles, which include important technological and sociological considerations (van Niekerk, Personal communication, 1991).

In semi-arid areas, dryland agriculture is defined as rainfed crop production characterized by irregular rainfall below 750 mm that fails to meet the potential evaporation demand during part of the year. Hillel and Yudelmen (1988) found that high yielding modern varieties of rice and wheat, when supplied with adequate water (irrigation or high rainfall) and nitrogenous fertilizers, give much higher yields than traditional varieties.

Canopy structure may be thought of as the amount and organization of above ground plant material. The leaf area index and orientation represent the amount of leaf material by the leaf angle distribution. Description of canopy structure is essential to achieve an understanding of plant processes because of the profound influence that structure has on plant-environment interactions. The vegetative architecture not only affects exchanges of mass and energy between the plant and its environment, but it may also reveal a strategy of the plant for dealing with long lasting evolutionary processes, such as adaptation to physical, chemical or biotic factors, by reflecting the organisms' vital activity or peculiarities in growth and development (Monteith, 1962, Norman & Campbell, 1983). The influence of canopy structure on wind and radiation environments within the canopy is perhaps the most obvious (Fritschen, 1985).

Measurements of radiant flux energy in physiological ecology are of primary importance because of their role in energy balance determinations and in photosynthesis measurements (Pearcy *et al.*, 1989). The relation between radiation environment within a canopy and canopy structure is much better quantified than the interaction between structure and wind (Ross, 1981). In fact, the coupling between radiation exchange and canopy structure is so strong that measurements of radiation may be used to infer canopy features.

Canopy structure affects other environmental factors such as air temperature, leaf temperature, atmospheric moisture, soil evaporation below the canopy, soil heat storage and soil temperature, precipitation interception, leaf wetness duration and others. However, these effects may be subtle and may require complex models to quantify them (Goudriaan, 1977; Norman & Campbell, 1983). Canopy structure, through its impact on canopy environment, affects not only plants, but also other organisms that may live within or below the canopy.

1.2 Study aim

The main aim of the study was to determine how the rate of photosynthesis affects the productivity, in different treatments, of a sole and intercrop system. The efficiency of photosynthesis of the whole plant is crucial to agriculture when it comes to analyzing productivity for food, and many other product uses. The quality and quantity of incident photosynthetically active radiation (PAR), temperature and water stresses, availability and utilization of mineral nutrients, photorespiratory losses, are some of the factors which affect plant productivity. How these factors interact with the changing environment is the subject of much practical and basic research. More attention will also be paid to how the rate of photosynthesis of leaves at various heights in the canopy changes under water stress.

Management of the radiation resource is a crucial but exciting problem. Theoretically, it is known that high radiation intensity will improve the rate of photosynthesis, which results in improvement of primary production. Determination of productivity amongst the treatments of sole cropping and intercropping using maize and soybeans should be measured.

1.2.1 The specific objectives

1. To quantify the photosynthetic potential of the whole plant (maize and bean) under different treatments (Sole beans, Sole maize and intercrop sole maize and bean).

2. To determine how the soil water content affects the development and biomass production of the crop.
3. To assess physiological changes that occurred during a stress period.
4. To evaluate the response of photosynthesis to growth and development under different treatments of water stress.

1.2.2 Hypothesis

This study compared the sole and intercrop cropping systems of beans and maize under irrigated and rainfed conditions. The assumption was that intercropping is considered to be less stressful than sole cropping as it consumes water more effectively and since irrigated treatments would be less stressed than rainfed treatments.

1.3 Environmental factors affecting photosynthesis

Plant growth has two distinctly different features: phasic and morphological development. Phasic development involving changes in stages of growth is always associated with major changes in biomass partitioning patterns (Table. 1.1).

Morphological development refers to the changes of plant organ development within the whole plant life cycle. The most important environmental factor that affects phasic and morphological development is the temperature of the growing part of the plant. The genotypic characteristics affecting plant response to photoperiod are also important determinants of the duration of growth in addition to the temperature influence. Table 1.1 shows that vegetative expansion growth is more sensitive to water deficit than the other three processes.

Table 1.1 Factors influencing plant growth and development processes (i.e. duration) and sensitivity to stresses (Ritchie, 1991).

	Growth		Development	
	Mass	**Expansion**	**Phasic**	**Morphological**
Principal Environmental Factor	Solar radiation	Temperature	Temperature Photoperiod	Temperature
Degree of variation among genotypes	Low	Low	High	Low
Sensitivity to plant water deficit	Low- stomata Moderate- leaf wilting and rolling	High – vegetative stage Low – grain filling stage	Low – delay in vegetative stage	Low – main stem High - tillers and branches
Sensitivity to nitrogen deficiency	Low	High	Low	Low – main stem High - tillers and branches

Environmental responses of photosynthesis can be studied using five basic approaches (a) gas exchange of intact leaves; (b) chlorophyll fluorescence analysis; (c) biochemical analysis of enzyme activity and content; (d) biochemical analysis of metabolite pool sizes; and (e) molecular analysis of transcriptional, translational and post-translational regulation (Strasser *et al.* 1999). For this study chlorophyll fluorescence analysis has been used.

1.3.1 Radiant flux density

Each plant is the product of its genetics and the total environment in which it is grown. The total growth environment is constantly changing during the lifetime of the plant. Because of the growth and developmental processes associated with adaptation to the many environmental variables, plants of the same genotype can differ significantly in size and chemical composition. Photomorphogenesis is plant growth and development, influenced by photoperiod, radiation quality and radiation quantity. Plants contain photoreceptor systems that sense, or measure, various aspects of the radiation environment and initiate physiological processes that regulate adaptation of the plant to increase its probability of survival and reproduction in that environment (Kasperbauer, 1994).

The various species of plants differ greatly with respect to the radiation dependency of their carbon dioxide fixation rates. The leaves of C_4 species, e.g. maize, show a virtually linear increase in carbon dioxide uptake rate with increasing level of radiation. C_3 species, e.g. soybean, are less productive and may become radiation saturated at lower levels of irradiance (Rosenberg *et al.*, 1983).

Radiation is a conservative quantity of major importance in crop ecology. Radiation use efficiency is the amount of dry matter produced per unit of radiation intercepted by the crop canopy. Intercepted radiation is the product of two quantities: radiation incident on a crop stand per unit area and the fraction of that radiation which is intercepted. The corresponding mean efficiency of photosynthesis is therefore conservative and the main discriminant of growth rate is the fraction of incident radiation absorbed by leaves, a quantity depending on the area and structure of the canopy as determined by factors such as plant population, water supply and or nutrient availability.

Day *et al.* (1978) found that when barley (*Hordeum vulgare*) grown on water stored in a soil profile was compared with irrigated barley in adjacent plots, the fraction of radiation intercepted over the growing season was 42% lower but the dry matter of leaves was only 20% less. The lower leaf biomass reported as a response both to dry soil and to a dry atmosphere is likely to be a consequence of stomatal closure. Rinaldi *et al.* (2003) also described biomass accumulation as a product of radiation use efficiency (RUE) and intercepted radiation (IPAR). Leaf absorptance is a measure of the fraction of the incident photon or energy flux that is absorbed by the leaf. It can be specified for each single wavelength. When leaf absorptances are expressed for a particular waveband (between 400 and 700 nm), the irradiance source (sunlight) must also be specified (Pearcy *et al.* 1989).

1.3.2 Water

Water availability is an important factor affecting plant growth and yield, mainly in arid and semi-arid regions, where plants are often subjected to periods of drought. The occurrence of morphological and physiological responses, which may lead to some adaptation to drought stress, may vary considerably among species. In general, strategies of drought avoidance or drought tolerance can be recognized, both involving diverse plant mechanisms that provide the plants the ability to respond to and survive drought (Levitt, 1980). Maize (*Zea mays*) is a species in which yield is limited by drought that usually occurs during the reproductive period (Karrou *et* *al.* 1988). Controlling the density of a plant population is one of the most important practices to match water use to anticipated soil water availability (Waldren, 1983). Karrou, *et al.*, (1988) demonstrated for maize that when precipitation was below average from planting through silking, different plant populations depleted the available soil water to near the wilting point at later stages and evapotranspiration remained about the same for each population, so the efficiency of water use varied with yield. Waldren (1983) concluded that water stress within 2 weeks after silking reduced the number of kernels/plant by about 15%, with little influence on kernel weight.

Rainfall determines the cropping potential in rainfed agricultural areas. Water is the essential component in the photosynthetic reaction. Shortages of soil water or extreme dryness of the atmosphere creates a water deficit that affects the efficiency of the photosynthetic reaction in the plant (Rosenberg *et al.,* 1983). Water stress affects photosynthesis through a number of mechanisms: by affecting the levels of metabolic intermediates; by inhibiting the photosynthetic electron transport system; by causing stomatal closure and by altering rates of respiration (Boyer, 1970). The increasing soil water stress and atmospheric evaporative demand on photosynthesis at varying levels of irradiance, results in the optimum photosynthetic rate being reached at lower irradiance. High atmospheric stress and, particularly, extreme atmospheric stress will reduce photosynthesis, probably because rapid evaporation reduces turgor in the guard cells causing stomates to close, limiting the availability of CO_2 (Moss, 1965).

Plant response to water stress can be categorized at two major growth stages: preanthesis (vegetative stage) and postanthesis (reproductive stage). These response phases coincide with different major physiological and biochemical changes in the plant. Seed yield under severe water stress has also been associated with maintenance of leaf, stem and silk extension, canopy temperature (transpiration) at anthesis and of green leaf area during grain filling (Duncan, 1994). Plants generally require a high water content, mostly greater than 75%, and a correspondingly high tissue water potential, mostly greater than –2MPa. The process of carbon uptake and fixation require an exchange of gases, thus giving rise to mechanisms capable of balancing the uptake of carbon dioxide with the loss of water to the atmosphere (Hinckley & Breathe, 1994).

Water use efficiency is the ratio of dry matter produced to the amount of water used (Gregory, 1988). The agronomic definition of water efficiency involves two major terms: a biological component (the transpiration efficiency) that specifies the amount of dry matter produced per unit of water transpired, and management component that specifies the fraction of the total water supply used for transpiration. Transpiration efficiency is affected by the saturation deficit of the atmosphere and also varies between species because of differences in photosynthetic pathways and in the carbon assimilates contributing to dry matter.

Monteith (1988) found that there is substantial evidence from field measurements on many species that the amount of dry matter produced by a crop per unit of water transpired (q) (water use efficiency) is almost inversely proportional to the mean value of the saturation vapour pressure deficit (D) of the atmosphere to which the canopy is exposed during the day. This implies that qD is a conservative quantity. It's physiological basis, conservative of the intercellular CO_2 concentrations of leaves. For C_3 species, qD is smaller than for C_4, corresponding to a well-documented difference in the characteristic intercellular CO_2 concentration of the two groups of species.

1.3.3 Temperature

Temperature is an environmental condition which is continually changing, both through the day and with the seasonal cycle through the year. Each plant species has an optimum range of air temperature for growth and reproduction. Many plants of temperate zones undergo a number of changes in response to the shortening days in late summer and autumn, accentuated by the decreasing temperatures of that season.

Many plant species that are originally found and thus adapted to warm habitats are very susceptible to injury by low-temperature exposure. Stomatal closure due to chilling-induced water stress can be responsible for part of the decrease in photosynthesis. Decreased fluorescence from intact tissue or isolated chloroplasts suggests that the oxidative side of photosystem II is the site of injury (Bowers, 1994).

The process of photosynthesis is not strongly affected by ambient temperature when a plant is grown in the normal region to which it is adapted. However, temperature does affect photosynthetic performance, but the effects may vary according to prior acclimation to hot or cold conditions (Rosenberg *et al.*, 1983). The C_4 plants generally have a greater photosynthetic potential under higher temperatures. Studies have shown that maize assimilates carbon dioxide more effectively as temperature increases from 10 to 30°C (Moss 1965), with an optimum temperature existing somewhere between 30 and 35°C.

1.3.4 Carbon dioxide and growth

The flux of CO_2 in the air above a crop canopy is a measure of the net exchange of CO_2 between soil-plant system and the atmosphere (Monteith & Unsworth 1990). The photosynthetic system begins to assimilate part of the respired CO_2 and the upward flux decreases to zero when solar irradiance reaches the light compensation point for the stand, usually 1 to 2 hours after sunrise over actively growing vegetation. After the irradiance exceeds the CO_2 compensation point, there is a down flux of CO_2 representing the atmospheric contribution to photosynthesis (Monteith & Unsworth, 1990).

The accumulation of carbon progresses in cycles corresponding to the succession of radiation and dark periods when the crop gains and loses CO_2. Large differences in photosynthesis from day to day are correlated with the daily radiation (Monteith & Unsworth, 1990).

Increasing the ambient concentration of CO_2 generally increases carbon dioxide fixation. In C_4 plants a linear increase in photosynthetic rate was found with increasing carbon dioxide concentration in the range 220-400 ppm (Rosenberg *et al.,* 1983). In the case of C_3 species, the increase in ambient CO_2 concentration may also act to suppress photorespiration since that process proceeds at a rate that depends on competition between oxygen molecules and carbon dioxide molecules for the active site on Rubisco (Chollet, 1977; Ehleringer & Bjorkman, 1977). The direct influence of CO_2 concentration on the photosynthetic rate of C_4 species is smaller than in C_3 species.

Assmann (1999) found that stomata are the main routes for leaf gas exchange controlling CO_2 uptake and transpiration. Stomatal movements are regulated by both internal and external factors. Low CO_2 concentrations, blue light and other photosynthetically active wavelengths stimulate opening of stomata, whereas stomatal closure occurs in response to a number of environmental cues namely darkness, low air humidity and high temperature. Stomatal movements are brought about through changes in turgor within guard cells and accessory cells.

Rates of CO_2 uptake and water loss are used to determine the response of net CO_2 assimilation, stomatal conductance and the intercellular partial pressure of CO_2 to the environmental variable in question. Calculation of intercellular partial pressure of CO_2 factors out stomatal and boundary layer effects on photosynthesis and allows assessment of the separate effects of the treatment on stomata and the photosynthetic biochemistry in intact leaves (Bowers, 1994; Sage & Reid., 1994).

Wand *et al.* (1999a) found that under well-watered conditions, atmospheric CO_2 enrichment increased rates of photosynthesis for C_3 and C_4 plants. The C_4 plants exhibited absolute rates of net photosynthesis that were about 60-160% greater than C_3 plants depending upon the atmospheric CO_2 concentration. Under water-stressed conditions, C_3 plants attained lower leaf areas to a greater extent than C_4 plants, regardless of atmospheric CO_2 concentration. Similarly, C_3 plants exhibited a greater average reduction in photosynthesis than C_4 plants. Thus, total plant dry mass was affected less by drought in C_4 than in C_3, plants.

1.3.5 Agricultural practices

The development of agriculture over the last 10 000 years has involved not only the selection and breeding of wild plants to form productive crops but also the development of methods of planting which maximize yields and maintain soil fertility. Indigenous agriculture all over the world commonly makes use of intercropping, which is the practice of growing two or more crops at once in the same field. Mostly, the grain and legume crops are maize and beans, millet and cowpeas in Africa, wheat and chickpeas in the Middle East, sorghum and pigeon peas in India, rice and soybeans in China, oats or barley and peas or beans in Europe (Innis, 1997, Liphadzi, *et al.*, 1997) and even peppermint and soybean (Maffei & Muccialli 2003).

Multiple cropping (intercropping) systems are important because of their potential for producing greater overall yields than single (sole) crop systems, because the judicious combination of crops may make better use of growth resources than sole cropping. Intercropping may make better use of resources at a given point in time because of complementary effects between the crops (Willey, 1988).

In sowing millet and groundnuts, Willey (1988) found that dry matter accumulation patterns of a one-row millet: three-rows groundnut system where the within-row spacing of each crop was the same as its sole crop and plant populations were, equivalent to row proportions (25%: 75%). For most growing periods, he found that the dry matter accumulation of the intercropped groundnut was a little less than the expected level of 75% of the sole crop because of competition from the millet. But later discovery resulted in a final dry matter yield equivalent to the expected 75%

level. In contrast, dry matter accumulation of the more competitive millet was much greater than its expected 25% level, reaching 62% of the sole crop by final harvest.

Intercropping can effect almost all the mechanisms that determine water use. Where intercropping provides a greater canopy cover because of higher leaf area index, it may protect the soil surface from the impact of rain and improve infiltration and increase the amount of water available in the soil (Lal, 1974). Several intercropping systems have been shown to extract more water than their sole crops (Willey, 1979).

The improvement of productivity is the common aim of farmers and agricultural scientists. The main reason for using a multicropping system is the fact that it integrates crops efficiently using space and labour (Baldy & Stigter, 1997). In particular, cereal and legume intercropping is recognized as a common cropping system throughout tropical developing countries (Ofori & Stern, 1987). It has been concluded that intercropping may be beneficial by giving a higher production (Tsubo, 2000).

Generally, in southern Africa, maize (*Zea mays*) is the main staple and is commonly grown with dry beans (*Phaseolus vulgaris*) as a supplementary crop adopted by the. smallholder farmers Rainfall is the single most important natural resource input under a rainfed intercropping system (Walker & Ogindo, 2003). Crop productivity of sole cropping systems is assessed by using mass yield (weight per unit area). Direct comparison for intercropping systems is complicated due to the fact that the composition of yields are different for different plant species growing on one piece of land (Beets, 1982). Mukhala *et al.,* (1999) reported an advantage in maize-bean intercropping over the sole cropping of either, in a South African semi-arid region. Rainfall plays a pivotal role in successful farming in semi-arid environments. The analysis of the cropping system is incomplete without consideration of the soil-plant-atmosphere system.

Intercrop environments are composed of two crops of differing stature and growth dynamics that may create characteristics that convey a favourably direct effect on transpiration efficiency (Biomass produced per unit of water transpired is water use efficiency). Intercrop canopies are generally rough due to the differences in plant height and architecture between the components (Jones, 1976). Dense canopy cover by the intercrop has an effect on soil temperature and contributes to reduced soil erosion and hence better fertility (Stoop, 1986, Olasantan, 1988).

Sole cropping systems are particularly well adapted to the length of the growing season. The crops grow faster during the rains and then often mature in sunny conditions on the residual soil water. In the short growing season, sole cropping system can be efficient because they inevitably involve rapid-growing, early-maturing crops that can make good use of the short period of available water. Long growing season crops, such as pigeonpea, castor bean and cotton are extremely slow growing and make poor use of resources at early stages. Long growing season crops such as late maturing cereals may be biologically efficient in that they are rapid-growing and make good use of resources (Willey, 1988).

1.3.6 C_3 and C_4 plants

Green plants are classified into three major groups according to their photosynthetic mechanism. C_4 plants utilize the C_4-dicarboxylic acid chemical pathway for photosynthesis. C_4 species are generally the tropical grasses, for example agronomic crops such as maize, millet, sorghum and sugar cane (Figure 1.2). C_3 plants utilize a photosynthetic pathway involving a three carbon intermediate product. C_3 groups includes virtually all other species i.e. small grains and leguminous species. CAM plants maintain open stomata at night during which time they fix CO_2 in the form of organic acids. During the day, the stored CO_2 is then reduced photosynthetically to save water when stomata are closed, for example many desert plants (Chollet, 1977).

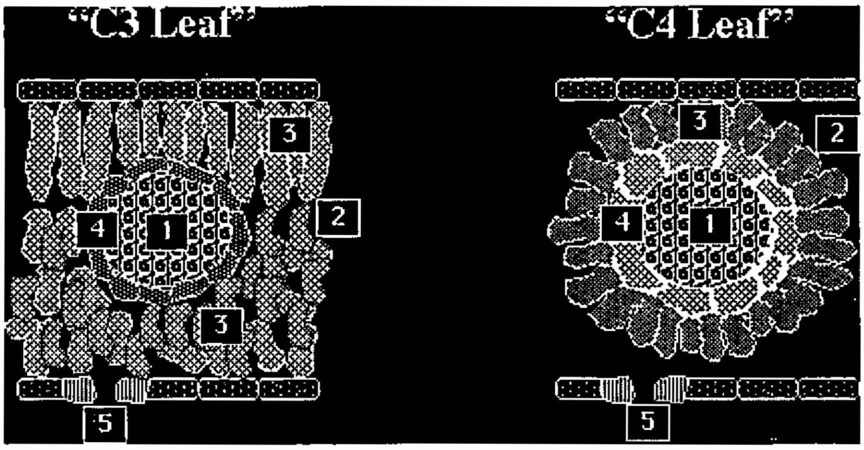


Figure 1.2. Illustration of the structural differences between C_3 and C_4 leaves (Wand *et al.*, 1999b).

Parts of the leaf structure are as follows:

1. Vein (site of transport of materials to and from the leaf).

2. Air space (in contact with the mesophyll in C_3 plants, thus permitting photorespiration; not in contact with the bundle sheath cells which are the sites of the Calvin cycle in C_4 plants).
3. Mesophyll cells (sites of photosynthesis and photorespiration in C_3 plants; chloroplast containing cells where CO_2 is incorporated into organic acids in C_4 plants).
4. Bundle sheath cell (in C_3 leaves, these cells surrounding the vein are nonphotosynthetic; in C_4 leaves these cells are the site of the Calvin cycle).
5. Stomata (one of the many openings on the undersurface of the leaf through which air enters the mesophyll).

C_3 plants use Rubisco to produce a three-carbon compound as the first stable product of carbon fixation. However, these plants may lose up to 50% of their recently fixed carbon through photorespiration. More than 95% of the earth's plant species can be characterized as C_3 plants. C_4 photosynthetic pathway is a biochemical pathway used by certain plants to obtain carbon during photosynthesis. Such plants possess biochemical and anatomical CO_2-concentrating mechanisms that increase the intercellular CO_2 concentration at the site of fixation, which greatly reduces carbon losses by photorespiration. It is thought that the primary selective mechanism for the development of C_4 photosynthesis is the low level of CO_2 that has prevailed during the last 50 to 60 million years (Wand *et al.,* 1999b).

Wand *et al.* (1999a) also found that after analyzing approximately 40 and 80 individual responses of C_4 and C_3 grasses respectively to elevated CO_2, it was determined that both types of grasses respond favorably to atmospheric CO_2 enrichment. Photosynthetic rates, for example, increased by an average of 25 and 33% for C_4 and C_3 grasses respectively, in response to a doubling of the atmospheric CO_2 concentration. In addition, atmospheric CO_2 enrichment increased total biomass of C_4 and C_3 grasses by 33 and 44%, respectively. Thus, it is abundantly clear that C_4 plants can (and do!) respond robustly to increases in the CO_2 content of the air. As the atmospheric CO_2 concentration continues to rise, C_4 plants will be likely to exhibit significant increases in photosynthesis and biomass production that will closely parallel those of C_3 plants, which often have been implicated to respond much more favorably to elevated CO_2 than do C_4 plants. Consequently, literature review suggests that it may be premature to predict that C_4 grass species will lose their competitive advantage over C_3 grass species in elevated CO_2. Thus, as the atmospheric CO_2 content of the air continues to rise, it is highly unlikely that C_3

plants will displace C_4 species. Indeed, rising atmospheric CO_2 concentrations should help to maintain biodiversity in ecosystems where C_4 and C_3 plants coexist.

C_3 concerns a type of photosynthesis in which 3-phosphoglycerate is the first stable product and ribulose bisphosphate is the CO_2 receptor. This photosynthetic pathway is also known as the Calvin Cycle. Plants that only exhibit this phenomenon are called C3 plants. C_4 concerns a form of photosynthesis in which oxaloacetate is the first stable product and phosphoenolpyruvate is the CO_2 acceptor. Another name for this photosynthetic pathway is the Hatch-Slack pathway. Plants exhibiting this phenomenon (called C_4 plants) ultimately perform the reactions of the Calvin Cycle as well.

1.3.7 Chlorophyll fluorescence

Chlorophyll fluorescence research began in the early 1930's by Kautsky and Hirsch (1931), who were the first to report that, upon illumination of a dark adapted photosynthetic sample, the *chl a* fluorescence emission is not constant but exhibits a fast rise to a maximum followed by a decline to reach, finally, a steady level witin a range of some minutes. They postulated that the rising phase of this transient, [found to be unaffected by temperature changes (up to 30°C) and the presence of poison (potassium cyanide)], reflects the primary reactions of photosynthesis. They further showed that the declining phase of the fluorescence transient is correlated with an increase in the CO_2 assimilation rate.

Chlorophyll fluorescence determines the quantum yield of photosystem II (PSII). PSII is a large multisubunit protein complex which catalyses water oxidation through an electron transport chain leading to the accumulation of positive charges on a manganese cluster and reduction of tightly bound (Q_A) and a diffusible (Q_B) plastoquinone (Santabarbara *et al.*, 2003). Chlorophyll fluorescence analysis has become one of the most powerful and widely used techniques available to plant physiologists. The radiant flux density absorbed by chlorophyll molecules in a leaf undergoes three processes: it can be used through photosynthesis (photochemistry), excess energy can be dissipated as heat or it can be re-emitted as light called chlorophyll fluorescence. Fluorescence yield can be quantified by exposing a leaf to radiation of a defined wavelength and measuring the amount of radiation re-emitted at longer wavelengths (Maxwell & Johnson, 2000).

1.3.8 Biomass and yield

Basically, the total biomass of a crop is the product of the average growth rate and the growth duration. The PAR fraction can range from practically 0.0 for crops with severe stresses at critical times to more than 0.5 for crops that are grown under optimum conditions. (Ritchie, 1991). Plant biomass assessment can be thought of as a combination of carbon fixation, maintenance respiration and growth respiration.

Plant development varies within a field due to the spatial variability of soil characteristics and agricultural inputs. Determination of the variations in plant development can be valuable, especially where development is affected by a stress condition that could be corrected. Plant parameters such as leaf area index (LAI) and dry matter production can be used as indicators of plant performance as these parameters play crucial roles in plant growth. Wiegand *et al.* (1979) noted that the LAI could be used to characterize crops for interception and penetration of photosynthetically active radiation (PAR) that is needed for photosynthesis or the simulation of plant growth by crop growth models.

In sole cropping systems, the assessment of crop yields is expressed as mass yield per unit area. For intercropping systems, direct comparison is difficult because products are different for the different plant species growing on the same piece of land (Beets, 1982). Beets (1982) introduced a quantitative method for evaluating intercrop productivity based on intensity of land use, production of constituents and capital return. Osiru and Willey (1972) observed that intercrop systems produced higher yield than the sole crop system, due to better utilization of environmental resources. However, various researchers have also reported a decrease in yield due to adverse competitive effects.

It has been observed that dry matter production of the various yield components in inter-cropped beans were similar to sole crop beans 43 day after planting. Thereafter, dry matter production reduced in intercropping. Gardner *et al.* (1990) found that maize/bean intercropping although they reported equal dry matter production in intercrop and sole crop up to 34 days after planting. This could be attributed to differences in the plant densities used in the studies.

A more functional approach to biomass growth is to assume constant dry matter radiation use efficiency (DMRUE) and calculate growth rate as directly proportional to intercepted PAR. Monteith (1977) provided a rationale why the DMRUE coefficients may vary, including: (a) the time interval involved, i.e. hourly, weekly, or seasonal; (b) the form of carbon, i.e. dry matter above-ground, dry matter including roots or the CO_2 uptake by the plant top, and (c) description of the radiation, i.e. solar radiation interception, PAR intercepted.

Chapter 2

MATERIALS AND METHODS

2.1 Field experiment

The field experiment was conducted during the summer months January to May of 2003. The experiment was located at the Agrometeorology site, West Campus of the University of the Free State (latitude: 29° 01'S, longitude: 26°1'E, altitude 1354 meters above the sea level). The topography of the site can be described as flat to a gentle slope from south to north and east to west, with micro-relief being the dominant landform. No surface crusting was noted. Run-off was negligible during the experiment season. An automatic weather station and a pivot irrigation facility at the site were used during the experiment. They were tools in terms of collecting weather data and irrigation application on the irrigated treatment.

According to the Soil Classification Working Group (1991) the soil type at the site is described as fine sandy loam Bloemdal Vrede (3100). The southern part of the site, which has almost similar textural composition, was used to locate the experimental blocks. According to de Jager (1987), Mukhala (1998) and Ogindo (2003) the experimental site has a clay content that varies from 8-22%. The textural composition of the topsoil can be considered to be predominantly sand. The northern part of the site has a higher clay content in the A-horizon.

2.2 Experimental design

The treatments were planted in a Randomised Complete Block Design. A block occupied an area of 1620 m^2 and each plot measured 18m x 12m. Each block consisted of three treatments: sole bean (SB), sole maize (SM), and intercrop maize and bean (IMB) (Fig. 2.1, Fig. 2.2 and Fig. 2.3). Each treatment had three replications.

The intercrop components were sown simultaneously using an additive scheme (Willey, 1979; Connolly *et al.*, 2001; Ogindo, 2003) with full maize and bean sole crop population. The plots were planted by hand. The intercrop had two rows of bean between every row of maize. Each planting hole had two plants for both sole and intercrops. The plant density for bean was 8 plants per square meter and for maize 4 plants per square meter. The row spacing for maize was 1.00 m, and for beans was 0.40 m (Table 2.1).

Table 2.1: Cropping system, spacing and densities adopted during the experimental season (January to May 2003)

Cropping system	Crop	Spacing	Plant density (Plant m^{-2})
Sole cropping	Maize	1m x 0.5 m	4
	Bean	0.4 m x 0.5 m	8
Intercropping	Maize	1 m x 0.5m	4
	Bean	0.4 m x 0.5 m	8

Figure 2.1: Sole bean crop 5 weeks after planting, growing season January-May 2003.

Figure 2.2: Sole maize 5 weeks after planting, growing season January-May 2003.

Figure 2.3: Intercrop maize/bean 5 weeks after planting, growing season January-May 2003.

2.3 Agronomic information

(*Zea mays* L cv. PAN 6804), a short maize cultivar, was planted with the indeterminate bean cultivar (*Phaseoulus vulgaris* L cv. PAN 148). The maturity period was 120 days for both species.

Table 2.1 shows the plant density and plant spacing adopted for this research. The land preparation, e.g. fertilizer application, sowing, weeding and harvesting was done by hand. Weeding was done repetitively to ensure a weed free crop. The fertilizer was applied as a single dose at sowing (basal) at the rate of 240 kg N, and 96 kg K per ha^{-1}.

Since one plot was rainfed and the other was irrigated, irrigation was applied using the center pivot system. Four rain gauges were placed within the blocks to measure the amount of precipitation received. The agronomic characteristics of maize and bean are presented in Table 2.2.

Table 2.2: Agronomic characteristics of maize PAN 6804 and bean PAN 148.

Period (days)	Maize	Bean
From planting to flowering	65-102	50-55
From planting to maturity	130-160	105-115

According to Penning de Vries *et al.* (1989) crop production models based on environmental resource factors which limit plant growth, have been successfully applied in agronomic research. The models can be classified into three main production levels: (i) weather dependence (unlimited water and nutrients, the first production level), (ii) water dependence (limited water and unlimited nutrients, the second level) and (iii) water and nutrient dependence (limited water and nutrients, the third production level). In the third production, nutrients may be subdivided into several levels such as nitrogen, phosphorus and potassium, *etc.* and/or the second and third production levels, weather (meteorological factors) influences plant growth. The first production level, namely the potential level, is often referred to as a radiation-based crop model.

2.4 Climatic variables

2.4.1. Long term climatic variables

Adverse weather conditions and droughts throughout southern Africa increase food insecurity. Variable rainfall is characteristic in southern Africa, with annual rainfall varying from 100 mm in the arid zones to 1500 mm in the humid zones. This results in high variation in the potential of natural resource based farming (Le Houérou *et al.*, 1993). Semi- arid areas are characterized by less precipitation than evaporation.

The climate of the study area (Bloemfontein, Free State, South Africa) is a cold and dry climate with mean annual temperature below 18°C, characterized as semi-arid warm climate (Schulze, 1947). Mean monthly weather data (South African Weather Bureau) for Bloemfontein Airport over 30 years (1961-1990), (latitude 29° 06'S, longitude 29° 18' E, altitude 1351 m above sea level) is presented in Table 2.3. The mean annual temperature is 15.9°C, the annual rainfall is 559 mm and the mean global solar radiation is 244 Wm^{-2}. An amount of 80% of rainfall occurs during summer months between November and April.

Table 2.3 Long term mean monthly climate data for Bloemfontein Airport, South Africa , (latitude 29° 06'S, longitude 29° 18' E, altitude 1351 m above sea level; for 30 years till 1990).

Month	Average Max. Temp °C	Average Min. Temp °C	Average Temp. °C	Monthly Rainfall °C	Global Radiation Wm^{-2}
Jan	30.8	15.4	23.1	81.4	311
Feb	29.0	14.7	21.9	99.9	285
Mar	27.0	12.4	19.7	74.2	244
Apr	23.3	7.7	15.5	56.3	204
May	20.3	2.4	11.3	18.0	175
Jun	16.9	-1.5	7.7	12.6	156
Jul	17.5	-1.9	7.8	8.9	168
Aug	20.0	0.5	10.3	14.4	201
Sep	24.0	5.3	14.7	21.7	246
Oct	26.0	9.1	17.6	46.7	285
Nov	28.1	11.7	19.9	61.2	320
Dec	30.1	13.8	22.0	61.1	337

2.4.2. Seasonal climatic trend

During the growing season 11 January to May 2003 meteorological weather variables were recorded at an automatic weather station located at the West Campus Agrometeorological experimental site. Rainfall was recorded within the blocks by using four raingauges per block as the experiment had rainfed and irrigated treatments. The amount of rainfall received (Figure 2.4) and the amount of irrigation (Figure 2.5) in shown below. The daily mean temperature and solar radiation is also represented in Figure 2.6 and Figure 2.7. This field experiment was only conducted for one season.

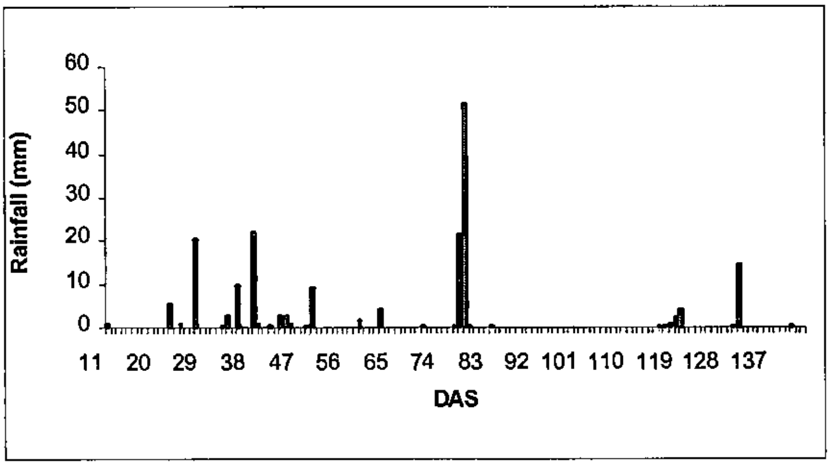


Figure 2.4 Amount of rainfall received during the growing season (11 January- May 2003)in Bloemfontein, University of the Free State Agrometeorology experimental site.

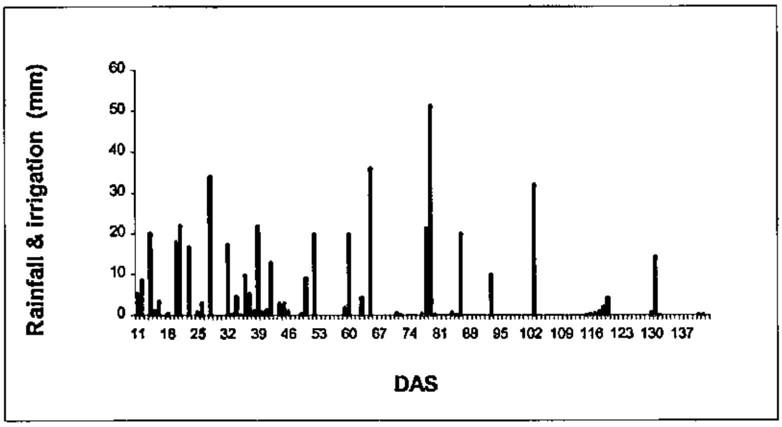


Figure 2.5: Amount of rainfall and irrigation received under the irrigated treatments through the growing season (11 January- May 2003)

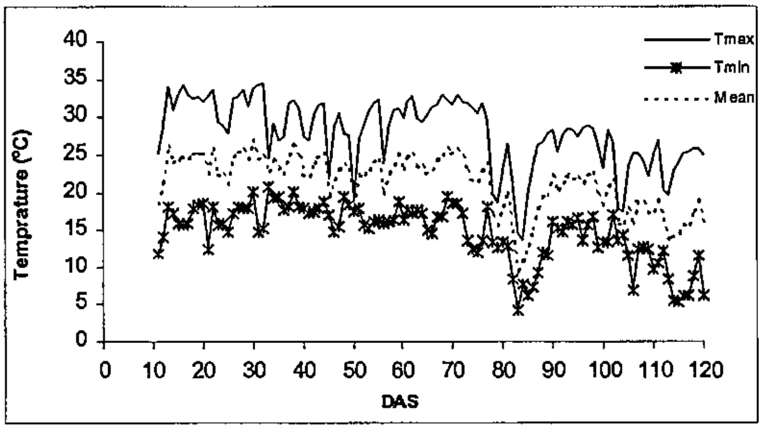


Figure 2.6: Daily maximum and minimum temperature during the growing season (11 January to May) after sowing

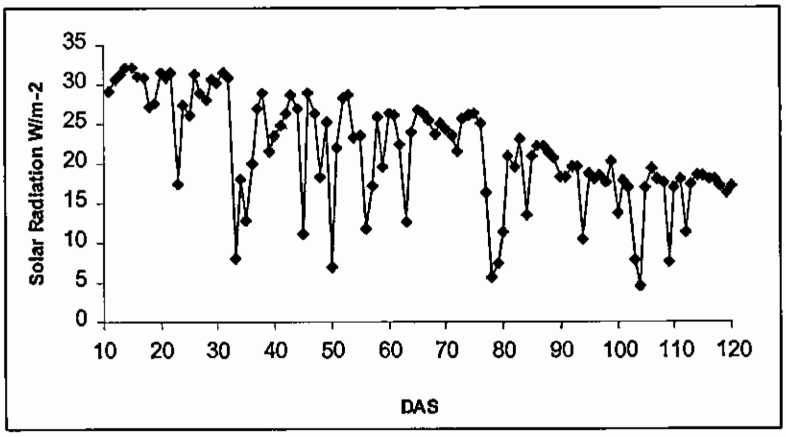


Figure 2.7: Daily solar radiation during the growing season as from the sowing date (11 January 2003) at Agrometeorology experimental site.

2.5 Crop variables

2.5.1 Dry matter production

Above ground biomass was done within a period of seven to ten days. Maize and bean plants were cut at the soil surface and separated into leaves, stem, cobs or pods. Flowers on bean plants were included with the pods and tassels with the stem. The separated plant parts were put in brown paper bags and oven dried at 80°C for three days, after which they were weighed for dry mass. The measurements for the above ground biomass were taken initially 30 days after sowing (DAS). The final harvest was done from an area of 12 m^2 for each treatment, separated into cobs or pods, stems, leaves and weighed. After drying the plant material, it was weighed again.

2.5.2 Leaf water potential

The pressure chamber has been widely adopted as a means of measuring total water potential (Turner, 1988; Leah *et al.*, 1982). The leaf water potential for maize and bean was determined in the field using the pressure chamber technique. The measurements were taken on clear sky between 12 h00 and 14 h00. The samples were taken from the most expanded top leaf, middle leaf and bottom leaf. The instrument was carried into the field to avoid evaporation. The time between leaf excision to measurement in the chamber is critical and should be less than 15 seconds to minimize evaporation along the cut surface. The water potential was recorded immediately a water bubble was noticed on the stem protruding from the chamber. The measurements were made every 7-10 days.

2.6 Measurement of fluorescence

Chl a fluorescence was measured for maize bean at three-height levels for irrigated and rainfed plots using a Plant Efficiency Analyzer (PEA, Hansatech Ltd., King's Lynn, Norfolk, England). Excitation light of 600 Wm^{-2}, from an array of six light emitting diodes (peak wavelength at 650 nm), was focused on the leaf disk to provide a homogeneous illumination light spot of about 4 mm in diameter. *Chl a* fluorescence signals were detected using a PIN photocell after passing through a long pass filter (50% transmission at 720 nm). The fast fluorescence transients were recorded and digitized on line with 12-bit resolution from 10 μs to 1 s.

PEA Fluorometer is an instrument by which the fast *Chl a* fluorescence kinetics can be measured, *in vivo* and *in situ*, with a 10μs time resolution and a measuring time of one second. PEA provides a detailed assessment of the photochemical and non-photochemical process suppressing (quenching) chlorophyll *a* fluorescence. Important fluorescence parameters include minimal fluorescence, Fo, the amount of fluorescence occurring when all photosystem II (PSII) reaction centers are open and the primary electron acceptor, Qa, is fully oxidized; Fm, the maximum fluorescence occurring when PSII reaction centers are closed (Qa is reduced); steady-state fluorescence, Fs, the level of fluorescence occurring during steady-state photosynthesis, and variable fluorescence, Fv, which is the difference between Fm and Fo (Strasser, *et.al.,* 1999 & Sage & Reid 1994).

2.6.1 Dark adaptation

During the course of this study the treatments were dark adapted for a duration of 15 minutes to close all the reaction centers for the plants, as to drive ten chosen fluorescence parameters; minimal fluorescence in dark adapted tissue Fo/Fm, exciton transfer efficiency in dark adapted tissue Fv/Fo, probability that an absorbed photon will move into an electron into the electron transport chain φ_{Eo}, dissipated flux φ_{Do}, absorption per reaction center ABS/RC, energy flux for trapping per reaction center TRo/RC, energy flux for electron transport per reaction center ETo/RC, dissipated flux per reaction center DIo/RC, performance PI (abs) and the driving force (D.F.).

Table 2.4 shows the summary of various energy fluxes, the flux ratios and derivation of formulas. The samples were dark adapted for a period of 15 minutes using special clips from

Hansatech (UK). Incubating samples in the dark reduces fluorescence to the minimum level Fo, where all the PSII reaction centers are open. It is known that it takes much longer for the complete reduction of PSII, hence to starndardise care was taken to ensure that all samples were dark adapted for exactly 15 minutes. The plastic clips used for dark-adapting the leaves were not exposed to direct heat from the sun, as this can produce physiological artifacts (Marler and Lawton, 1994).

Table 2.4 Summary of the JIP-test formulae using data derived from the fast fluorescence transient

Derived and technical fluorescence parameters

Fo = $F_{50\mu s}$, fluorescence intensity at 50μs

F_J = fluorescence intensity at the J-step (at 2ms)

F_M = maximal fluorescence intensity

T_{Fmax} = time to reach F_M, in ms

V_J = (F_{2ms} – Fo) / (F_M – Fo)

Area = area between fluorescence curve and F_M

Mo or dV/dt = 4.(F_{300} –Fo) / (F_M –Fo)

Flux ratios

TRo/ABS or .Po = [1-(Fo/F_M)] or Fv / F_M

ETo/ ABS or .Eo = [1-(Fo/F_M)] . .o

ETo/TRo or .o = (1 –V_J)

Specific Fluxes

ABS/RC = Mo . (1 –V_J) . (1/ . Po)

TRo/RC = Mo . (1 –V_J)

ETo/ RC = Mo . (1 –V_J) . .o

DIo/RC = (ABS/RC) – (TRo/RC)

Driving force

DF_{Po} = log (PI_{Po})

DF_{No} = log (PI_{No}) = -log (PI_{Po})

Vitality indexes

SFI_{Po} = (RC/ABS) . .Po . .o

SFI_{No} = (1- .Po) . (1 - .o)

$$PI_{Po} = (SFI_{Po}) / SFI_{No}$$
$$PI_{No} = 1/ PI_{Po}$$

2.6.2 Sample selection

The samples were selected from each plot and several measurements were made per week, prior to a severe hailstorm on day 74. After the hail damage leaf samples were selected with minimal damage for further measurements. Three samples were selected per plot and three fluorescence measurements were taken per plant (top, middle and lower leaf). The spider plots have a range of 0-2. All the parameters are normalized to the control plant where this is set at 1. Responses less than 1 would indicate stress while stress >1 would indicate achievement. The data was collected from the field for all treatments every 7-10 days. The measurements were taken between 08:00 and 14:00 under full exposure of the sun.

2.7 Measurement of soil water content

2.7.1 Neutron Water Meter

Soil water content was required to calculate the degree of water limitation experienced by the crop, which affected both biomass accumulation and leaf area production. Measurements of soil water content were done using the neutron water meter (NWM) Campbell Pacific Nuclear (CPN), model 503DR. The tubes were installed to a depth of 1200 mm. They were installed both within and between the rows for sole cropping, and for the intercrop an additional one between maize and bean plant. The gravimetric samples were taken at each depth (150, 450, 750, 1050 and 1200 mm) during installation for calibration purposes. The readings were taken in counts at intervals of 32 seconds and converted into count ratios using readings taken at the beginning and end of each measurement. The measurements were made on a 7 to 10 day period. At a time when the NWM had a problem, a second one was borrowed to continue the study. Taking readings from three standard PVC pipes of different diameters using both NWMs, a cross calibration was made.

2.7.2 Neutron water meter calibration

Two pits were dug to a depth of 1500 mm at representative sites on the eastern and western parts of the experimental site. Bulk density values were determined using the core method. Three replicate core samples were taken at depths of 0-300 mm, 400-700 mm, 700-900 mm and 900-

1200 mm. The soil profile layers were reasonably homogenous. Bulk density values for the same depths were used to convert mass water content (θm) to volumetric water content (θv). The linear regressions of volumetric water content (%) values against NWM count ratios for the corresponding depths provide the calibration regression line each depth (Ogindo, 2003).

The volumetric water content of the gravimetric samples often differed considerably. The samples often with volumetric water content values falling above porosity were excluded from the calibration. The equations obtained from regressions are shown in Table 2.5.

Table 2.5 Linear regression of volumetric water content (%) for each depth on count ratio.

Profile Depth (mm)	Calibration equation %	R^2	S.E
0-300	WC = (21.34 X CR) – 0.69	0.86	2.93
400-700	WC = (28.89 x CR) – 13.02	0.96	1.41
700 – 900	WC = (38.97 x CR) – 25.76	0.80	3.99
900 – 12000	WC = (31.88 x CR) – 17.72	0.87	2.62

Chapter 3

WATER STRESS IN MAIZE AND BEAN

3.1 Introduction

Crops growing in semi-arid environments routinely encounter high radiation levels, insufficient soil water, high daytime temperatures and low night temperatures throughout their growth and development. Though a combination of morphological and biochemical changes have been reported to occur in crops grown in semi-arid environments, these changes serve primarily to ensure plant survival. They seem to have only a minor impact of 50% or greater decline in yield and biomass when compared with irrigated crops. Plants in semi-arid regions experience water requirements of as much as 9 mm day^{-1}, and decrease in available soil water between rainfall events can result in shortages that make it impossible for the plant to meet its daily atmospheric demands. Foliage temperatures increase as a consequence of the decline in water available for transpirational cooling, and the differential between air temperature (Ta) and leaf temperature (Tc) increases. The observation of the decrease in Ta-Tc associated with declining soil water comprises the backbone for the crop water stress index (CWSI) sometimes used in irrigation management (Burke, 1990).

The dependence of leaf water potential (LWP) on transpiration flux and soil water supply and the dependence of physiological processes on plant water status make LWP an important parameter for assessing plant-environment relationships. Plant leaf temperatures are a measure of the plant's response to many environmental variables acting in seclusion or in combination (Hattendorf *et al.*, 1988).

Water stress causes severe decrease in photosynthetic CO_2 assimilation (Ort & Boyer, 1985). However, studies have indicated that photosynthate translocation is less sensitive than photosynthesis response to decreases in plant LWP (total water potential) (Daie, 1988; Sung & Krieg, 1979). The concept of water potential is one key to the understanding of the soil-plant-atmosphere continuum. Jeffrey (1987) stated that, by observing the free energy of water in different parts of a system, it is possible to predict its behaviour quantitatively. Movement of water within the plant, and from soil to air via the plant, is driven by gradients in water potential. The value of water potential, ψ, and its algebraic sign (+ or -), represent the extent to which the free energy of water is altered. Interactions of water with solutes, with a matrix of surfaces, or by exposure to less than standard pressure lead to reduced free energy and negative values. In plants, water potential can be resolved into two predominant components, namely:

(i) ψ_s, osmotic potential, which is always negative and ordinarily covers the range –1.0 to –2.5 MPa. It is generated by organic and inorganic solutes in cell cytoplasm and vacuoles. Photosynthesis and ion absorption are the basis for metabolic control of solute potential and absorption of water.

(ii) Pressure potential, ψ_P, may be generated either in turgid cells (positive) or in water columns under tension in xylem (negative). The phenomenon of root pressure may also result in a transient positive ψ_P in xylem (Jeffrey, 1987). Inman-Bamber (1986) investigated using potted sugarcane plants, that plant extension rate was reduced and the youngest unfurled leaf began to roll at –0.8 MPa, stomatal resistance started to rise at –0.8 to –1.0 MPa, green leaf area was reduced at –1.0 to –1.7 MPa, plant extension rate ceased and stomatal conductance reached a minimum at –1.3 to –1.7 MPa, youngest unfurled leaves became fully rolled at –2.0 MPa and the number of living leaves per stalk was reduced to two at –2.8 MPa. Therefore, LWP is a measure of how tightly or strongly a leaf holds its water. To measure LWP, a leaf is clipped off and inserted into a pressure chamber. Pressure in the chamber is increased just until water starts to ooze out of the cut end of the leaf. The greater the pressure needed to exude water from the leaf, the more tightly the leaf is holding on to its water, indicating that the leaf may have been experiencing water stress.

If metabolic processes give rise to water absorption, the sustained flow of water through plants and vegetation, evapotranspiration is caused by the water potential difference between soil and air. Many researchers have investigated the role of water in plant and leaf extension. Attaining a high leaf area index is normally associated with high yields regardless of which part of the plant is of value. The highest seed yields in sunflower subjected to water stress under a rain shelter were obtained from a variety that developed a high leaf area index value after stress was relieved (Rawson & Turner, 1982). Leaf angle is likely to be important in sugarcane recovering from stress since the penetration of radiation into the canopy is increased by a more erect leaf arrangement and this favours the recovery of small stalks (MacColl, 1976).

3.1.1 Wilting

Wilting of vegetation means that the pressure potential of tissue is relatively low, usually because water loss is greater than uptake, due to the following:

a. Rapid transpirational loss by leaves is not matched because of internal resistance to flow,

b. Soil water is low and matrix potential. ψ_m soil is more negative than $(\psi_o + \psi_p)$ tissues.

c. Transpirational loss cannot be replaced because of deficiencies in the root system, including freezing, anaerobic conditions and predator or pathogen damage (Jeffrey 1987).

Taylor (1983) suggested that the tendency of roots to preferentially grow in deeper, wetter soil zones during water deficit might be due to the inverse correlation between soil penetration resistance (strength) and soil water content. When a range of soil bulk densities was used to vary soil strength, and soils were wetted to ψ_w of -0.02 to -1.25 MPa, peanut root elongation rate was inversely correlated with soil strength, not soil ψ_w (Taylor & Ratliff, 1969). Soil strength also affects root branching, thickness and root-hair formation. Goss and Russell (1980) indicated that root physical contact with soil particles was a triggering event that induced changes in root growth and morphology.

Whole plant growth is a function of cell division and expansion. Leaf and root growth involve turgor-driven cell expansion of which the rate may be limited by wall-yielding properties and water transport. When expansion rate decreases during stress, photosynthate import can continue, but at a lower rate (Finn and Brun, 1980). In maize roots, a downhill solute concentration gradient was observed from phloem sieve tubes to elongating and meristematic cells (Warmbrodt, 1987), consistent with pathway for imported photosynthate in root and expanding leaf sinks via plasmodesmatal connections in the symplast. Factors governing cell expansion rates may be primary determinants of photosynthate partitioning between expanding leaf and root sinks.

The close relationship between the functioning and condition of the photosynthetic apparatus and of its pigments (chlorophyll a and b and carotenoids) means that the process of photosynthesis and carotenoid content cannot really be considered in isolation. Factors which affect photosynthesis, one way or another, generally affect these pigments. Photoinhibition which results from stress factors (drought, chilling, etc.) is becoming increasingly important in field situations under natural conditions (Young & Britton, 1990).

Leaf turgor pressure is important because it provides the internal cellular force that causes leaves to expand and grow. Hattendorf *et al.* (1988) found that during vegetative growth, elevated CO_2 caused an increase in the turgor pressure of leaves via an increase of osmotic pressure of cellular contents. This finding explains why soybean leaves grown in elevated CO_2 are larger. However, later in the life of soybean (during seed fill), they found no change in osmotic pressure at elevated CO_2 although the leaves were maintained more turgid, in both well-watered and stressed plants. Growth of plants in elevated CO_2 should be less affected by stress than plants grown at ambient CO_2.

3.1.2 Role of water stress in yield production

Yield variability results from complex interactions between the environment, genetics, management and biotic stress that occur across a field. Of these factors, water stress is one of the major causes of yield variability across fields. Water stress occurs when roots cannot supply enough water to satisfy evaporative demand of water transpiring from leaves. Root water uptake is a function of soil water availability, root depth and density, and location of roots relative to water in the soil. Plant genetics can also influence root growth and development, and subsequently water uptake, by influencing location of roots relative to water in the soil. Daily evaporative demand driving transpiration and potential water stress is a function of uncontrollable environmental factors, including solar radiation temperature, relative humidity and wind speed. Water stress reduces photosynthesis, resulting in reduced crop growth and yield. Minor water stress often occurs for short periods during the hottest part of the day, especially late in the season. Water stress can vary across a field, depending upon soil type, water-holding capacity and drainage characteristics. The integration of variable water stress each day over the season can result in reduced photosynthesis and variable yield loss across a field. Because of the dynamic nature of water stress, it is very difficult to measure and correlate to a single final yield (Batchelor, 1998).

3.2 Definitions

Water potential is defined as the potential energy per mole per unit mass per unit volume or per unit weight of water with reference to pure water at zero potential. In thermodynamic terms, the energy per mole is the molar Gibbs free energy of the water in the system. A gradient of the water potential is the driving force for liquid water movement in a system. Energy per unit volume (J/m^3) is dimensionally equivalent to pressure (kPa or MPa), these units are frequently used for water potential (Campbell & Norman, 1998).

The water potential is made up of several components. The total potential is written as the sum of the components:

$$\psi_L = \psi_g + \psi_m + \psi_p + \psi_o$$

where the subscripts, *g, m, p,* and *o*, are for gravitational, matric, pressure, and osmotic components. In this study, total leaf water potential was determined by the use of a pressure bomb chamber to measure the water potential in leaves. Leaf water potential is a common physiological measurement used to assess the general water status of a plant. A value of zero indicates the absence of water stress, while increasingly negative values depict increasing severity of water stress (Blondel & Aronson, 1999).

Water from the soil moves through roots, through the xylem of plants, to the leaves and eventually evaporates in the substomatal cavities of the leaf. The driving force for this flow is a water potential gradient. For water to flow, the leaf water potential must be at a value below that of the soil. Ohm's law is used to describe the flow of water in the soil-plant-atmosphere system. The main resistances for liquid water are in the root and in the leaf, so the rate of uptake, U, of water from the soil is calculated as follows:

$$U = \frac{\psi_s - \psi_L}{R_R + R_L} = \frac{\psi_s - \psi_L}{R_P}$$

where ψ_s is the soil water potential, ψ_L is the leaf water potential, and R_R, R_L, and R_P are the root, leaf and total plant resistances. The uptake (U) should be thought of as uptake per unit area of soil, not per plant. Campbell (1985) has shown that distribution of roots and soil water potential can be represented by a single equivalent potential, which is the ψ_s. The relative humidity inside the stomata of leaves is nearly 100%. Even in severely stressed leaves, it does not drop below –0.5 MPa during daytime. The control of water loss is indirect, through effects of leaf water potential on the stomatal diffusive conductance for water vapor. At high leaf water potential, the stomatal conductance is determined by radiation, temperature and CO$_2$ concentration. As leaf water potential decreases below some threshold, conductance begins to drop rapidly.

3.3 Study objectives

- To compare the leaf water potential for maize and bean intercropping and sole cropping under irrigated and rainfed conditions.
- To determine the efficiency of photosynthesis (φEo) at different soil water content and leaf water potential throughout the growing season.
- To characterize the leaf water potential gradient through the plant by measuring leaf water potential at different heights of the canopy (bottom, B, middle, M and top, T).
- To compare the leaf water potential before and after hail damage.

Movement of water takes place from a high pressure to a low pressure, thus leaf water potential close to zero would indicate that the plant water needs are sufficient for its use. A low negative value would indicate stressful conditions (Boyer, 1969). Plant water potential indicates the demand for water within a plant. It integrates the soil water tension in the rooting zone, the resistance to water movement within the plant and the demands for transpiration imposed by the atmosphere (temperature, humidity, wind, etc.). Leaf water potential also indicates how the environment affects the plants, which could be used to evaluate the adaptation of the plant to its environment.

3.4 Results and discussion

3.4.1 Leaf water potential changes with time

The discussion will focus on data collected from day 47 until day 74 due to the fact that the crops were severely damaged by hail on day 74. Similar comparison will also be made of data after hail damage. The leaf water potential trend is clearly shown up to day 74. Figure 3 shows that the crops recovered well after the hail damage although the final yield was affected.

Figure 3.1 shows comparative data of measurement of LWP for IMB taken at different plant heights (top, middle and bottom) and the intercrop maize under irrigated (IMI) conditions at different leaf heights, top, middle and bottom. Day 47 was the initial date for taking readings, where the water status of the leaves was almost the same across the treatments. On day 53 the leaves in all treatments were stressed because irrigation was not done for a period of almost a week. Day 67 shows the top leaf to be more stressed, which could be due to high temperature from high radiation exposure. The leaf water potential for intercrop irrigated maize (IMI) ranged from –0.6 MPa to –1.25 MPa compared to –0.8 MPa to –1.9 MPa for IMR. Rainfed intercrop maize (IMR) (Figure 3.2) shows that from day 47-74 the top leaf was more stressed due to sunlight exposure. The bottom leaf was less stressed because it is at the bottom of the canopy and is the most shaded leaf. On day 74, the leaves were more stressed due to physical hail damage, despite the improved water status of the soil after receiving 51 mm rainfall.

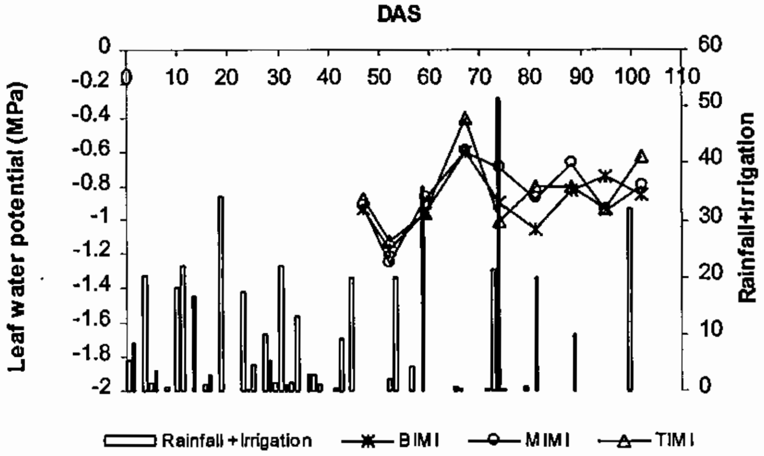


Figure 3.1: Maize leaf water potential under irrigation at different leaf height (bottom, B, middle, M and top, T).

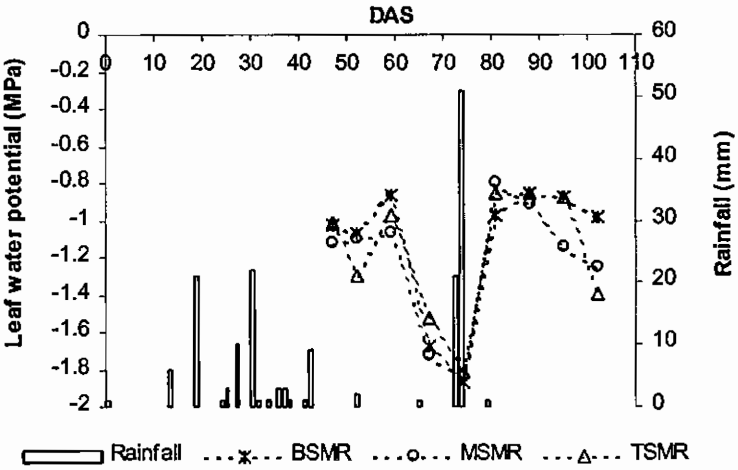


Figure 3.2: Intercrop maize leaf water potential under rainfed conditions at different leaf height (TIMR= top intercrop maize rainfed; M= middle; B= bottom; T= top)

Figure 3.3 shows no major difference between the leaf water potential between day 47 and day 59 across the treatments. On day 67 the middle leaf was more stressed; this could be due to variation in the sunlight exposure. The leaf water potential ranged from –0.7 MPa to-1.42 MPa for irrigated sole maize (SMI). Figure 3.4 shows the sole maize rainfed (SMR) performance, which seemed to be very stressed compared to the SMI. The leaf water potential for SMR ranged from –0.9 MPa to –1.9 MPa. The top and the middle leaf seem to be more stressed than the bottom leaves.

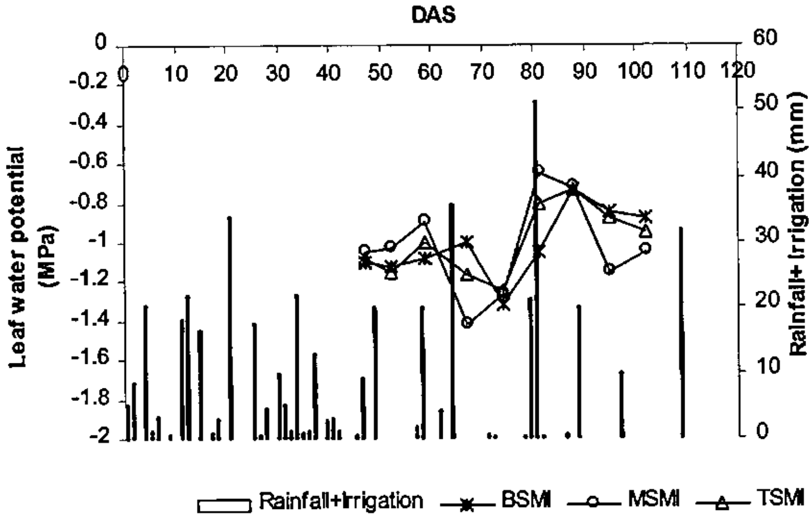


Figure 3.3: The leaf water potential for sole maize under irrigation (SMI) at different leaf height.

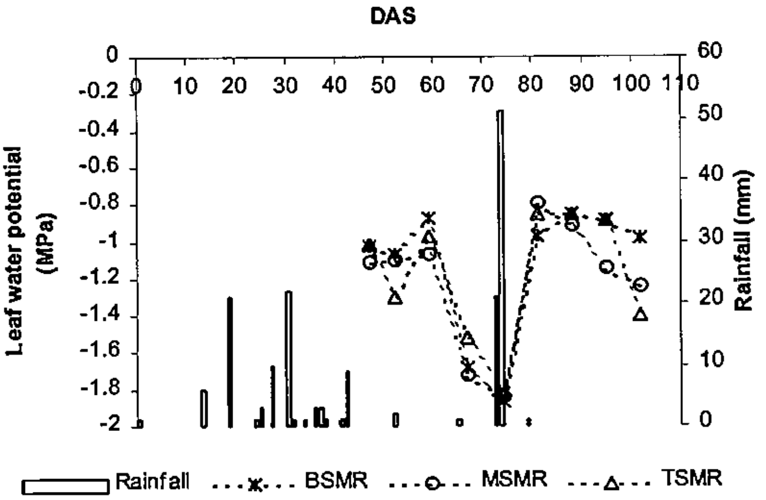


Figure 3.4: The water potential for sole maize under rainfed (SMR) conditions at different leaf height.

Bean plants are very sensitive to soil water conditions and quality and yield can suffer greatly from even brief periods of water shortage. Figure 3.5 shows irrigated sole bean (SBI) whereby the middle leaf seems to be more stressed.This could be due to aging or sunlight exposure. On day 67 the irrigated treatment sole bean plants were more stressed due to low soil water since irrigation was done after a week and the small rainfalls received had little or no effect. The leaf water potential (.$_L$) for SBI ranged from –0.1 MPa to –1.1 MPa. Figure 3.6 represents rainfed sole bean (SBR) whereby the initial readings are low negative or severely stressed on day 47. From Table A.1 SBI values drawn closer to zero than SBR except on two days (76 & 88) when SBI there was a delay in applying irrigation and so it quickly went into stress. However, SBR, which had gradual developing stress, was able to maintain a reasonable value of LWP through a greater part of the season, although at a slightly lower value than SBI. The topmost leaf measured was the most stressed due to sun exposure. The SBR samples ranged from -0.2 MPa to –0.9 MPa. Although high yields depend heavily upon adequate soil water during the post-bloom stage, the need for high amounts of water during the pre-bloom stage is more controversial (Bunce, 1977).

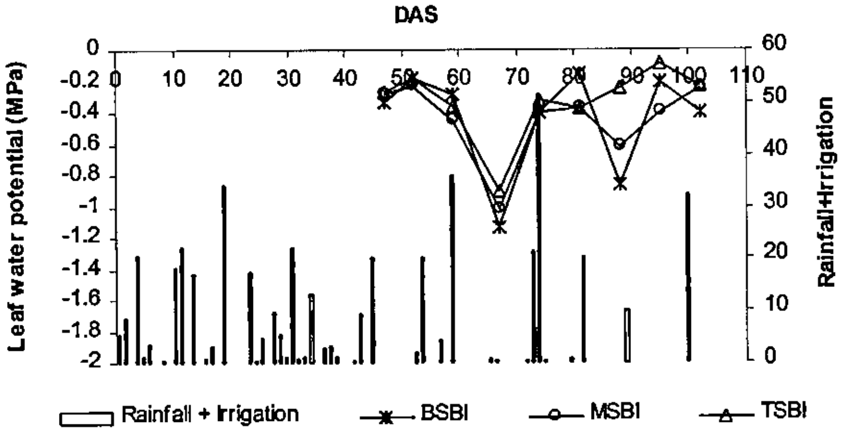


Figure 3.5: Leaf water potential for sole beans under irrigation (SBI) at different leaf canopy heights.

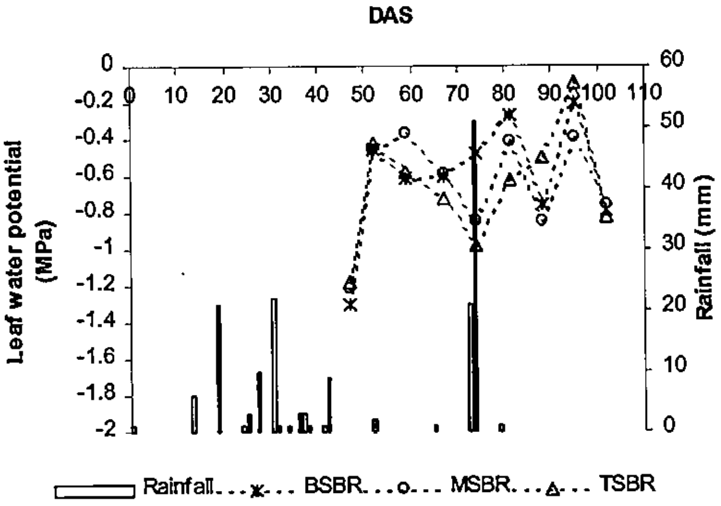


Figure 3.6: Leaf water potential for sole beans under rainfed (SBR) conditions at different leaf canopy heights.

Figure 3.7 shows the relationship and trend of leaf water potential at different height for rainfed intercrop bean (IBR). Initial readings were very stressed until an amount of 5 mm rainfall was received. The leaf water potential ranged between –0.1 MPa and –1.1 MPa. The figure shows that day 67 the soil water was insufficient for the crop needs. The leaf water potential from day 47 to day 60 was almost the same. For intercrop bean irrigated (IBI), Figure 3.8, the top leaf is the most stressed leaf due to sunlight exposure. The IBI leaf water potential ranged between –0.2 MPa and -0.9 MPa.

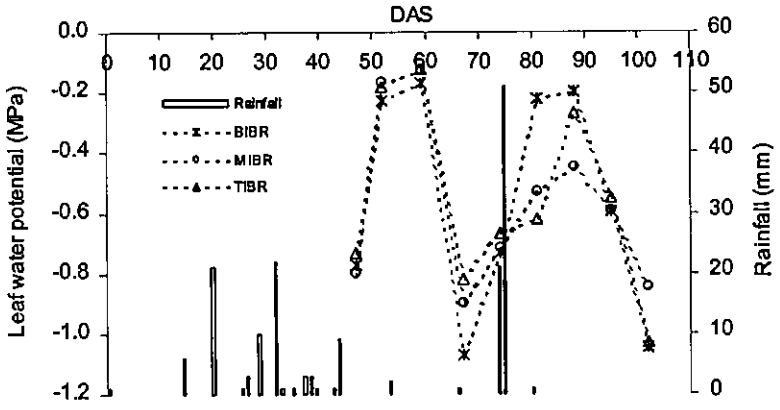


Figure 3.7 Leaf water potential for intercrop beans under rainfed (IBR) conditions at different leaf height.

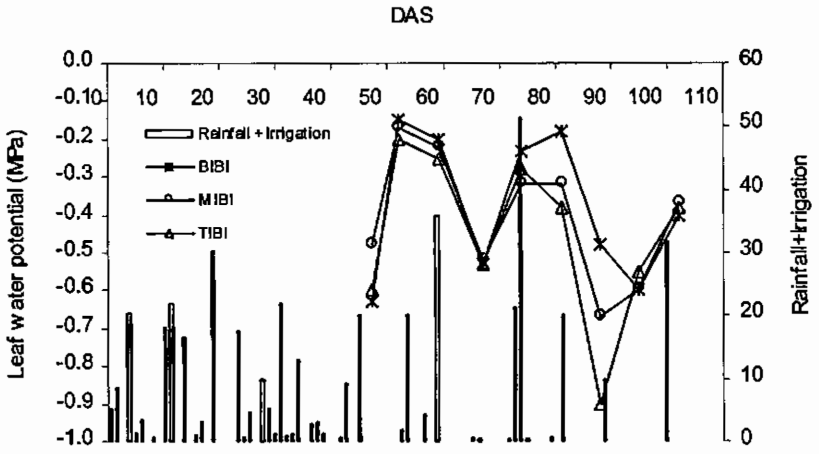


Figure 3.8: Leaf water potential for intercrop beans under irrigation (IBI) at different leaf heights.

In order to assess the water status of the whole plant in each treatment, the average of the values over the three measurement sample heights was used. It can be considered that LWP at each height is the driving force for transpiration for the leaves in that section of the canopy Then the sum of the driving forces would be representative of driving force active over the whole plant simultaneously.

The whole plant average leaf water potential per leaf height was averaged to determine the total driving force of the whole crop throughout the season, as shown in Figure 3. 9 and 3.10 for maize and bean rainfed and irrigated conditions throughout the season. Figure 3.9 shows that the rainfed crops were more affected by water stress than the irrigated ones. The rainfed maize crops were the most stressed from day 60 up to the days just before hail on day 74. IMI indicates that the plots had enough soil water available for the crop. The IMR and SMR were almost the same and had a lower negative plant leaf water potential than IMI and SMI. From the beginning of the season till day 74, rainfall amounting to 87.7 mm was received, therefore rainfed treatments were developing stress symptoms from about 60 days after planting. Following the hail storm, damage (day 74) accompanied by heavy rainfall amount of 51.4 mm. The water stress was relieved, but a further stress was introduced, namely physiological damage to leaves. However, this physiological damage will not really be reflected in the LWP readings since, following the hail storm, the LWP measurements were conducted on intact leaves and not on the damaged leaves from days after planting 81 onwards.

For beans, figure 3.10 shows the whole plant average leaf water potential for sole and intercrop beans under rainfed and irrigated conditions. The bean plant requires a rich, well-drained soil with 500-1000 mm of rainfall during the growing season for optimum germination and growth (Davis *et al.*, 1977). Flowering and pod maturation are usually controlled by the available water regime rather than by length of day. According to Nelson (1962) water stress during flowering and pod development reduced yields by an average of 22%. Mark *et al.* (2001) also found beans to be most sensitive to water stress during flowering and seed formation. Robins and Doming (1986) found water stress during flowering to reduce both pod number and the number of seeds per pod, and water stress prior to harvest was observed to reduce seed weight. All these references show that the bean plant is very sensitive to water stress. SBR and IBR from day 47 up to just before hail on day 74, show far larger negative leaf water potential results, which indicate insufficient water for the plant needs. Irrigated plants were taller, heavier, and produced more pods than rainfed plants. According to Wright (1978) physiological growth stages which are affected by water stress include the following: emergence = 6-10 days after sowing; development of first trifoliate leaves = 15 days after emergence; beginning of flowering = 34 days after emergence; row closure = 42 days after emergence; full cover = 46 days after emergence.

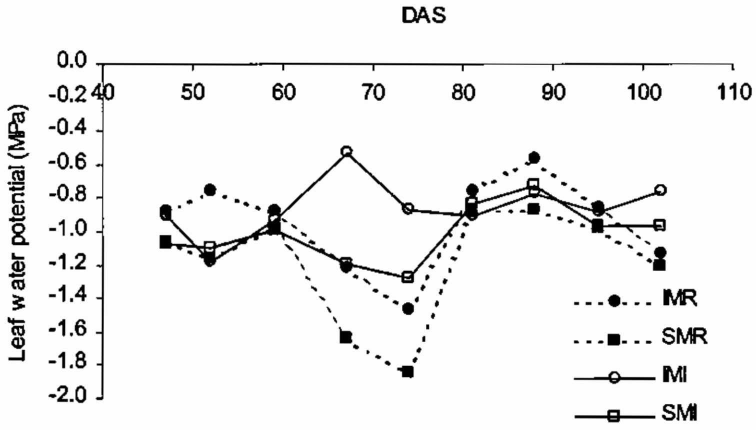


Figure 3.9: The total whole plant leaf water potential for sole and intercrop under rainfed and irrigated conditions throughout the growing season for maize.

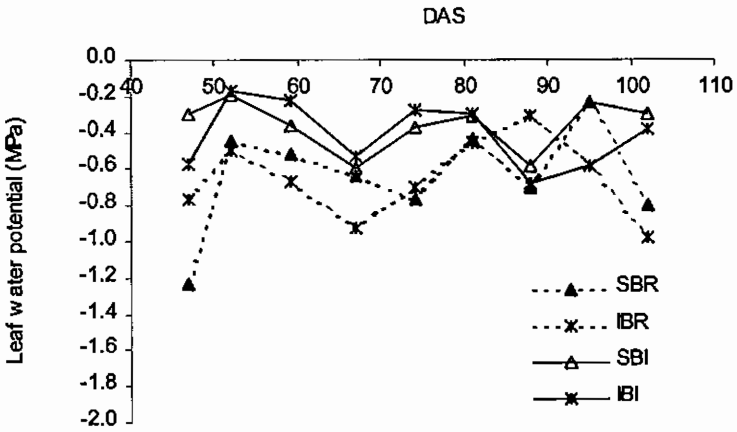


Figure 3.10: For beans, the total whole plant leaf water potential for sole and intercrop under rainfed and irrigated conditions throughout the growing season.

3.3.2 Leaf water potential before hail

The purpose of the study was to determine the leaf water potential for leaves at different heights in the canopy (bottom, middle, and top). Figures 3.11,3.12,3.13 and 3.14 compare the leaf water potential values at the same height for different treatments Figure 11, for instance, compares the lowest leaves for IMI, IMR, SMI and SMR. The analysis is done from day 47 up to day 74 due to the effect of hail after day 74.

Figure 3.11 shows that the bottom SMR leaves were most stressed. The behaviour of bean (Figure 3.14) under water stress is seen when compared with irrigated, as the bottom leaf of IMI had sufficient water. The middle leaves as seen in Figure 3.12 clearly show that the rainfed treatments were far more stressed than irrigated treatments, though the middle SMR was the most stressed during the data collection. The top leaves are prone to low negative water stress due to full sun exposure Figure 3.13. Mallet (1972) found that the water stress at different stages during the growth cycle of the maize plant causes yield reductions which are related to the length, timing and severity of the stress. He also reported that soil water is required just after emergence for the slow growth that takes place. It is very crucial to understand the interaction between water status of the plant and the right planting date because if these are ignored the production will not be at the potential level. Mallet (1972) also found that water stress during the vegetative stage delays enlargement of plant parts and, although plants can recover fully once water is administered, the smaller plant size was accompanied by a lower final dry matter and grain yield. According to Mallet (1972) stress occurring during ear filling had a more direct effect upon yield as it reduces assimilation during the critical period when daily assimilation rates are normally high and when most of the assimilates are being used for grain production.

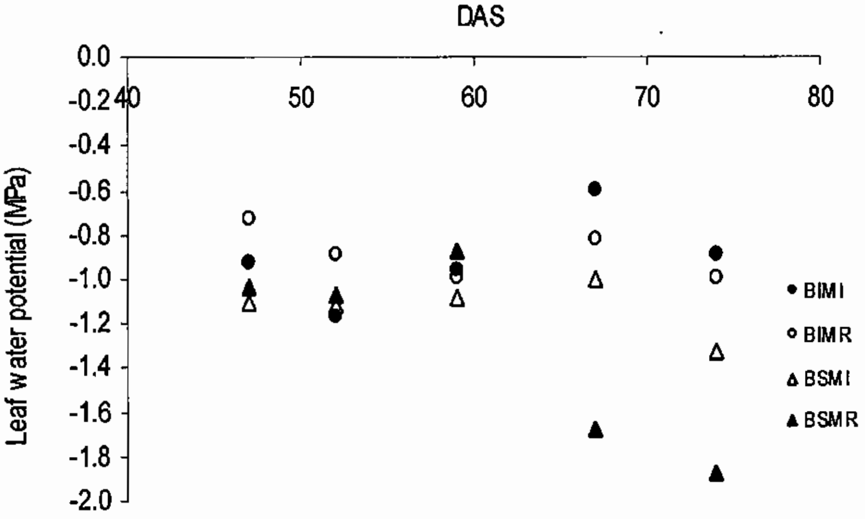


Figure 3.11: The leaf water potential trend for maize lowest leaves under the different treatments.

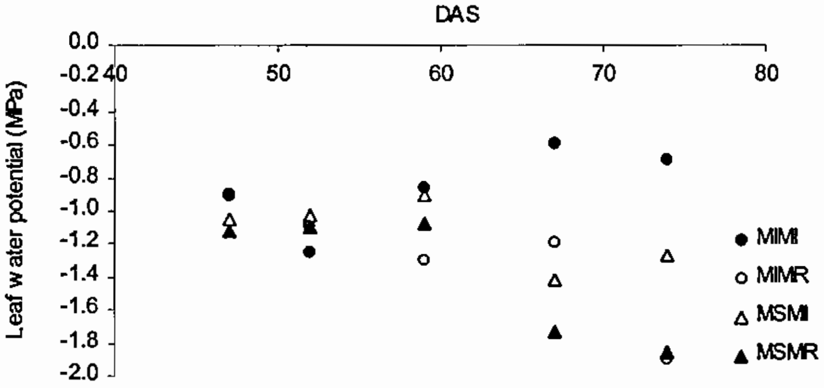


Figure 3.12 The leaf water potential trend for maize middle leaves for different treatments.

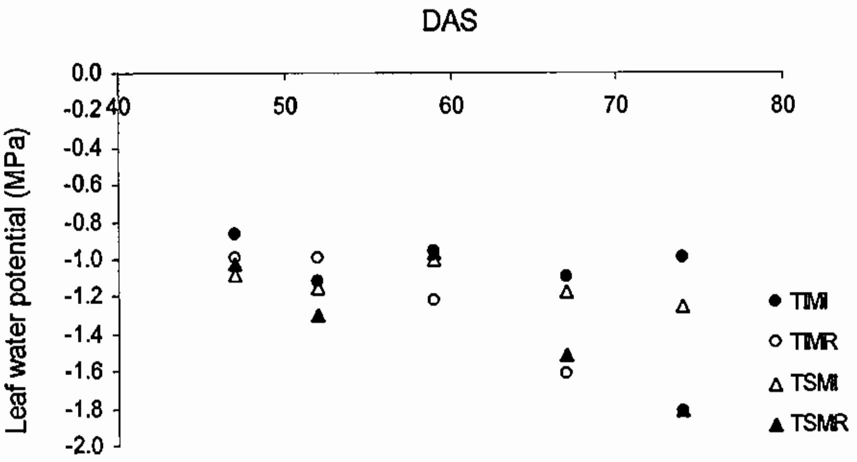
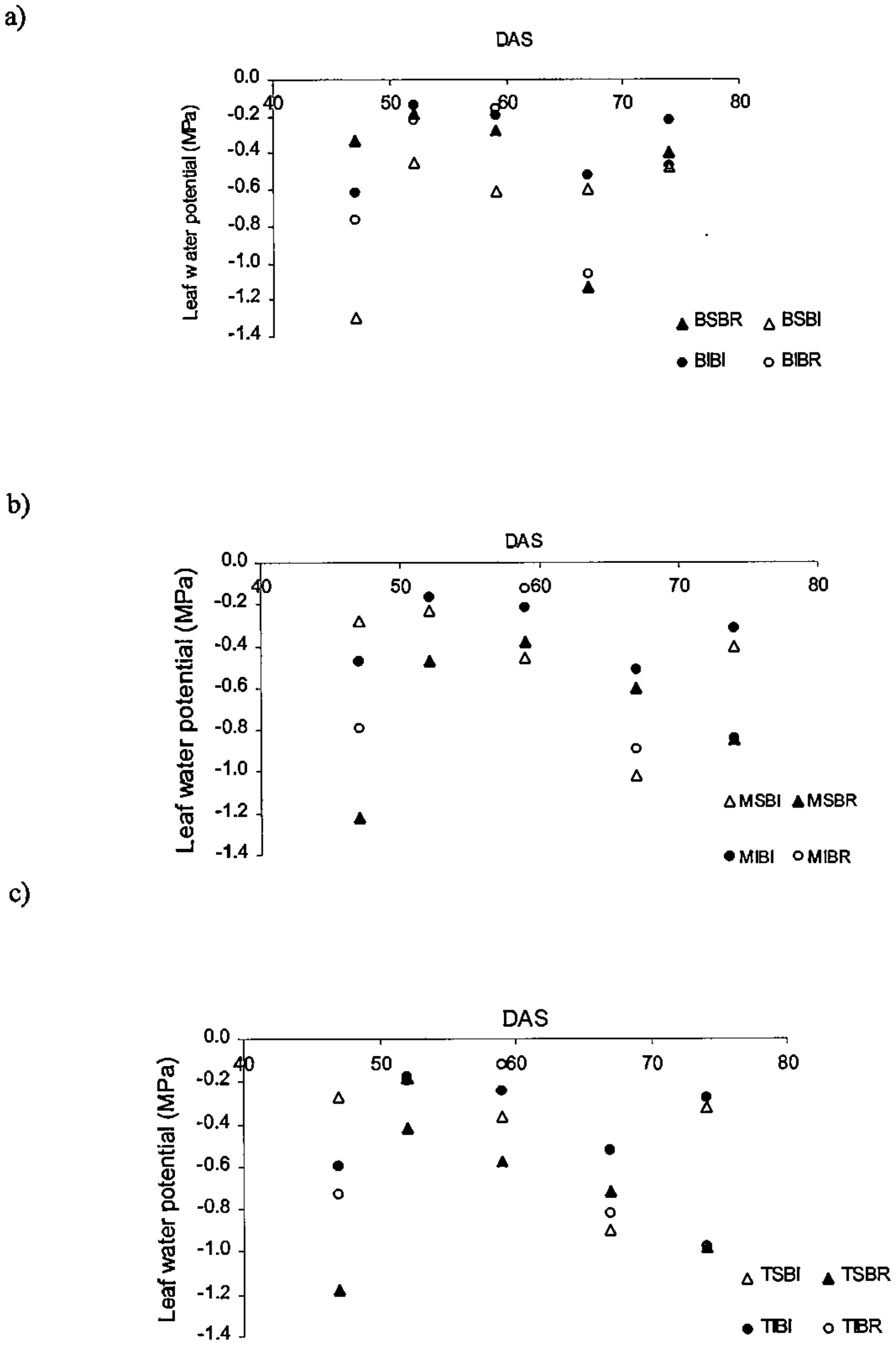


Figure 3.13 The leaf water potential trend for top (T) sole and intercrop maize leaves under rainfed and irrigated conditions.

Figures 3.14 a, b and c show the leaf water stress status for beans at different leaf heights for different treatments under rainfed and irrigated conditions. At all levels, the rainfed treatments were the most stressed. Davis *et al.* (1977) and other investigators found that an available soil water content of at least 70% was shown to be necessary for maximum growth and yield of beans and in the post flowering period available soil water content should exceed 80%. Unlike maize, beans have a shallow root system and are thus particularly responsive to frequent irrigation. Stegman and Olsen (1976) observed that the root zone depth of beans advances to near 100 cm by the time of full cover. Figure 3.14 shows the behaviour of the bottom leaves for beans. Bottom leaves SBI were severely stressed; this should be due to the aging of the leaves and the fact that the canopy was not fully covered. From day 59 to day 74 the plants recovered as the water stress rose from –1.3 to –0.4 MPa. On day 67 the plants were also severely stressed because no rainfall was received for a period of 8-10 days. The middle leaf for SBR was severely stressed initially but recovered later as it rose from –1.2 to –0.9 MPa (Figure 3.15). Later in the season the middle SBI was also severely stressed as it started from –0.3 MPa and went down to –1.0 MPa. The lower leaves SBR were severely stressed which could be due to leaf aging as the plant recovered from –1.2 to –0.4 MPa from day 47 to day 52. The rainfed treatments suffered even more stress on day 67 as they went as low as –1.2 MPa and the irrigated treatments remained at -0.6 MPa for BSBI and –0.5MPa for BIBI (Figure 14 c).



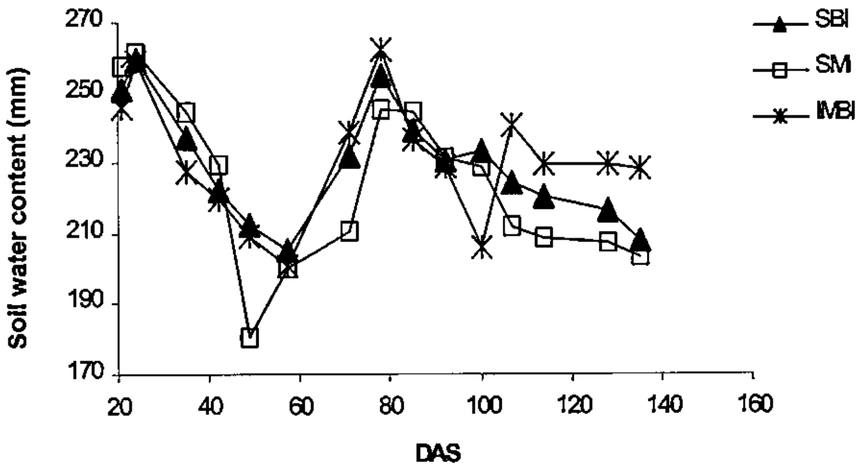
Figures 3.14 a, b and c: The leaf water potential trend for bottom, middle and top sole and intercrop bean leaves under rainfed and irrigated conditions.

3.3.3 Leaf water potential changes with soil water content

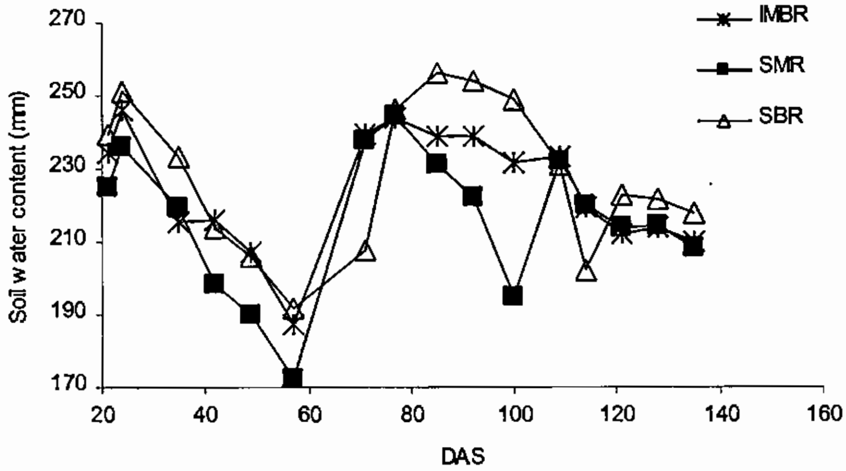
The soil water data was diligently collected each week throughout the season. Representative graphs illustrate the necessary points for discussion and conclusions of this chapter. The detailed data set shows that there are differences between the rainfed and irrigated treatments in terms of leaf water potential.

Figures 3.15b and 3.16b show that under well-watered conditions the leaf water potential was higher negative or simply closer to zero, the water profile maintained water available to the plant. Figures 3.15a and 3.16a show that under stressed conditions the leaf water potential is at lower negative values. The utilization of water by sole and intercropped maize and bean are compared by the crop production per unit area. Morris and Garrity (1993) mentioned that water utilization efficiency by intercrops differs only slightly from water capture by sole crops (usually between –6 and + 7%). Efficient use of water in irrigated crop production requires that the optimum amount of water be applied at the correct time.

a)

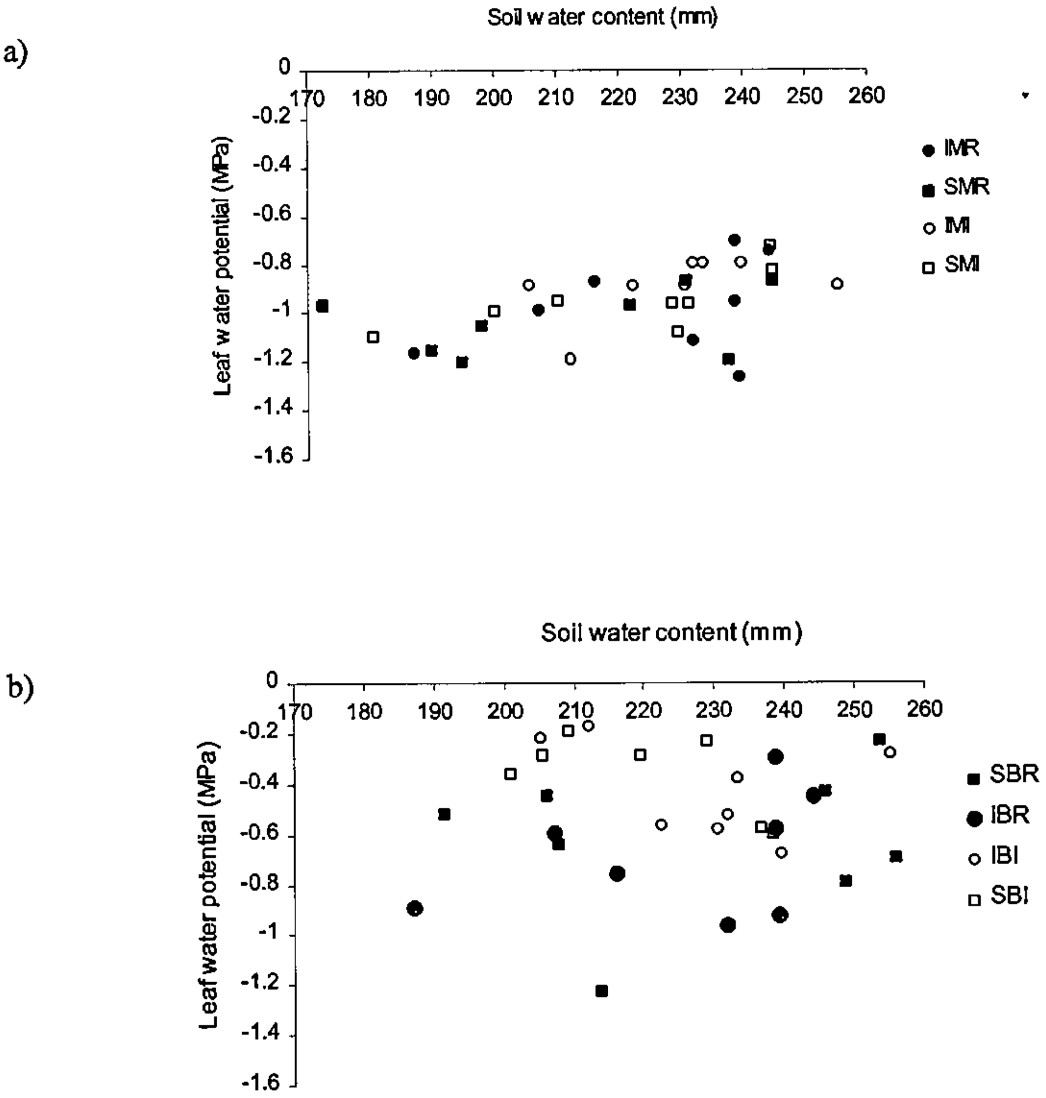


b)

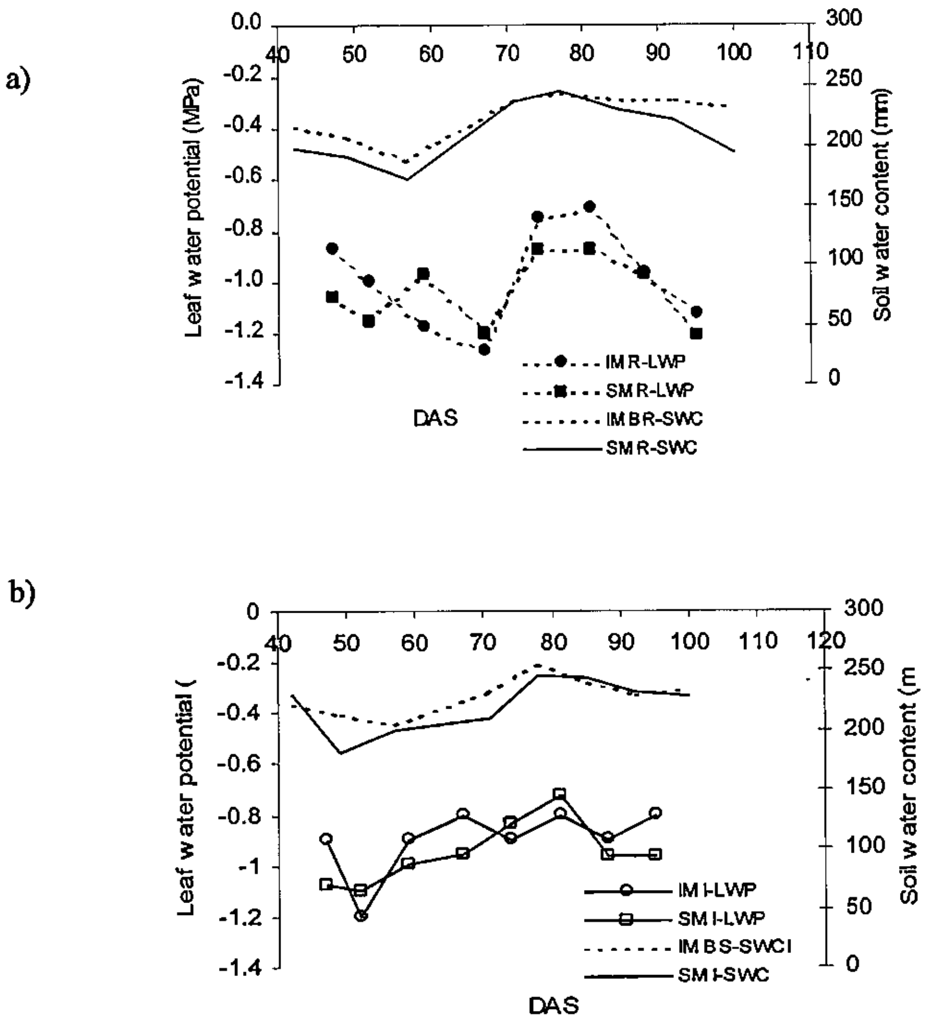


Figures 3.15 a and b: Soil water content trend for the sole and intercropping system maize and bean under rainfed and irrigated conditions.

Figures 3.16 a and b show the relationship between leaf water potential and soil water content for maize and bean treatments. The maize treatments showed a better trend line compared to that of the beans, as most points are concentrated along the same line, although some points are out of the trend, which could be due to other environmental stresses. Figure 3.16 b shows that for the bean treatments there is no consistent relationship, which could be due to various limitations, including errors on the instrument used. It was noted also that the rubbers used to insert the petiole in the chamber pressure were not good for beans. Maize treatments performed better than the bean treatments. In general, as the soil water content increases the leaf water potential tends closer to zero. The far negative values are experienced when there is a lower soil water content, as shown is Figure 3.17 a and b under different maize treatments.

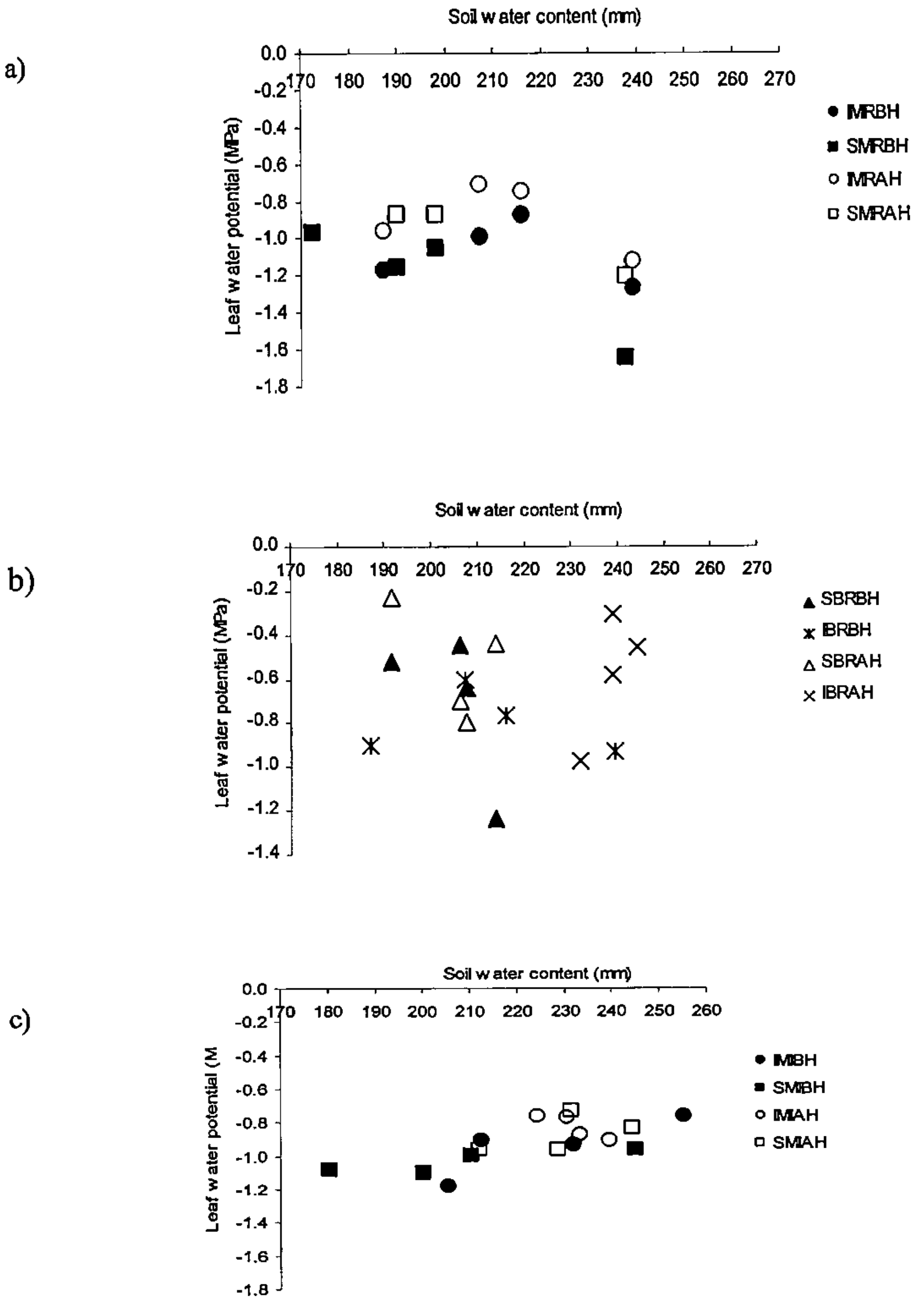


Figures 3.16 a and b: Maize and bean comparison for soil water content and leaf water potential under stressed and unstressed condition.



Figures 3.17 a and b: Maize intercrop and sole cropping leaf water potential relationship with soil water content under stressed (a) and unstressed (b) conditions.

Figures 3.18 a, b, c and d show the relationship between leaf water potential and soil water content before and after the hail damage on day 74. Figures 3.17 a and c show the maize treatments under rainfed and irrigated conditions. The maize treatments show a better relationship than bean treatments. A good trend appears for leaf water potential and soil water content. Figures 3.17 a and c clearly show that as the amount of soil water content increases the leaf water potential becomes less negative except in Figure 3.18 a when the soil water content was 240 mm and hence the plants were affected by other environmental stressors. Figures 3.18 b and d show that the bean treatments under rainfed and irrigated conditions displayed no linear relationship among the treatments. This shows that the environmental stress was dominant over water stress since there is no correlation amongst the treatments. The assumption is that maize treatments will respond more slowly to stress than bean treatments, which respond rapidly. Intercrop treatments are also slower to stress than sole cropped treatments.



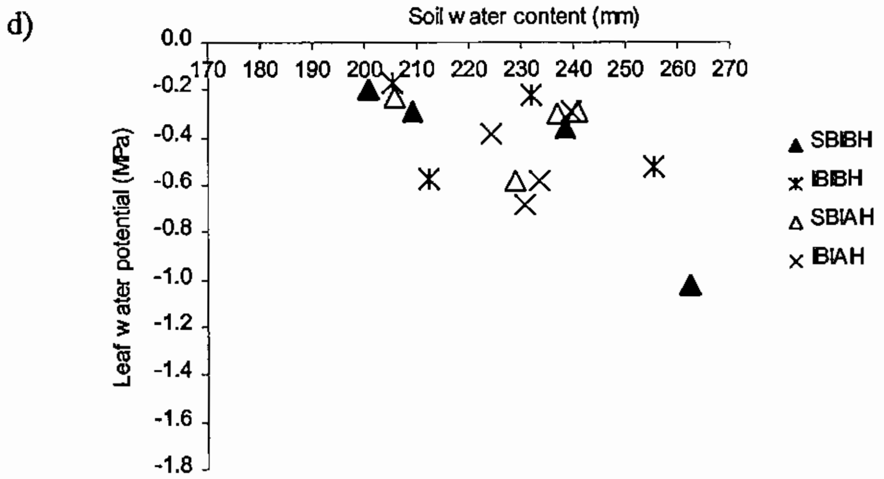


Figure 3.18 a: Rainfed maize treatments; b: Rainfed bean treatments; c: Irrigated maize treatments and d: Irrigated bean treatments. A comparison of leaf water potential against soil water content on days before (BH) and after (AH) hail.

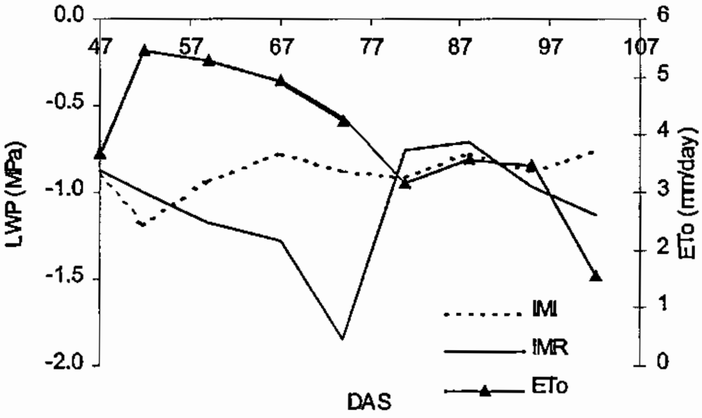
3.3.5 Evapotranspiration

Evaporation and transpiration occur simultaneously and there is no easy way of distinguishing between the two processes. Together with the water availability in the topsoil, the evaporation from a cropped soil is mainly determined by the fraction of the solar radiation reaching the soil surface. This fraction decreases over the growing period as the crop develops and the crop canopy shades more and more of the ground surface area. When the crop is small, water is predominately lost by soil evaporation, but once the crop is well developed and completely covers the soil, transpiration becomes the main process (Allen *et al.*, 1998).

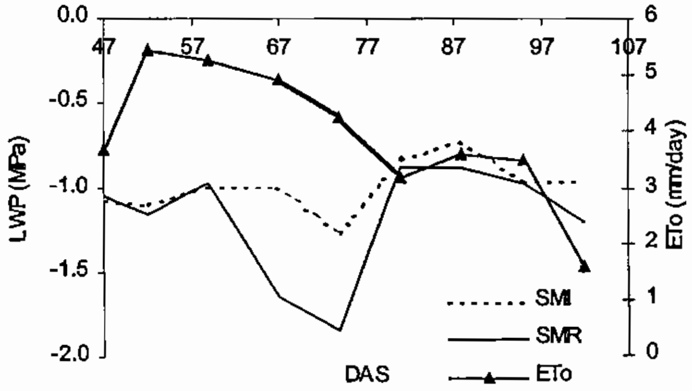
Evapotranspiration for this study was calculated using the REF-ET computer program (www.kimberly.uidaho.edu/ref-et/logo.htm) The REF-ET program provides standardized calculations of reference evapotranspiration and other intermediate micrometeorological parameters that can be compared to calculations by other programs for error checking. The evapotranspiration rate is normally expressed in millimeters (mm) per unit time. The rate expresses the amount of water lost from a cropped surface in units of water depth. The time unit can be an hour, day, decade, month or even an entire growing period or year. For the purpose of this study the Penman-Monteith equation (Allen *et al.*, 1998) was used and calculated by the REF-ET program. Figures 3.19 and 3.20 show the rate of evapotranspiration through the growing season. The figure clearly illustrates the potential amount of water loss during this growing season. The figure also shows the season progression of evapotranspiration (ETo) declining due to the shift towards autumn and winter. Potential evapotranspiration decreased from 5.48 mm per day on day 52 to 3.19 mm per day on day 81, increased slightly on day 88 and 95 and dropped again to 1.58 mm per day on day 102.

Figure 3.19 shows that as the potential evapotranspiration amount increases, which points to a high rate of evapotranspiration, the plant loses its water and undergoes water stress. This may affect the plant growth and development. In Figures 3.19a and b, and 3.20a and b, a comparison between leaf water potential for maize treatments and evapotranspiration (ETo) is illustrated. At the beginning of the season, much water was lost through ETo, whereas the crops from day 47 there were no differences between rainfed and irrigated plots. As the season continues the intercrop maize rainfed (IMR) suffered more stress than the intercrop maize irrigated (IMI) plots. The sole and intercrop bean treatments under rainfed and irrigated conditions are shown in Figure 3.20 a and b as these treatments showed only small difference in terms of stress.

a)



b)



a)

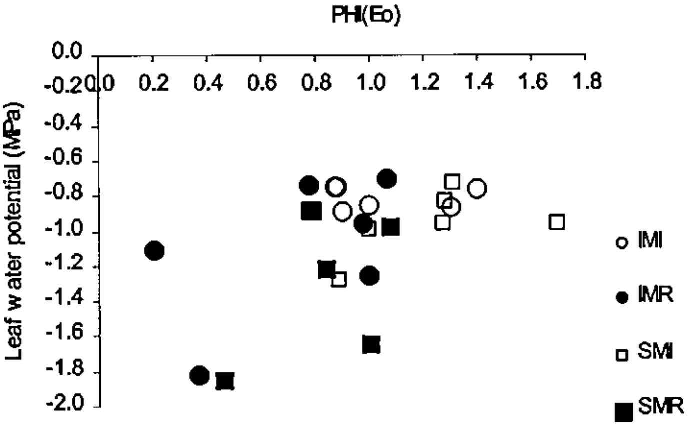


Figure 3.21: Maize calculated photosynthetic efficiency (PHI(Eo)) and LWP for the growing season for intercrop and sole maize under stressed and unstressed conditions.

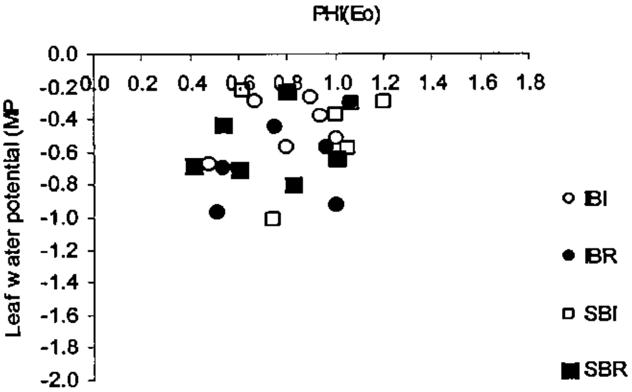


Figure 3.22: Calculated photosynthetic efficiency (PHI(Eo)) and LWP for the 2003 January growing season for intercrop and sole bean under stressed and unstressed conditions.

3.4 Conclusion

In general the top leaves, which are exposed to the sun, have the lowest leaf water potential and the highest driving force for transpiration. Rainfed intercrop maize was more severely stressed than irrigated intercrop maize. At the time of the hailstorm the rainfed intercrop maize suffered even more damage than irrigated intercrop maize. After the hailstorm the irrigated intercrop maize recovered better with respect to leaf water potential and photosynthetic efficiency than the rainfed intercrop maize. Irrigated sole maize performed better for leaf water potential than rainfed sole maize, which was more stressed due to scarcity of soil water. Sole maize rainfed was more stressed than irrigated sole maize.

Looking at Table A.1, the extreme lowest values over the season show that the rainfed treatments were the most negative. Irrigated sole bean (SBI) on day 67 proves that the bottom leaves were more negative compared to the middle leaves, as the top leaves performed better. Irrigated intercrop bean (IBI) shows that the top leaves were more negative to middle leaves, as the bottom leaves performed better. Rainfed sole bean (SBR) shows that the bottom leaves were the most stressed and top and middles leaves were at the same status in terms of leaf water potential. Rainfed intercrop bean (IBR) shows that the bottom leaves were more negative than the top leaves. The middle leaves performed better and were less stressed.

Table A.2 shows the leaf water potential for maize treatment under rainfed and irrigated conditions. Rainfed maize treatments were the most negative compared to irrigated maize treatments. Irrigated intercrop maize (IMI) shows that the middle leaves were more negative than the bottom leaves. Irrigated sole maize (SMI) shows that the middle leaves suffered more stress and that the top and the bottom leaves were at the same stress level. Rainfed maize intercrop (IMR) shows that the middle leaves were more affected than the top leaves and that the bottom leaves performed better. The rainfed sole maize (SMR) shows that the bottom and the middle leaves of the plant were the leaves most affected by water stress and that the top leaves were less stressed.

When comparing the irrigated treatments with the rainfed treatments from Table A.1 and A.2 for maize and bean at height level, it is expected that the irrigated treatments will perform better than the rainfed treatments. The irrigated sole bean (SBI) was more negative than the rainfed sole bean although the top leaves for SBI were less negative. Irrigated intercrop bean (IBI) actually displays more negative values than rainfed intercrop bean (IBR). The maize treatments show different results from that of the bean treatments. The leaf water potential of the maize rainfed treatments were more negative than irrigated treatments. Irrigated intercrop maize (IMI) and Irrigated sole maize (SMI) performed better than rainfed maize intercrop (IMR) and rainfed sole maize (SMR).

The photosynthetic efficiency is affected most when the plant shows more negative values and the plant development is eventually retarded due to water shortage. Treatments under irrigation had a higher photosynthetic efficiency than rainfed treatments. Figure 3.22 illustrates that the irrigated sole maize had the highest photosynthetic efficiency, followed by irrigated intercrop maize, followed by rainfed intercrop maize and lastly by rainfed sole maize. Figure 3.21 for bean treatments shows that the irrigated sole bean had the highest photosynthetic efficiency, followed by irrigated intercrop bean, followed by rainfed intercrop bean and lastly by rainfed sole bean.

Chapter 4

FLUORESCENCE AND PHOTOSYNTHESIS

4.1 Introduction

Photosynthesis is the process by which plants, algae, cynobacteria and photosynthetic bacteria convert radiant energy into a chemically stable form. The process is initiated when radiant flux energy is absorbed by the antenna molecules within the photosynthetic membrane. The absorbed energy is transferred as excitation energy and is either trapped at a reaction centre and used to do chemically useful work, or dissipated mainly as heat and less as emitted radiation-fluorescence (Strasser, 2000; Harbinson & Rosenqvist, 2003).

Chlorophyll fluorescence research began in the early 1930s with experiments done by Kautsky (Kautsky & Hirsch, 1931). Chlorophyll fluorescence is red and far-red light that is emitted from photosynthetic green plants when exposed to photosynthetically active radiation. Although the total amount of light that is emitted is small (typically less than 5% of total irradiance absorbed), it can be quantified with sensitive instrumentation such as the Plant Efficiency Analyzer (PEA) as used in this study. Biolyzer (http://come.to/bionrj) is a tool developed to analyse the fluorescence data, which can rapidly screen many samples and provide adequate information about the structure, conformation and function of their photosynthetic apparatuses (Strasser *et al.*, 1995). Over the years, manufacturers have developed instruments that can quantify all kinds of problems, especially regarding stress reactions in plants. Quantum yield of PSII photochemistry is the result of a combination of photochemical and non-photochemical processes that determine the overall efficiency of PSII. The relative contribution of the two differs between species (Foyer & Harbinson, 1994).

According to Strasser *et al.* (1999) the development of smaller electronic components and optical systems has had the effect that instruments are becoming more readily usable in the field, as done in this study. The use of a far-red background light, which oxidises the plastoquinone pool, allows the determination of the minimum fluorescence (Fo) signal in pre-illuminated leaves. Radiant energy utilised in photosynthesis by higher plants and algae cells is absorbed by a number of photosynthetic pigments with absorption spectra covering a large range of available irradiancies.

The most prominent pigments that absorb this energy are chlorophyll-a and -b. The radiant energy flux absorbed by the chloroplast first excites pigment molecules of light harvesting chlorophyll proteins (LHC). These LHC proteins transfer their energy to Photosystem I (PSI) or Photosystem II (PSII). These photosystems contain the reaction centre pigments for the conversion of absorbed radiant energy into oxidation and reduction potential to drive dark electron transport. Radiant energy absorbed initially by the LHC and transferred to the reaction centers (RCs) is lost through a number of different mechanisms. Approximately 3-9% of the radiant energy absorbed by chlorophyll pigments is re-emitted mainly from PSII from the first excited state as fluorescence. The emission peak is of longer wavelength than the excitation energy. This effect was first observed more than 100 years ago by Muller (1874), visually using coloured glass filters. He also noted that fluorescence changes that occur in green leaves correlate with photosynthetic assimilation. The radiant energy absorbed (ABS) by the reaction centres (RC) drives photosynthetic electron transport (ET) through PSII and PSI, leading to oxidation of water, oxygen evolution, the reduction of NADP+ to NADPH, membrane proton transport and eventually to ATP synthesis (Strasser *et al.*, 1999).

As stated before, most fluorescence comes from PSII. When the chloroplast or leaves have been dark-adapted, the pools of oxidation or reduction intermediates for the electron transport pathways return to a common level, or relaxed state. Upon excessive illumination of a dark-adapted leaf, there is a rapid rise in radiant emission from PSII fluorescence, followed by a series of slow oscillations. This is referred to as the "Kautsky Effect" (Kautsky and Hirsch 1931).

The energy cascade from PSII radiant energy absorption to electron transport, includes absorption of photons (ABS), which refers to the photon flux absorbed by the antenna pigments and consequent excited chlorophyll. Part of the excitation energy is dissipated, mainly as heat and less as fluorescence emission, and another part is channeled as trapping flux (TR) to the reaction centre, to be converted to redox energy by reducing the electron acceptor Q_A to Q_A^-, which is then re-oxidized to Q_A and creates an electron transport (ET) beyond Q_A^- that ultimately leads to CO_2 fixation (Strasser & Stirbet, 2001). The key expression of the JIP-test (Fig. 4.1) is TRo/RC, the specific trapping flux at time zero. At any time TR/RC expresses the rate by which an exciton is trapped by the RC, resulting in the reduction of Q_A to Q_A^-. The maximal value of this rate is given by TRo/RC, because at time zero of a dark adapted sample all RCs are open.

4.1.1 The derivation of energy fluxes

The membrane model, Fig. 4.1, also includes a demonstration of the average "antenna size", which follows the value of the ABS / RC. This value expresses the total absorption of PSII antenna chlorophylls divided by the number of active (in the sense of Q_A reducing) reaction centres. Thus, the antenna of inactivated reaction centres (non-Q_A reducing, here due to the depletion of the oxygen evolving side) is mathematically added to the antenna of the active reaction centers (Strasser *et al.*, 1999). The energy fluxes at time zero, ABS/RC, TRo/RC and ETo/RC, are derived as follows:

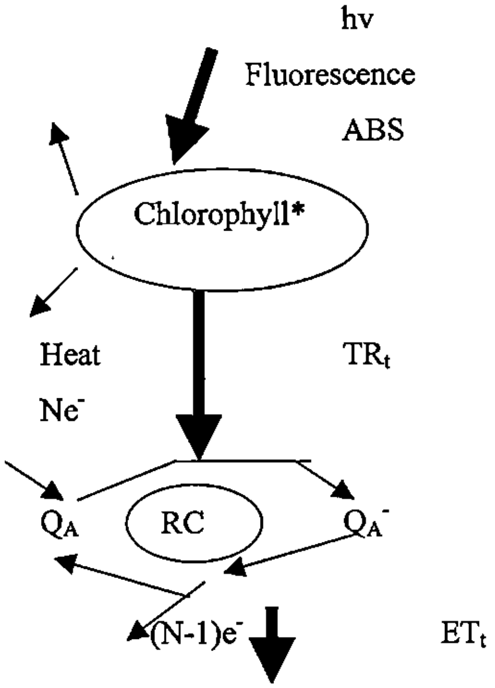


Figure 4.1: Pipeline model of photosynthetic unit where antenna size, energy and electron fluxes are symbolically represented. (redrawn from Strasser, *et al.* 1999).

The maximum quantum yield of primary photochemistry TRo/ABS $\equiv \varphi_{Po}$, the efficiency by which a trapped exciton can move an electron into the transport chain ETo/TRo $\equiv \psi o$, or the probability that an absorbed photon will move an electron into the transport chain ETo/ABS $\equiv \varphi_{Eo}$, are directly related to the three fluxes, as the ratios of any two of them (Figure 4.2). TR/RC expresses the rate by which an exciton is trapped by the RC, resulting in the reduction of Q_A to Q_A^-. TRo/RC gives the maximal value of this rate, because at time zero all RCs are open (Krause *et al.*, 1990).

4.1.2 JIP-test: A tool for screening

The JIP-test was developed to process the O-J-I-P fluorescence transient, which forms various peaks in the initial rise of the fluorescent signal following illumination. This test can be used as a tool for the rapid screening of many samples, providing adequate information about the structure, conformation and function of the photosynthetic apparatus (Strasser & Strasser, 1995). A measurement typically takes 1 second (Figure 4.3).

During the first second the data is stored. The flourescence intensity Fp will be measured. If the excitation intensity is high enough to permit the closure of all RCs then Fp = Fm as the maximal fluorescence intensity. The fluorescent intensities at 150 μs, 300 μs, 2ms (denoted as F_J) and at 60 ms (F_I) are also used in the various calculations (Figure 4.3). The time to reach F_M $t_{Fmax;}$ and the area between the transient and the line $F = F_M$ are also determined. These values are selected for the JIP-test and used for the calculation of phenomenological and biophysical expressions leading to the dynamic description of a photosynthetic sample at a given physiological state.

Based on the different ratios shown in Figure 4.2, the theory of energy fluxes in biomembranes, formulae for the specific energy fluxes (per reaction centre RC) and the phenomenological energy (per excited cross section CS), as well as for the ratios or yields, have been derived using the experimental values provided from the JIP-test. ABS refers to the flux of photons absorbed by the antenna pigments Chl*. (Strasser *et al.*,1995.) Table 2.4 explains the JIP-test derived fluorescence parameters used. Perfomance index is a multiparametric expression taking account of the major steps in the functiong of PSII, namely absorption and quantum efficiency of the conversion of trapped excitation energy to ET beyond Q_A.

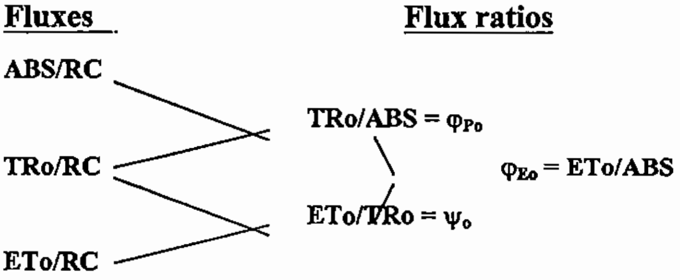


Figure 4.2: A simplified working model of the energy fluxes in a photosynthetic apparatus (Strasser & Strasser 1995).

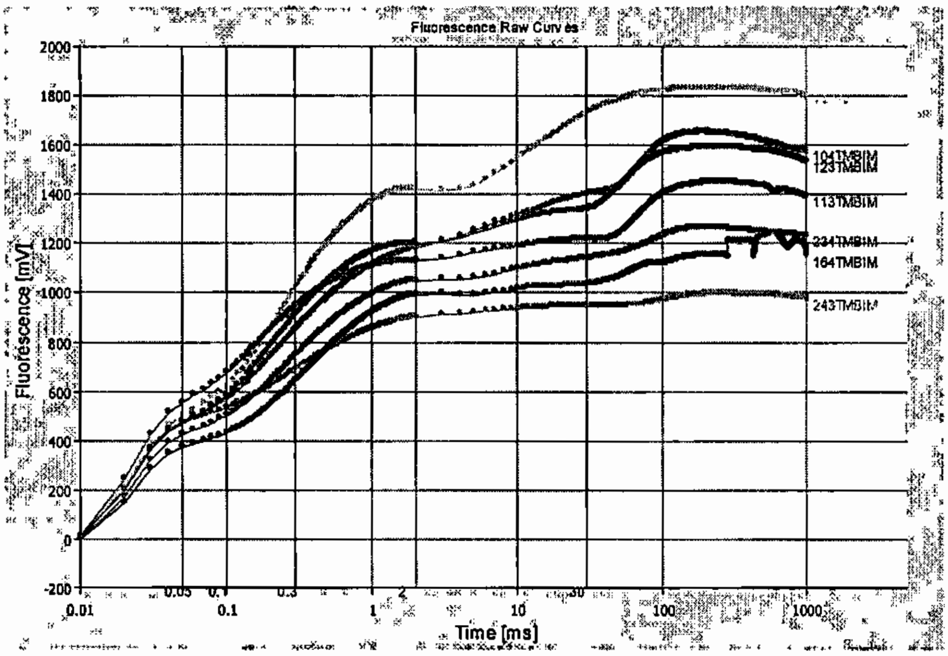


Figure 4.3: Examples of the fluorescence rise (measured with the PEA instrument) in maize leaves under irrigated conditions, taken weekly for the season with the control as the 24tmb sample. The fluorescence values at different time intervals were used in the calculation of the various photosynthetic parameters. Fo, $F_{50\,.s}$, F100 .s, F_{2ms}, F_{M}.

4.1.3 Spider plot presentation

Spider plots represent the constellation of selected photosynthetic parameters quantifying the behaviour of PSII for bean and maize leaves measured at the top, middle and bottom of the plants grown in intercrop and sole cropping under irrigated and rainfed conditions (Figures 4.5 and onwards). In the presentation the initial values (usually day 70) served as the reference and were set at unity against which all other days were compared. This type of presentation provides a direct visualisation of the behaviour of a sample and it can serve as a mapping for easy comparison of plant material and classification of the effect of environmental stressors and of the modifications plants undergo to adapt to new conditions.

4.2 Definitions

Kautsky already measured the fluorescence of chlorophyll in the 1930's. When a dark-adapted leaf is suddenly illuminated, it shows an oscillation in the fluorescence. The "Kautsky measuring protocol" is still applied in laboratories and in the field. Any photosynthetic sample at any physiological state exhibits, upon illumination, a fast fluorescence rise from an initial fluorescence intensity Fo to a maximal intensity F_M. Between these two extremes the fluorescence intensity F_t was found at intermediate steps like F_J (at about 2ms) and F_I (at about 30 ms), while F_M was reached after 300 ms (Strasser & Govindjee 1992, Strasser *et al.*, 1995). The photosynthesis efficiency (φ) is then calculated according to the formula:

$$\varphi = 1\text{-}F_V/F_M = F_V/F_M \qquad (1)$$

Initially it was thought that the photosynthesis rate (P) is then given by

$$P = \varphi.\ PAR \qquad (2)$$

where PAR denotes the photosynthetic active radiation (about 50% of total solar radiation). Research has shown that under intense solar radiation the photosystems are deactivated (Rosema *et al.*, 1998). Through this mechanism, F and Fm decrease simultaneously (fluorescence quenching) and the calculated photosynthetic efficiency φ does not necessarily change. Equation (2) should, therefore, be reformulated to be:

$$P = f_l\varphi.\ PAR \qquad (3)$$

where f_l is the fraction of active photosystems. At low irradiation levels, f = 1, a linear relation between f_l and φ exists as shown in Fig. 4.4. where the distribution of the measurements below the line is the fluorescence quenching due to photosystem deactivation. The unquenched fluorescence level (F*) by approximation satisfies:

$$F^* = a - b.\varphi \qquad (4)$$

and thus:

$$f = F/F^* = F/(a\text{-}b.\varphi) \qquad (5)$$

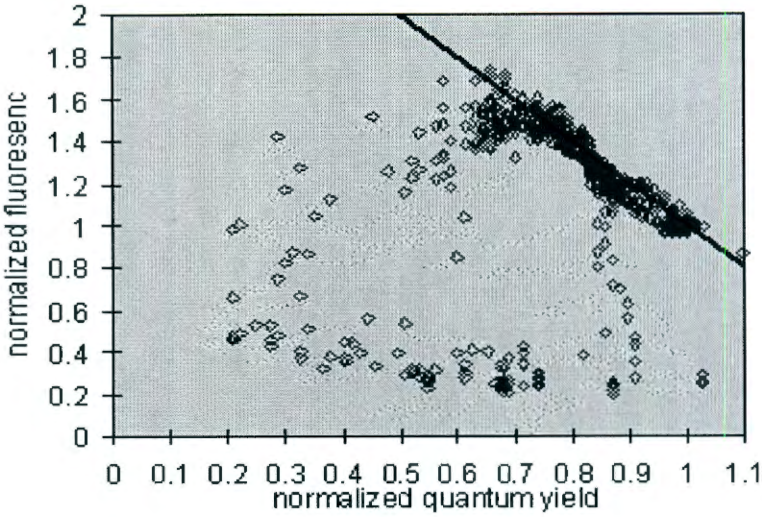


Figure 4.4: Fluorescence against photosynthesis efficiency (EAR-PPM, 2000).

The constants a and b can be determined from a series of PEA measurements at low light levels. The gross photosynthetic rate is then found by entering equation (5) into (3). The photosynthetic activity is expressed as the required radiation for photosynthesis per second. This can be converted to CO_2 assimilation, using:

$$P\ (\mu\text{mol PAR/m}^2\text{/s}) = c.\ P\ (\mu\text{mol CO}_2\ \text{/m}^2\text{/s}) \qquad (6)$$

Where 'c' denotes the number of photons needed to chemically bind one molecule of CO_2. For a C3 crop, c = 8, for a C4 crop, c = 12 to 13, which are theoretically minimum values, i.e. the minimum quantum requirement. Edward & Baker (1993) found that the CO_2 assimilation (A) for maize can be calculated accurately by:

$$A = \varphi.\ PAR - 5.9610^6\ (-4632/Ta) \qquad (7)$$

where φPAR is the gross photosynthesis rate and $5.96.10^6$ (-4632/Ta) is the respiration rate, which depends on the air temperature Ta.

4.3 Specific aim

The aim of this study was to use the JIP method of measuring of chlorophyll fluorescence using the PEA from Hansatech (UK) to determine the photosynthetic efficiency and other photosynthetic responses for maize/bean intercrop and sole cropping under irrigated and rainfed conditions.

4.4 Results and Discussion

Chlorophyll fluorescence correlates well with other methods of physiological analysis and is a sensitive indicator of photosynthetic disturbances. However, it is not prudent to consider it a complete replacement for measuring photosynthetic rates or other physiological features (Maxwell & Johnson, 2000; Mahommed *et al.*, 1995). Ten parameters were selected and calculated using the Biolyzer software for the PEA measurements. The chlorophyll fluorescence measurements supplemented the measurements done on leaf water potential and soil water content (Chapter 3). It is also known that chlorophyll fluorescence readings may vary according to biological factors such as leaf age, stage of development, leaf exposure to the sun and chlorophyll content (Gitelson *et al.*, 1999; Spunda *et al.*, 1998). The C3 and C4 plants differ in their capacity to transfer electrons. Maize (C4-plants) have a greater capacity for electron transport at high radiant flux density than bean (C3-plants) (Greer & Halligan, 2001).

4.4.1 Bean top leaves

Figure 4.5 shows a spider plot presentation of the constellation of selected parameters quantifying the behaviour of PSII of the top leaves irrigated of intercrop bean (TIBI-unstressed) and top leaf of rainfed intercrop bean top leaf (TIBR-stressed). The data are normalised to the control, where the controls were the initial readings of each treatment. Major energy dissipation (φ_{Do}) was seen on day 84 of the unstressed plant, resulting in a low photosynthetic efficiency PHI(Eo), low ET, low driving force (DF) and low performance index (PI(abs)) values. The electron transport per reaction center (RC) was also low and the results clearly show major stress on day 84, while for the experimental period minor differences were seen. For TIBR it is clear that lots of energy was dissipated on days 84, 87, and 93, indicating how stressed the plants were. The low values for the performance indices PI(abs) and φ_{Eo} also confirm the severe stress that these plants were experiencing. Using the youngest leaves (top) the chlorophyll fluorescence data clearly show that the irrigated plant was less stressed than the rainfed plant.

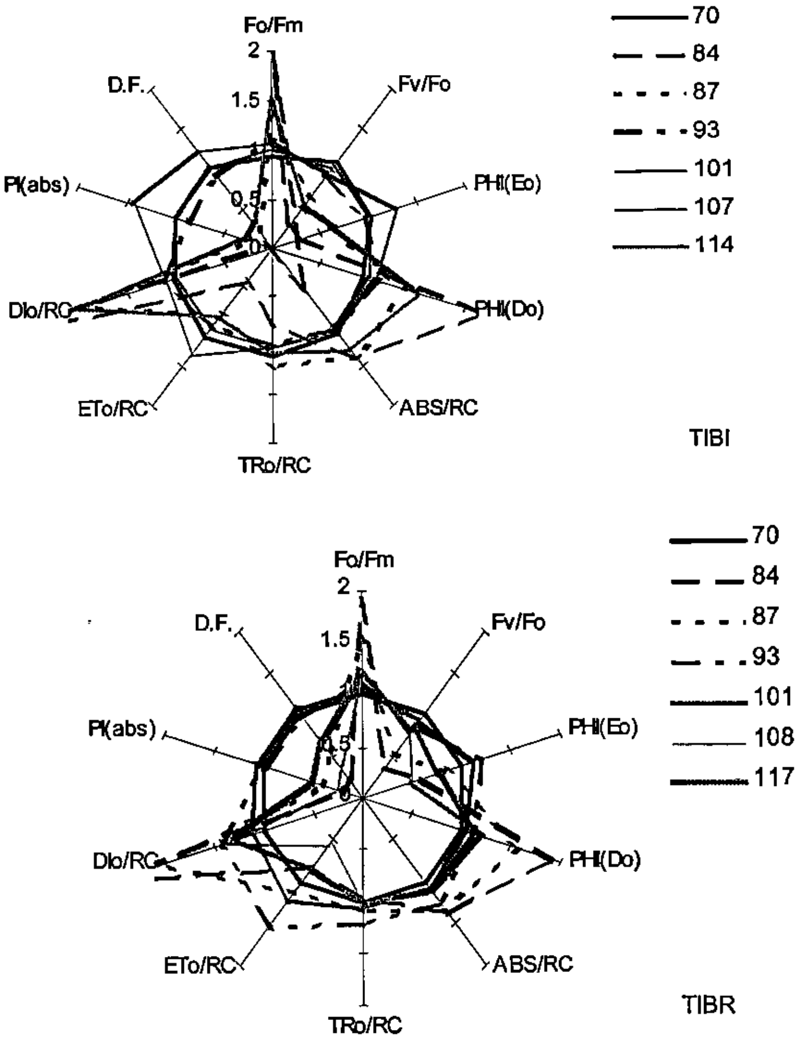


Figure 4.5: Spider plot representations for top leaves of irrigated intercrop bean (TIBI) and rainfed intercrop bean (TIBR). The different plots show the days following the initial measurements. Day 70 served as the control (i.e. 1.0).

Chlorophyll fluorescence measurements of the top leaf of the irrigated sole bean (TSBI) indicated that the plant was severely stressed on day 84 (Fig. 4.6), where major photosynthetic energy was lost as confirmed by the high dissipation (PHI(Do)) and DIo /RC low driving force and high Fo/Fm. Following this, the plant recovered and the parameters approached the control conditions. The data clearly show that the rainfed sole bean plant (TSBR) was severely stressed during the period under investigation. This is clear from the high PHI(Do), ABS/RC, DIo/RC and Fo/Fm values.

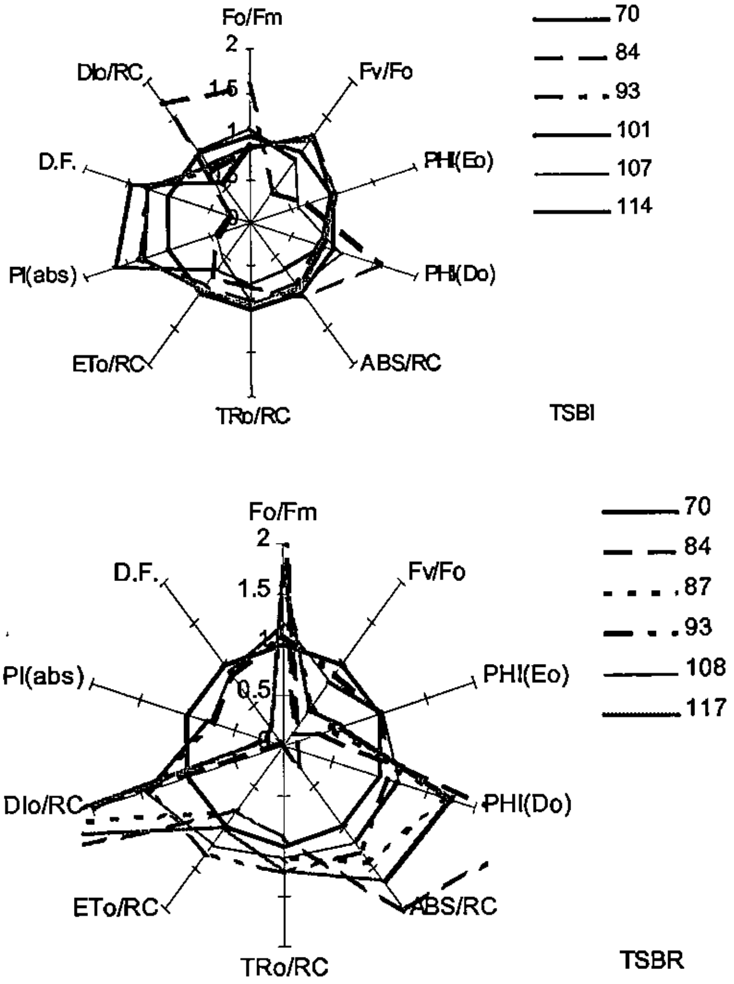


Figure 4.6: Spider plot representations for top leaf irrigated sole bean (TSBI) and top leaf rainfed sole bean (TSBR). The different plots are the days throughout the season, where day 70 served as the control.

4.4.2 Bean middle leaves

Chlorophyll fluorescence data from the middle leaves in Figure 4.7 also confirm major differences between the unstressed and stressed plants throughout the season. Major dissipation (DIo/RC and φ_{Do}) for MIBI, which confirms energy loss from the photosynthetic process, took place. MIBR also shows stressed conditions for rainfed intercrop bean plants, as φ_{Do}, ABS/RC, DIo/RC and Fo/Fm values were very high. This resulted in φ_{Eo} being very low, which shows that photosynthesis and the plants were photosynthetic highly stressed.

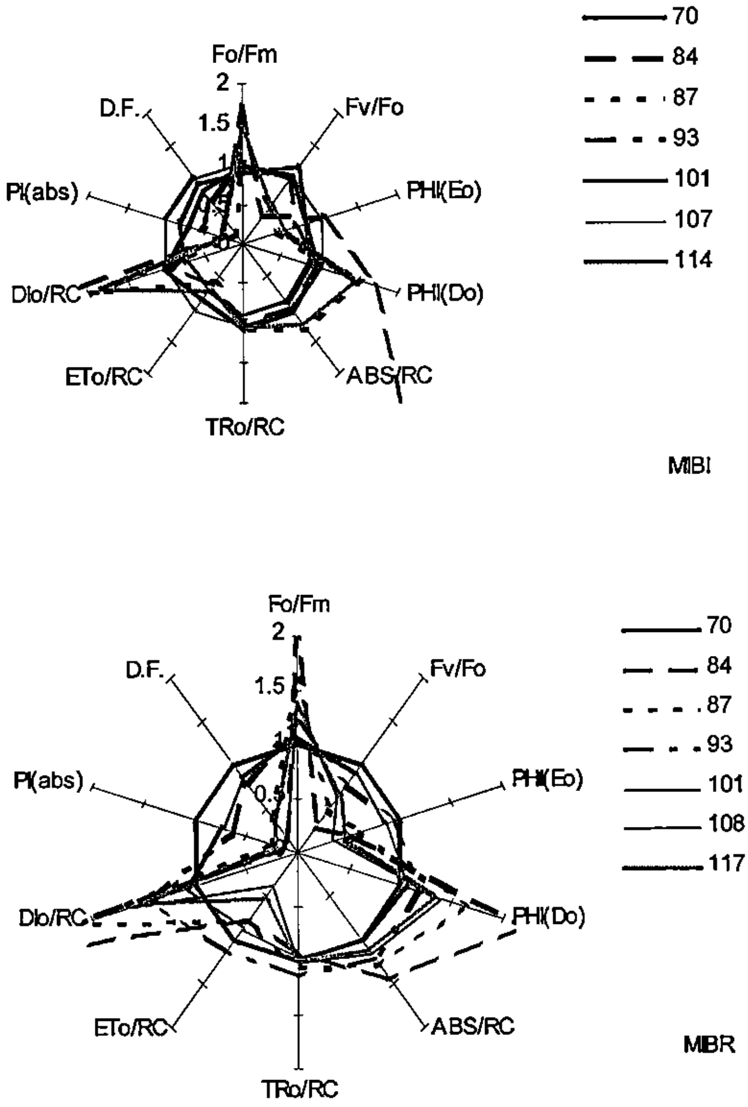


Figure 4.7: Spider plot representations for middle leaf irrigated intercrop bean (MIBI) and middle leaf rainfed intercrop bean (MIBR) where day 70 served as the control.

Major differences are clear between irrigated sole bean middle leaves (MSBI) and rainfed sole bean middle leaves (MSBR) (Figure 4.8). Except for day 84 MSBI was in a better condition than MSBR. This is clearly seen by the overall low D.F., PI(abs) values, high φ_{Do} and DIo/RC values of the MIBR plants. Again, day 84 shows that the plants were severely stressed due to a lack of water as no irrigation was applied for almost 13 days. The problem is that day 84 was stressed and consequently the rest of the values suggests major improvements which are not meaningful since day 87 was used as the control.

4.4.3 Bean bottom leaves

The bottom leaves are assumed to be the less stressed due to shading and less exposure to the sun. Figure 4.9 shows the results from the irrigated intercrop bean bottom leaves (BIBI) and rainfed intercrop bean bottom leaves (BIBR). Except for day 84 and 87, BIBR were in a better condition than BIBI.

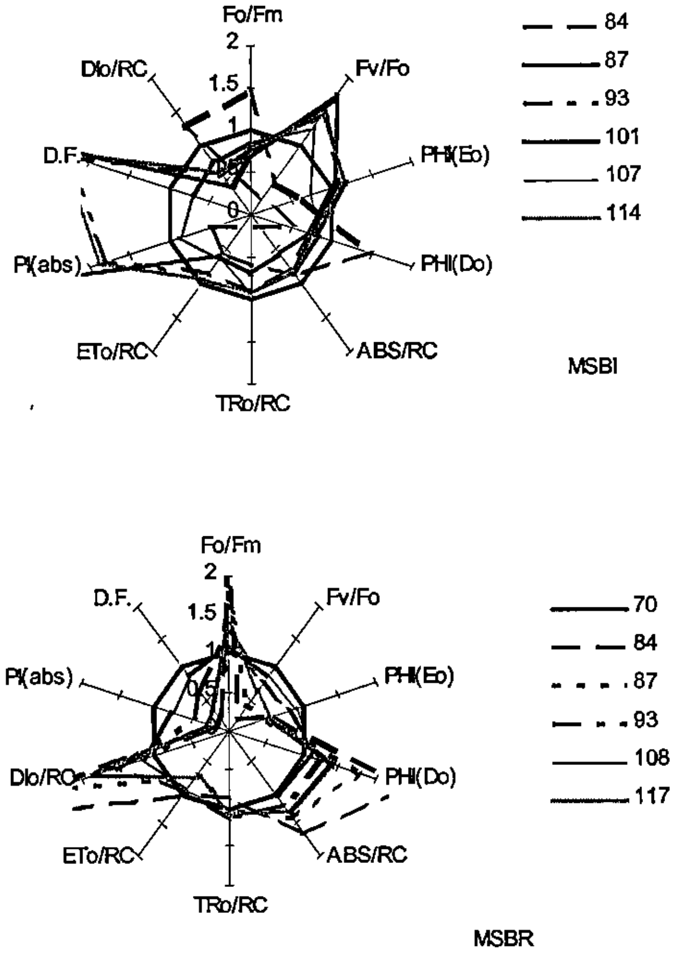
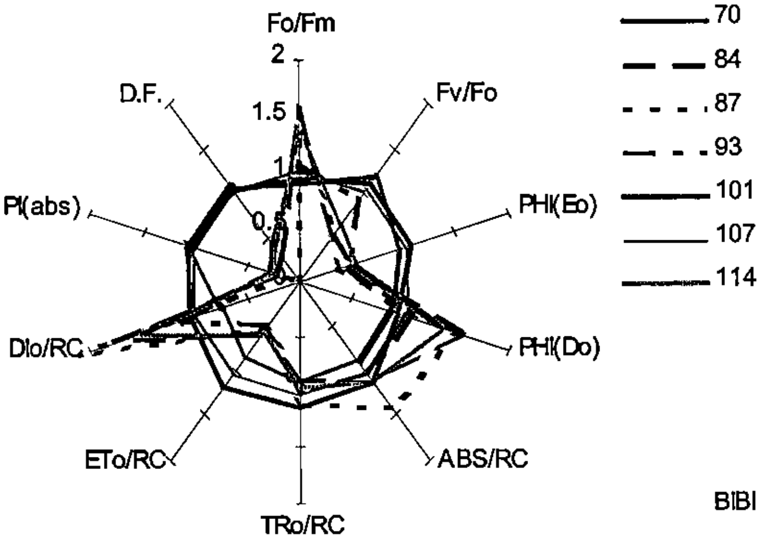


Figure 4.8: Spider plot representation for middle leaf irrigated sole bean (MSBI), where day 87 served as the control and for middle leaf rainfed sole bean (MSBR), day 70 served as the control.



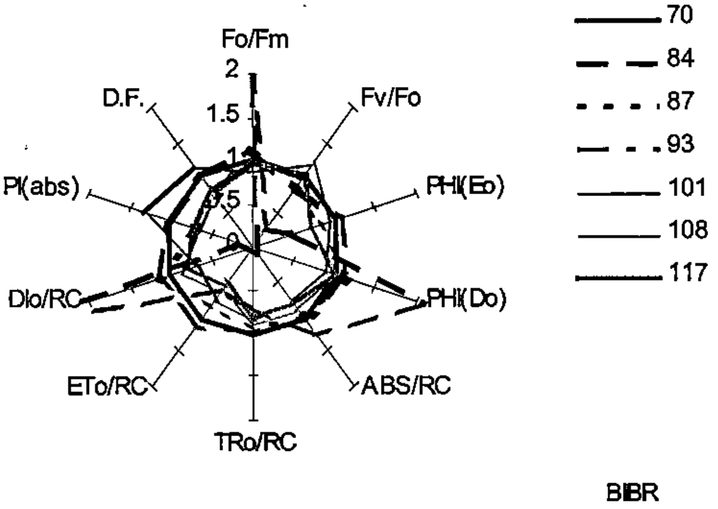


Figure 4.9: Spider plot representation for bottom leaf of irrigated intercrop bean (BIBI) and bottom leaf of rainfed intercrop bean (BIBR), where day 70 served as a control.

Results from the bottom leaves of irrigated sole bean leaves (BSBI) and rainfed sole bean leaves (BSBR) are shown in Figure 4.10. BSBI improved considerably over the experimental period as clearly shown by the increases in Fv/Fo, φ_{Eo} TRo/RC, PI(abs) and driving force (D.F.), and lower values for DIo/RC, Fo/Fm and φ_{Do}. However, the BSBR plants became severely stressed over the experimental period as shown by the lower values of Fv/Fo, φ_{Eo} , ETo/RC, PI(abs) and D.F., and the high dissipation of trapped energy as seen in the high values for DIo/RC and φ_{Do}.

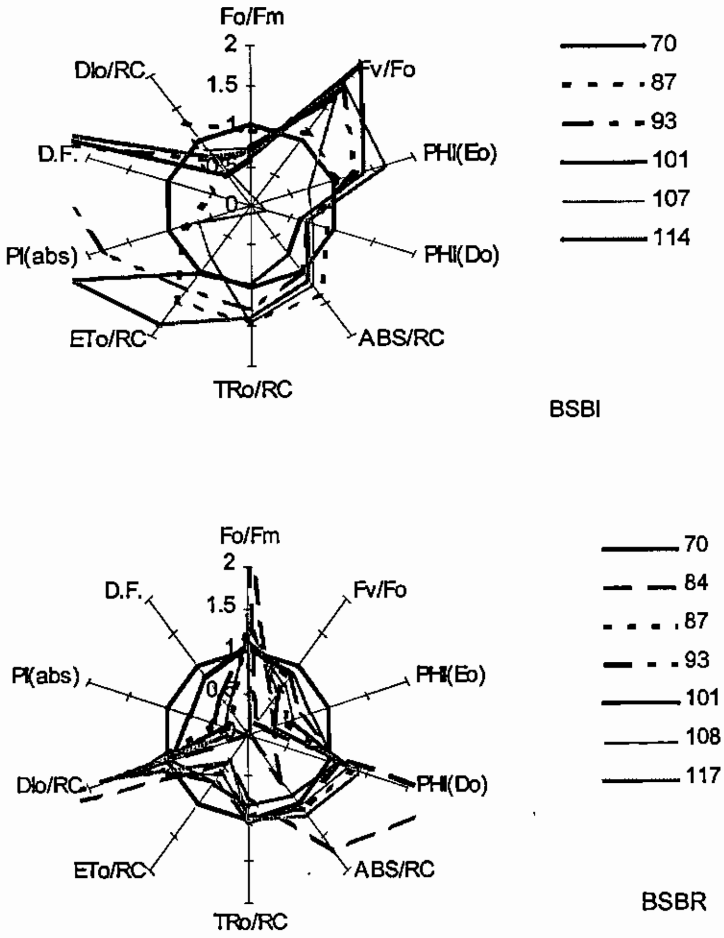
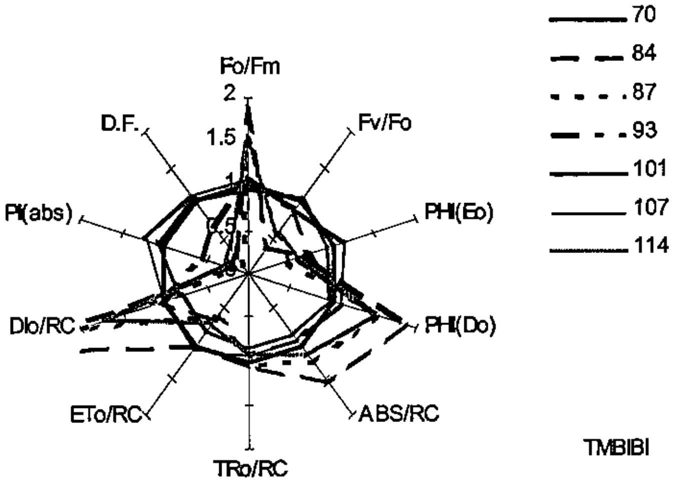


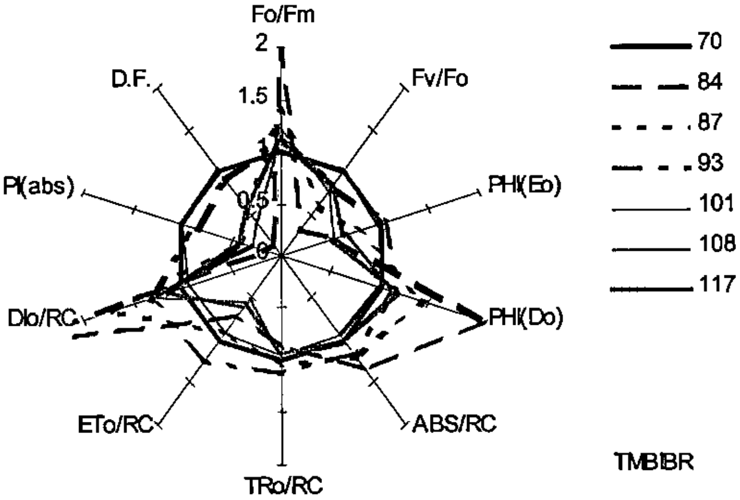
Figure 4.10: Spider plot representations for bottom leaves irrigated sole bean (BSBI) and bottom leaf rainfed sole bean (BSBR), where day 70 served as the control.

4.4.4 Bean whole plant

Figure 4.11 shows the whole plant averages over the experimental period. For all of these treatments (Figure 4.11) the control is day 70.The legend shows the number of days when the measurements were taken. Data for the TMBIBI plants indicated stress especially on days 84, 87 and 114, as indicated especially by the high dissipation of absorbed energy (φ_{Do} and DIo/RC) and low photosynthetic efficiencies (φ_{Eo}). DF TMBIBR appears to be more stressed than TMBIBI because on most days φ_{Eo}, D.F., PI(abs) and Fv/Fm were lower than the control and the most energy was dissipated. The irrigated sole bean plants (TMBSBI, Figure 4.11) experienced stress on days 84 and 101, but for the rest of the time the plants were in a better condition than at the onset of the experiment (day 70), as appeared under rainfed sole beans. (TMBSBR) were stressed on day 70, while on day 84 was partly severely stressed. Very low values for D.F., PI(abs) and

Fv/Fo were seen. These results for the whole plants clearly indicated that the irrigated plants performed better than the rainfed plants and that the sole plants did better than the intercrop plants.





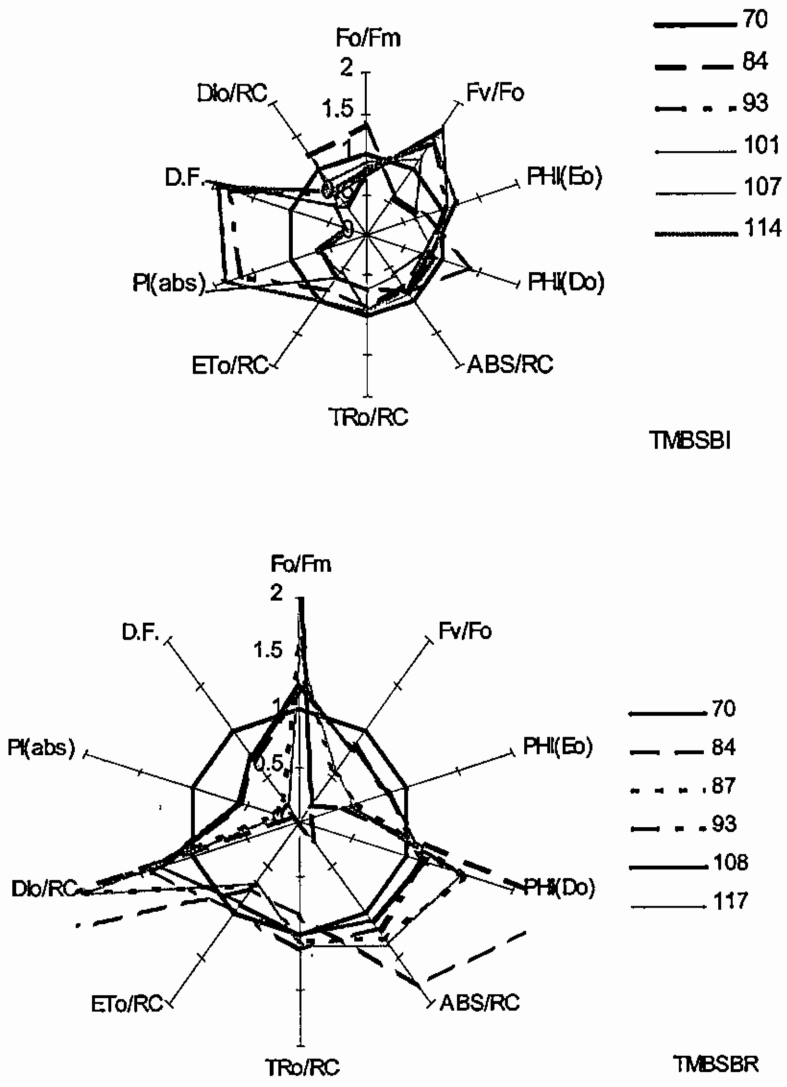


Figure 4.11: Bean whole plant average spider plot representation for TMB (top, middle and bottom) leaves under irrigated (I) and rainfed (R) conditions for the following treatments: irrigated intercrop bean (IBI), rainfed intercrop bean (IBR), irrigated sole bean (SBI), and rainfed sole bean (SBR), where day 70 served as the control.

4.4.5 Maize top leaves

It is well known that photosynthetic activity varies tremendously not only between cells of different taxonomic origin but also as a result of the physiological state defined by the environmental conditions. Figure 4.12 is a representation of the changes in the values of irrigated TIMI and rainfed TIMR intercrop maize top leaves. TIMI improved better over the experimental period as shown that from day 101, 107 the increase in φ_{Eo}. D.F., PI(abs) and Fv/Fo at 1. However, the TIMR plants were stressed as the season continued and the values for φ_{Eo}, D.F. and

PI(abs) were drawn closer to zero. Looking at day 87, 93 and 101 the values for φ_{Eo}. D.F. Fv/Fo and PI(abs) are at 1 and above. These results show that the C4 plants can tolerate drought considerably better than C3 plants.

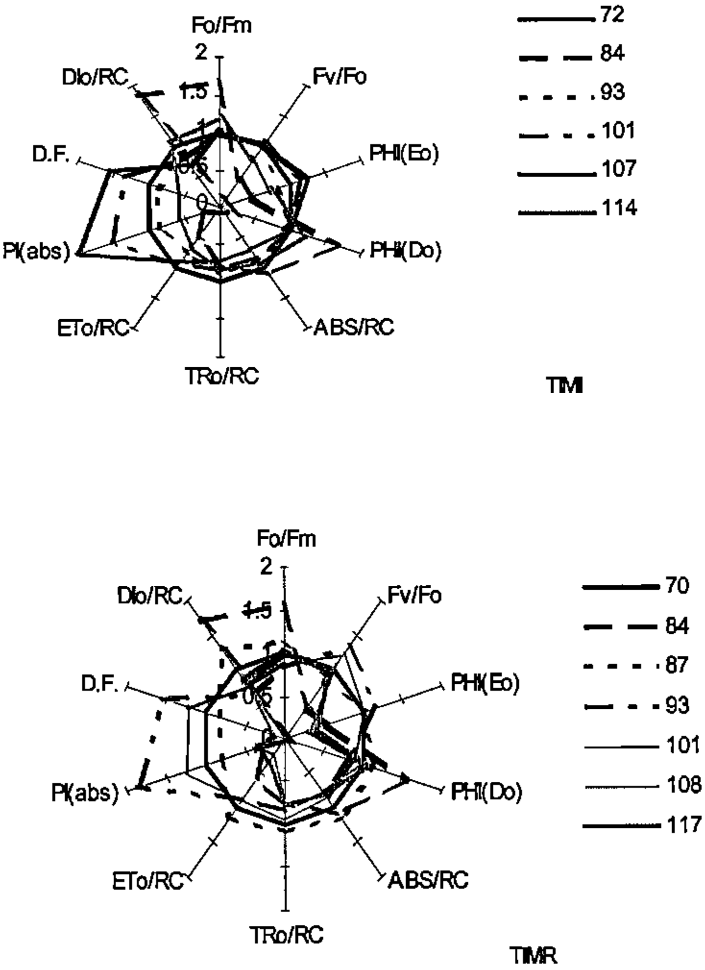


Figure 4.12: Spider plot representations for top leaf irrigated intercrop maize (TIMI) and top leaf rainfed intercrop maize (TIMR). Day 70 the initial measurements served as the control.

Results from irrigated sole maize top leaves (TSMI) and rainfed sole maize top leaves (TSMR) are shown in Figure 4.13. TSMI was much less stressed than TSMR. The TSMI plants responded similarly to the control (day 70) over the experimental period, except for day 84. TSMR shows major energy dissipation (φ_{Do} and DIo/RC) on days 84 and 87. On the rest of the days similar values were recorded to that on the onset (day 70).

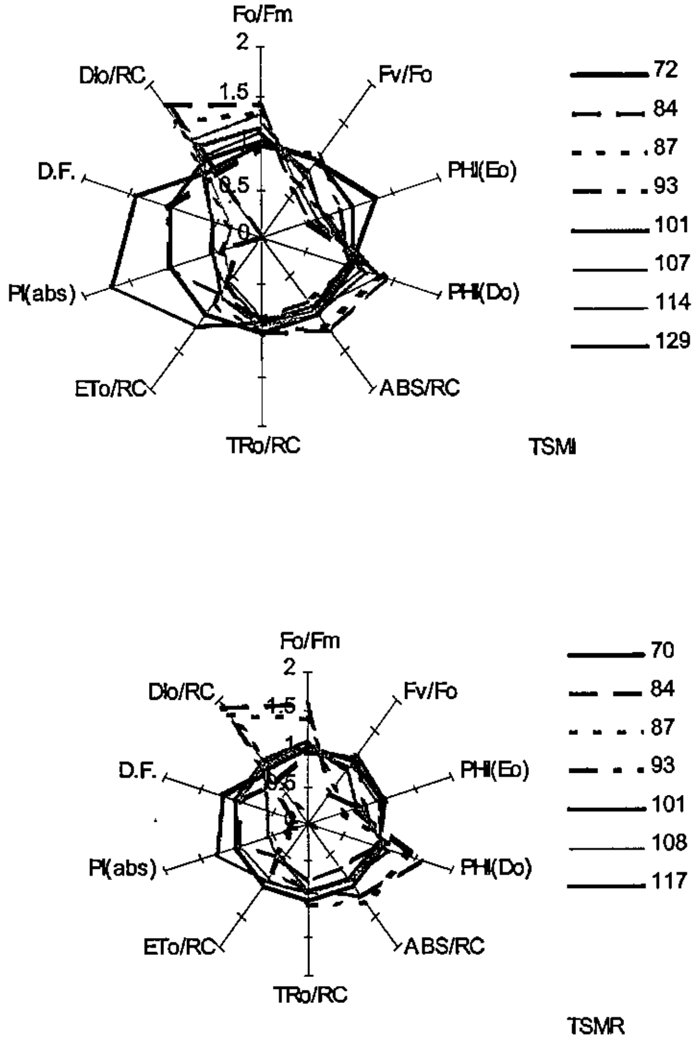


Figure 4.13: Spider plot representations for top leaf irrigated sole maize (TSMI) and top leaf rainfed sole maize (TSMR), where day 70 served as the control.

4.4.6 Maize middle leaves

The maize middle leaves are less exposed to direct sunlight compared to the top leaves. The photosynthetic parameters of irrigated intercrop maize middle leaves (MIMI) and rainfed intercrop maize middle leaves (MIMR) are sown in Figure 4.14. MIMI showed hardly any stress, except for day 84 and day 101 where it showed an improvement over day 70, the control. On day 101 also little deviation from the control of the stressed leaf (MIMR) was perceived. Definite stress is clear on all other days with high energy dissipation and little transport part absorption.

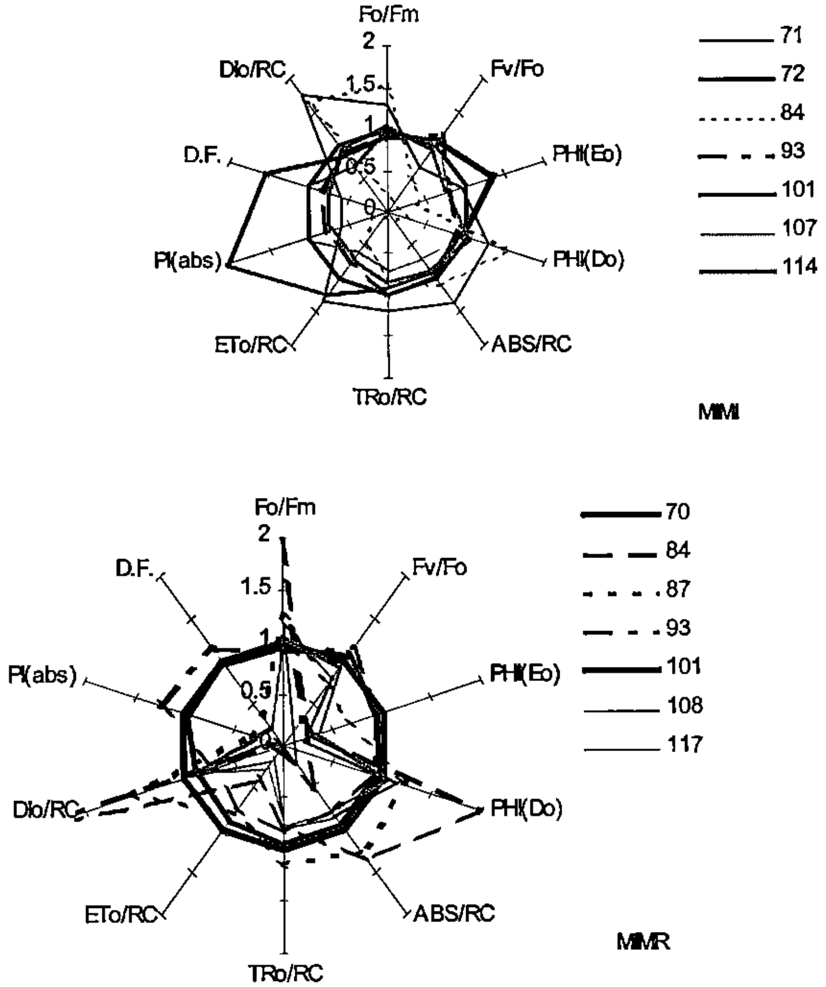


Figure 4.14: Spider plots representations for irrigated middle leaf intercrop maize (MIMI) and middle leaf rainfed intercrop maize (MIMR), where day 70 served as the control.

Results in irrigated sole maize middle leaves (MSMI) and rainfed sole maize middle leaves (MSMR) on Figure 4.15 showed that MSMI improved considerably as the season grew and the fact that values for DIo/RC, φ_{Do} were less compared to the control day 70. The most sensitive photosynthetic parameters φ_{Eo} , D.F. Fv/Fo and PI(abs) showed values greater than 1 as a result where most days performed very well except day 84 and 114. MSMR improved for the better as the season continued, as less energy was dissipated and most energy was used in the reaction center. The graph clearly shows a great increase in Fv/Fo, φ_{Eo}, D.F. Fv/Fo and PI(abs) values.

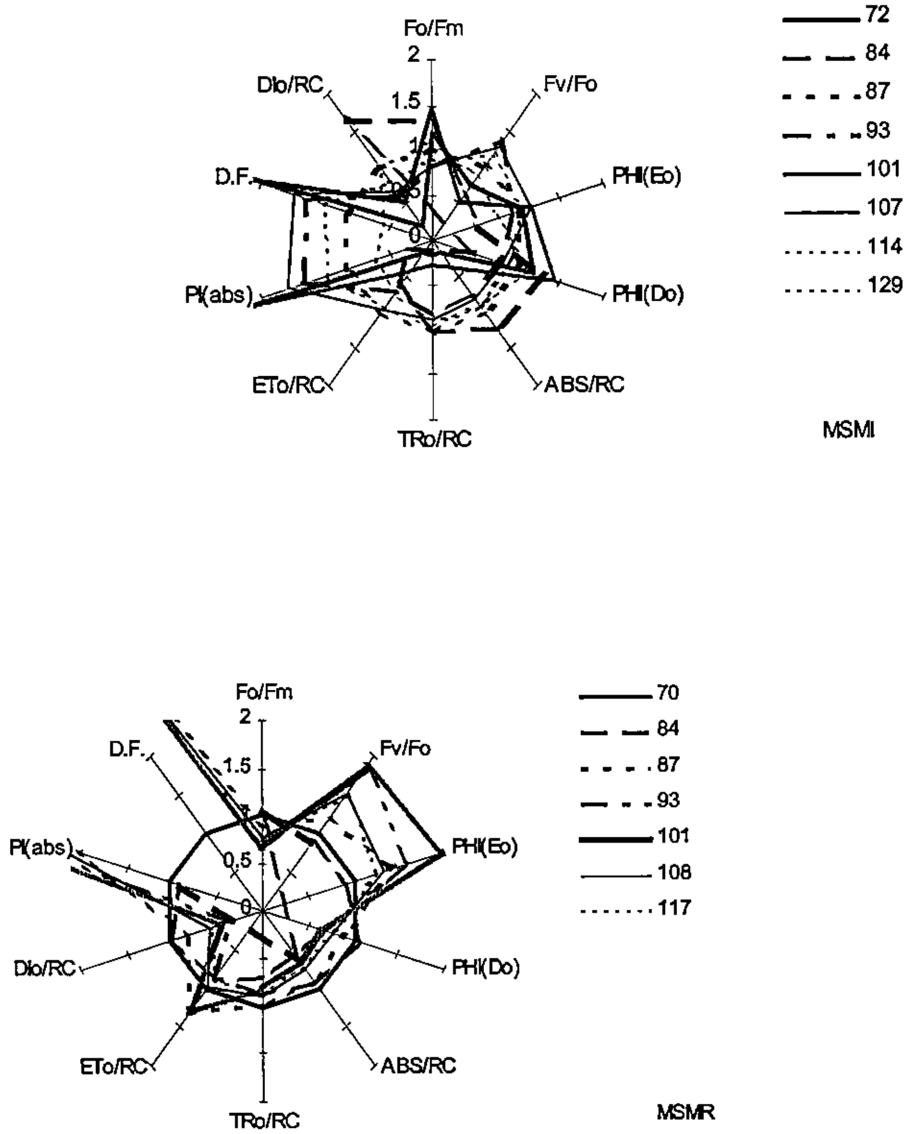


Figure 4.15: Spider plot representations for irrigated middle leaves sole maize (MSMI) and middle leaf rainfed sole maize (MSMR), with day 70 as the control.

4.4.7 Maize bottom leaves

Results show that BIMI was considerably stressed during the experimental period, and the graph shows that major energy dissipation occurred, since the photosythetic sensitive parameters were below the control and less than expected. High dissipation of trapped energy indicated by high values of (DIo/RC and φ_{Do}) were high above the control. This shows how stress affected plants during the experimental period. BIMR showed a considerable improvement to resisting water stress. Most of the plants display an improvement except for day 84, 108 and 117, although it showed that trapped energy was a little higher. It was only day 93 where the plants did not depict severe stress relative to the other days.

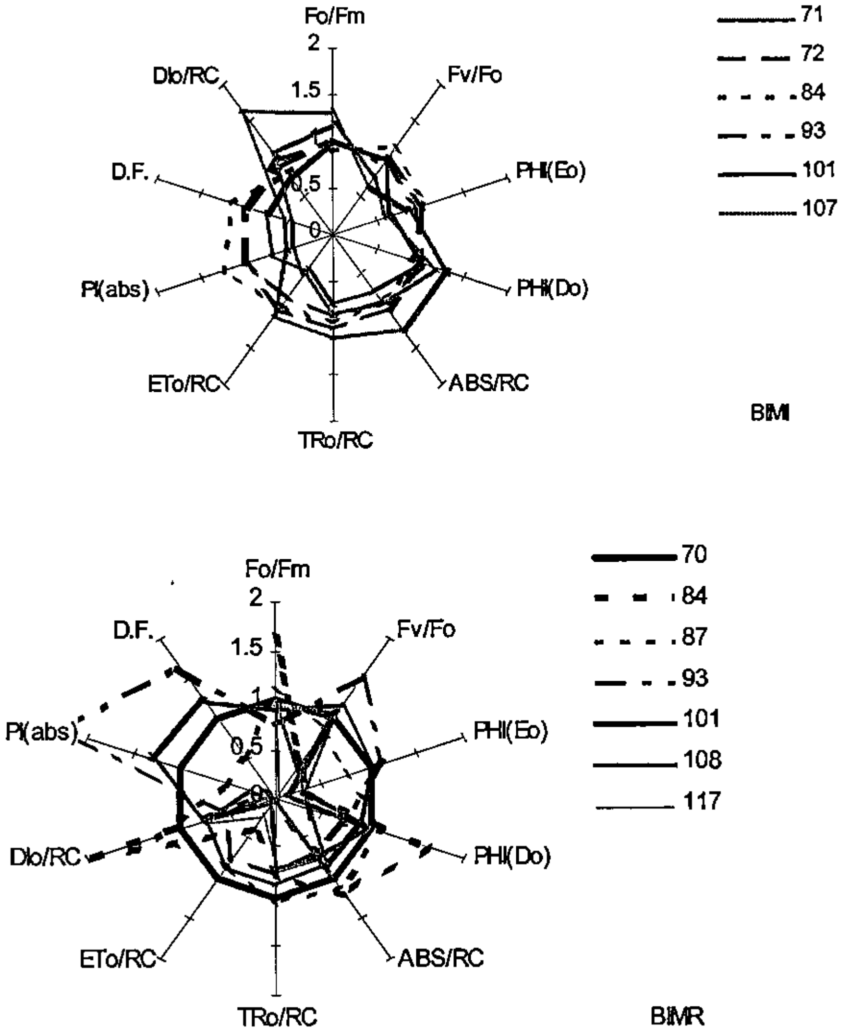


Figure 4.16: Spider plot representation for irrigated bottom leaf intercrop maize (BIMI) and bottom leaf rainfed intercrop maize (BIMR), with day 70 served as the control.

The results show that irrigated sole maize bottom leaves (BSMI) and rainfed sole maize bottom leaves (BSMR) in Figure 4.17 differed during the experimental period. BSMI is expected to be less stressed than BSMR. Lower values for Fv/Fo, D.F., TRo/RC. φEo, and PI(abs) clearly showed that the plants suffered severe stress throughout the season as major energy dissipated. This is evidenced by the high values for φDo, DIo/RC and Fo/Fm. BSMR showed considerable ability to survive severe stress during this season because on days 93, 101,108 and 117 the photosynthetic efficiency was normal with lower values for DIo/RC, as well as φDo on days 93, 101 and 108.

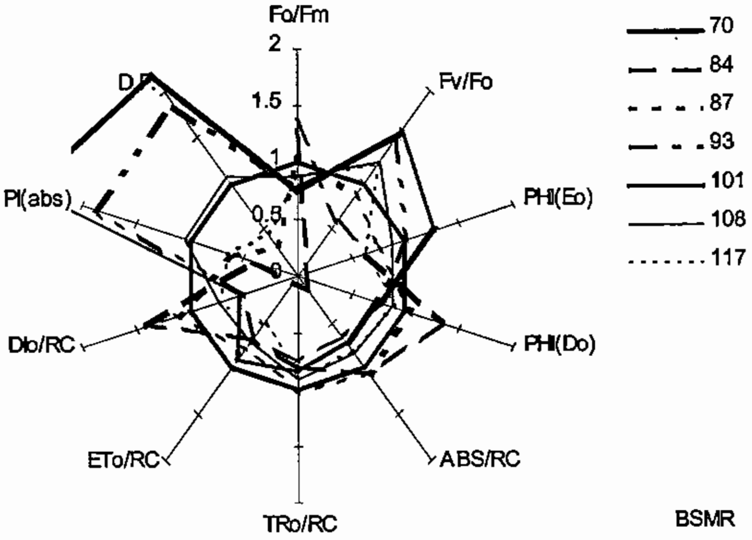
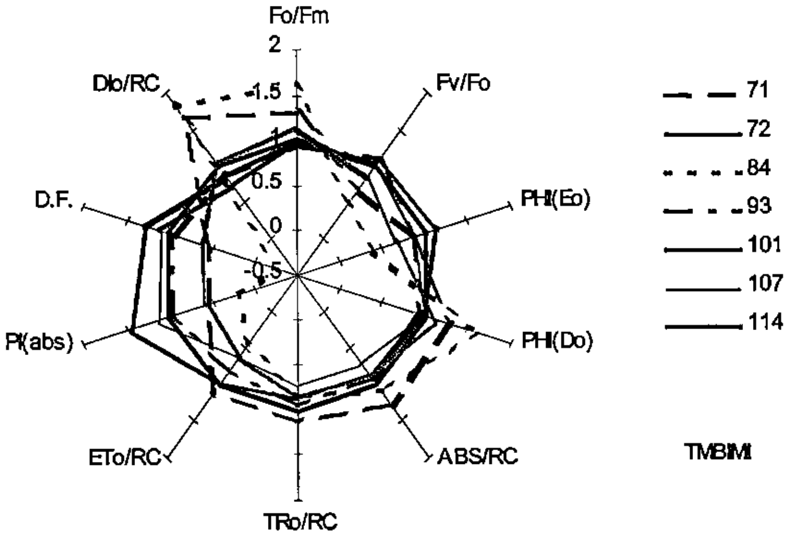


Figure 4.17: Spider plot representation for irrigated bottom leaf sole maize (BSMI) and bottom leaf rainfed sole maize (BSMR), with the control for BSMI on day 72 and for BSMR on day 70.

4.4.7 Maize whole plant

Average values of the top, middle and bottom leaves of the various treatments are shown in Figure 4.18. It can be seen that irrigated intercrop plants (TMBIMI) showed little variation in respect of water stress over the study period, with some stress on days 84 and 93. Much more variation was seen in the rainfed plants (TMBIMR) where definite stress was seen on all days except day 93. Not much stress was seen except on day 93. Not much stress was seen in the irrigated sole maize, (TMBSMI) except on days 84 and 87, where marked stress was evident. On the other hand the rainfed sole maize plants showed improvement from the initial control (day 70) with much higher D.F., PI(abs), Fv/Fo and φ_{Do}. These results indicate that irrigated intercrop maize performs better than rainfed intercrop maize, but that rainfed sole maize performs the best.


Fo/Fm
2
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Fv/Fo
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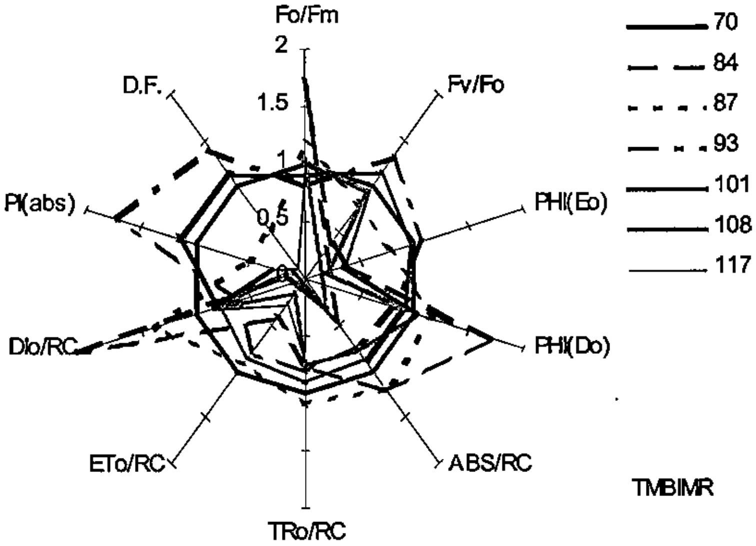
D.F.
DIo/RC
71
72
84
93
101
107
114
TMBIMI


Fo/Fm
2
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TMBIMR

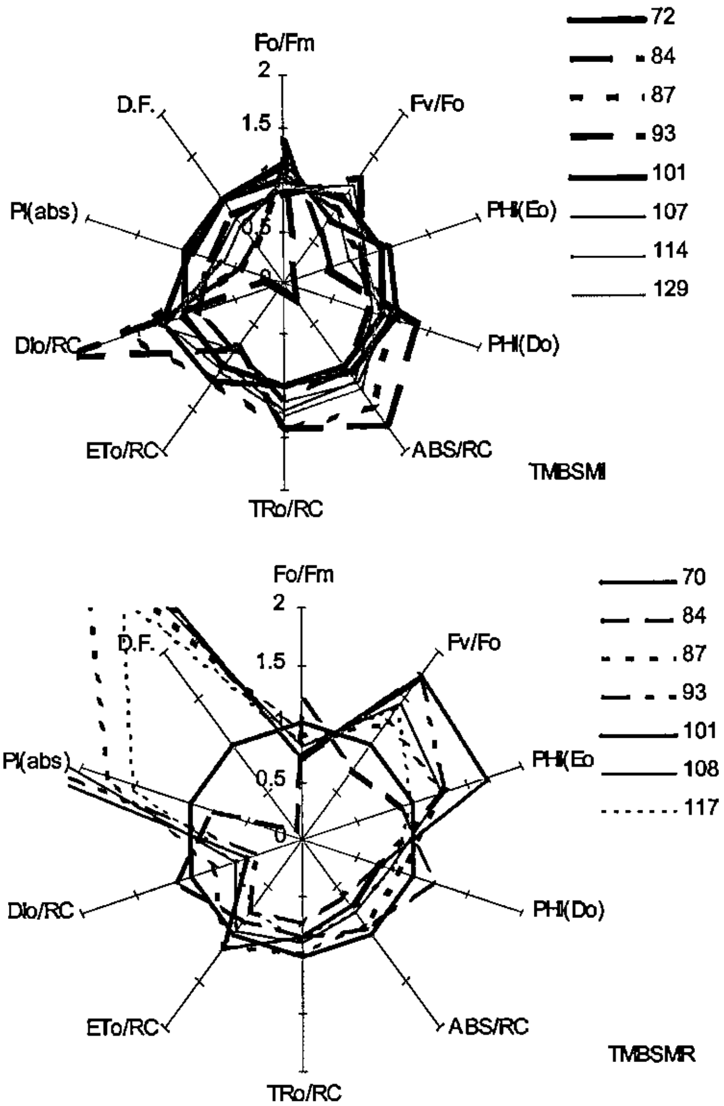

Figure 4.18: Spider plots of the averages of all the leaves for TMB top, middle and bottom under irrigated (I) and rainfed (R) conditions for irrigated intercrop maize (IMI), rainfed intercrop maize (IMR), irrigated sole maize (SMI), and rainfed sole maize (SMR), where day 70 served as the control for most treatments

4.5 Conclusion

The examples presented in this chapter illustrate how chlorophyll fluorescence can be used to study components of the photosynthesis apparatus and their reactions to changes in the environment, as well as photosynthesis as a whole.

Chlorophyll fluorescence is a powerful tool in photosynthesis research. Stress conditions have been detected by chlorophyll fluorescence for this study under irrigated and rainfed treatments whereby PSII was directly or indirectly included in the response. This means that several metabolic pathways in the chloroplast can substitute each other in the use of products from the electron transport chain, buffering changes in quantum efficiency for photochemistry.

PHI(Eo), PI(abs) and driving force were the backbone for this study to analyse the behaviour of the maize and bean crop under different cropping systems whether irrigated or rainfed. PHI(Do) has been a great measure for the amount of flux dissipated away from photosynthesis, indicating stress.

Irrigated intercrop maize does better than intercrop rainfed maize, but rainfed sole maize performs the best. The results from these treatments show that the JIP-test is very sensitive in measuring plant stress and also suggests that irrigated intercrop bean performed better than rainfed intercrop bean and rainfed sole bean performed better than irrigated sole bean, but most importantly rainfed sole bean in particular performed the best.

Chlorophyll fluorescence has been used in this study to study photosynthesis. Photosynthesis is a good indicator of adaptation of plants to their environment. Parameters (Chapter 2) were selected to interpret the behaviour of maize and bean under irrigation and rainfed conditions.

In conclusion, for bean plants, rainfed intercrop bean and irrigated sole bean appeared to be more stressed than irrigated intercrop bean and rainfed sole bean. For maize plants, irrigated intercrop maize and rainfed sole maize appeared to perform better than rainfed intercrop maize and irrigated sole maize. Strasser *et al* (1999) found that the indicator function of chlorophyll fluorescence arises from the fact that fluorescence emission is complementary to alternative pathways of de-excitation which are primarily photochemistry and heat dissipation. Generally, fluorescence yield is highest when photochemistry and heat dissipation are lowest. Therefore, changes in the fluorescence yield reflect changes in photochemical efficiency and heat dissipation.

Schreiber & Neubauer (1987) discovered that a lower value indicates that a proportion of PSII reaction centers are damaged, a phenomenon called photoinhibition, often observed in plants under stress conditions. Upon the onset of photochemical and heat dissipation processes, the fluorescence yield is quenched and reaches a steady state value. Haldimann *et al.* (1995) stated that upon exposure to low temperature, photosynthesis of maize leaves is strongly inhibited, because cold temperature inhibits the activity of the water splitting complex or electron transport possibly due to a decrease in the thylakoid membrane fluidity. According to Demming-Adams & Adams, (1996) upon increased energy dissipation as heat, non-photochemical quenching of chlorophyll fluorescence is observed and the efficiency of open PSII centers decreases.

Chapter 5

THE INFLUENCE OF PHOTOSYNTHETIC EFFICIENCY ON BIOMASS

5.1 Introduction

When the canopy of leaves are fully exposed to the sun, photosynthesis proceeds at a rate which depends on how photons are distributed over individual elements of the foliage and on the relationship between the photosynthetic rate and irradiance for each foliage element. Therefore, photosynthesis of a canopy, expressed per unit of ground area rather than unit leaf area, can be estimated from a statistical description of irradiance as a function of leaf position. The energy used in photosynthesis has been estimated from the amount of CO_2 absorbed, or from the amount of oxygen given off, and from the increase in dry weight (Blondel & Aronson, 1999).

Higher plants intercept incident radiation with their leaves, utilise the absorbed radiant energy for photosynthesis and the photosynthetic products eventually lead to the accumulation of plant mass. The leaf environment supplies the CO_2 and the radiation for photosynthesis and controls the temperature of the leaf. The enzymes that catalyze the photosynthetic reactions are all strongly temperature dependent, so leaf temperature can play an important role in determining the assimilation rate for a leaf. Most plant species fall into one of two major groupings with respect to carbon assimilation. In the most common group the primary product of photosynthesis is a three-carbon sugar, the C_3 plants such as the beans used in this study. A less common photosynthetic mechanism is present in tropical grasses, the C_4 plants, as the maize used in this study. Carbon dioxide and oxygen compete for the same enzyme in C_3 species, resulting in the loss of some of the CO_2 in a process called photorespiration. The fixing of CO_2 into the four-carbon compound in C_4 species concentrates the carbon dioxide and minimizes photorespiration. The concentration of CO_2 inside the leaves is therefore much higher in C_4 than in C_3 species, typically resulting in higher photosynthetic rates and higher water use efficiencies in the former (Campbell and Norman, 1998).

Each plant is the product of its genetics and the total environment in which it is grown. Some grow in harsh environments whereas others grow under milder conditions. The strategy of each plant is to survive in its environment long enough to reproduce the next generation. The total growth environment is constantly changing during the lifetime of a plant. It includes available soil water, quantities and solubility of mineral nutrients, air and soil temperature, etc. The growth and developmental processes associated with adaptation to the many environmental variables, brings about that plants of the same genotype can differ significantly in size and chemical composition (Kasperbauer, 1994).

Biomass is the dry mass of living plant material contained above and below a unit of ground surface area at a given point in time. Blackman (1919) defined production in terms of the compound interest law. The harvest index, the proportion of total plant dry matter accumulated into harvested plant organs, is largely determined by factors controlling carbon partitioning between alternative sinks. Plants have evolved adaptive mechanisms by which they respond to stressful environments and improve their chances of survival or production of offspring. Many of these mechanisms involve changes in partitioning. The generally accepted mechanism of phloem transport is by mass flow of solution in sieve tubes down hydrostatic pressure gradients from sources to sinks (Minchin and Thorpe, 1987). Thus, water deficit and other stresses which alter plant water relations (high temperature, salinity, etc.) might be expected to exert a substantial influence on such gradients, on carbon partitioning and on the harvest index (Settler, 1990).

Photosynthesis is fundamental to the conversion of solar radiation into stored biomass energy Its theoretically achievable efficiency is limited both by the limited wavelength range applicable to photosynthesis and the quantum requirements of the photosynthetic process. Only radiant energy within the wavelength range of 400 to 700 nm (photosynthetically active radiation, PAR) can be utilized by plants, effectively allowing only 45% of total solar energy to be utilized for photosynthesis. In addition, fixation of one CO_2 molecule during photosynthesis necessitates a quantum requirement of ten (or more), that could results in a maximum utilization of only 25% of the PAR absorbed by the photosynthetic system. On the basis of these limitations, the theoretical maximum efficiency of solar energy conversion is approximately 11%. In practice, however, the magnitude of photosynthetic efficiency observed in the field is further decreased by factors such as poor absorption of radiation due to a proportion being reflected, respiration requirements of photosynthesis and the need for optimal solar radiation levels. The net result is an overall photosynthetic efficiency of between 3 and 6% of total solar radiation (Hall & House, 1994).

The radiant energy captured by the plant enables CO_2 to be converted to carbohydrates and stored as biomass to produce yield. Intercrops have been documented to increase the plant available water through greater canopy cover and protection of the soil surface from raindrop impact, thereby increasing the proportion that infiltrates into the soil profile and hence becoming available for transpiration (Lal, 1974; Ogindo, 2003). A sole cropping system is assessed in terms of mass per unit area. However, for intercropping systems, direct comparison is difficult because the products are different plant species growing on one piece of land (Tsubo, 2000).

5.2 Plant Growth and Development

Growth is the process by which a plant increases the number and size of leaves and stems. According to Boyer (1968) plant growth is the irreversible increase in size of the organ, due predominantly to an increase in cellular water content accompanied by the simultaneous extension and synthesis of cell wall and accumulation of the solutes. Dennett (1975) defines plant growth as a process of cell division and cell elongation or as an increase in dry matter. Digby & Frin (1985) describe plant development as a physiological process involving the stages of anatomical development which a leaf passes through during its growth from primordium to maturity.

Plant growth and development are essential processes of the life and propagation of a species. These are continued during the life cycle, depending on availability of meristems, assimilate, hormones and other growth substances and a supportive environment (Gardner *et al.*, 1985). According to Digby & Frin (1985) a plant body grows gradually, tissues maturing progressively and being added to those matured earlier. As they grow and mature, these tissues are affected by the current environment in various ways. The plant body at any given moment is therefore an epitome of the effect of past environments including temperature variations.

5.3 Plant growth rate

Total biomass accumulation of many agricultural species is proportional to the solar radiation absorbed by the crop canopy. The transformation of radiant energy to chemical energy occurs in the chloroplast, and the chemical energy is utilised for dry matter production. Crop growth can generally be measured by biomass accumulation and the increase of leaf area during the growing season (Walker, 1988). According to Hunt (1982) crop growth rate is the weight gain of a community of plants on a unit of land in a unit of time This concept is defined as follows:

$$G = dW/dt \qquad (5.1)$$

where G is the instantaneous slope of the graph of total dry mass per plant (W) against time (t), thus constituting a plain and simple measure of the rate of increase in weight per plant.

Blackman (1919) and Walker (1988) described biomass accumulation by the "compound interest law" with an initial phase early in the season recognized as the exponential growth phase when the canopy was incomplete. The equation was as follows:

$$m = m_o \exp[K(t - t_o)] \qquad (5.2)$$

where m is biomass (g/m^2) at a given time (t), m_o is the initial biomass at time t_o , K the relative growth rate. This equation has been used by many researchers, who calculated relative growth rate of crops from biomass accumulation through the season for maize and for soybean (Hunt, 1982). This equation has not yet been tested for intercropping situations. Dry matter partitioning is closely associated with crop growth. Quantification of the temperature responses of dry matter distribution constitutes an important component in the analysis of the response of crop dry matter accumulation to temperature. The rate of development and leaf photosynthesis show a curvilinear response to temperature for maize, with a maximum at approximately 31°C (Tollenaar, 1989).

The genetic potential of dry mass growth rates can be limited by either solar and thermal energy input, or water. Growing a crop is an exercise in energy transformation, in which incident solar radiation is converted to more useful forms of chemical potential energy located in the dry matter. The yield (Y) of a crop over a given period of time can, therefore, be expressed by the equation:

$$Y = Q \times I \times \varepsilon \times H$$

where Q is the total quantity of incident solar radiation received over the period, I is the fraction of Q which is intercepted by the canopy, ε is the photosynthetic efficiency of the crop (the efficiency of conversion of radiant to chemical potential energy), commonly expressed in terms of the total plant dry matter produced per unit of intercepted radiant energy, and H is the fraction of the dry matter produced, which is allocated to the harvested parts. H is actually the harvest index of the crop stand, or the above ground production (Hay & Walker, 1989). The amount of solar radiation incident upon unit area of cropland (Q) per day, which depends upon day length and the diurnal pattern of irradiance, varies regularly with season and latitude, as the variation in Q is an aspect of environmental physics.

5.3.1 Specific aim

The aim of this chapter was to determine how efficiently plants covert radiation flux energy into chemical energy and its influence on dry matter production. The photosynthetic efficiency (PHI(Eo)) or ε was measured using the PEA. The comparison was between intercropping and sole cropping for maize and bean.

5.4 Results and Discussion

5.4.1 Dry matter accumulation

Photosynthetic pigments are localised in protein complexes of chloroplast membranes and their role in photosynthesis has long been established but their efficiency has not been measured in many species (Kathiresan & Moorthy, 1993). Any analysis of biomass energy production must consider the potential efficiency of the processes involved. Although photosynthesis is fundamental to the conversion of solar radiation into stored biomass energy, its theoretically achievable efficiency is limited both by the limited wavelength range applicable to photosynthesis and the quantum requirements of the photosynthetic process.

Bean is a C_3 plant as the CO_2 is first incorporated into a 3-carbon compound and the stomata are open during the day. RUBISCO, the enzyme involved in photosynthesis, is also the enzyme involved in the uptake of CO_2. Photosynthesis takes place throughout the leaf. Maize is a C_4 plant because the CO_2 is first incorporated into a 4-carbon compound and the stomata are open during the day. C_4 plants use PEP Carboxylase for the enzyme involved in the uptake of CO_2. This enzyme allows CO_2 to be taken into the plant very rapidly, and then it "delivers" the CO_2 directly to RUBISCO for photosynthesis. Photosynthesis takes place in inner cells called the Kranz Anatomy (Kathiresan & Moorthy, 1993).

Figure 5.1 show the results of bean dry matter production for intercrop and sole cropping under rainfed and irrigated conditions. Due to hail on day 74, the plants were severely damaged especially under rainfed conditions. However, as the season progressed the bean plants recovered for both rainfed and irrigated treatments. Irrigated sole bean (SBI) showed good recovery after the hail damage as indicated by higher final dry matter harvest of 443.82 g/m^2, relative to 187.29

g/m^2 produced by the irrigated intercrop bean. Rainfed sole bean and irrigated intercrop bean had almost the same dry matter production, which could be due to a high competition for water, nutrients, radiation etc. in the intercrop system. Rainfed intercrop bean was affected not only by water stress but also other environmental stresses, resulting in low dry matter production. In general, the irrigated treatments had higher production than rainfed treatments.

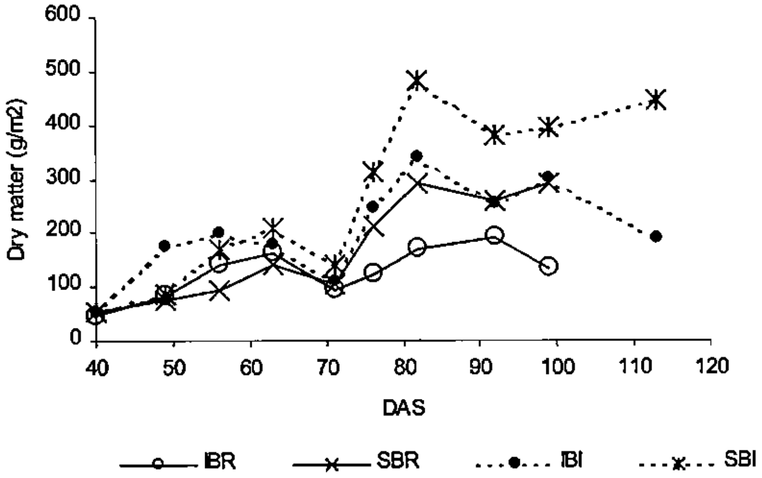

Figure 5.1: Bean intercrop and sole cropping dry matter accumulation trend under rainfed and irrigated condition.(IBR, rainfed intercrop bean; SBR, rainfed sole bean; IBI, irrigated intercrop bean; SBI, irrigated sole bean).

Furthermore a comparison was done between maize and bean sole and intercrop systems under rainfed and irrigated conditions. Figure 5.2 shows maize dry matter accumulation for the whole season. Irrigated sole maize (SMI) had the highest dry matter production with the final harvest of 794.09 g/m^2, while irrigated intercrop maize was 492.58 g/m^2. The maize treatments were also affected by common rust (*Puccinia sorghi*), which probably comes through wind and rain dispersal mechanism. The rainfed plot was the most affected by the rust, and was probably responsible for the low production rates of these plants.

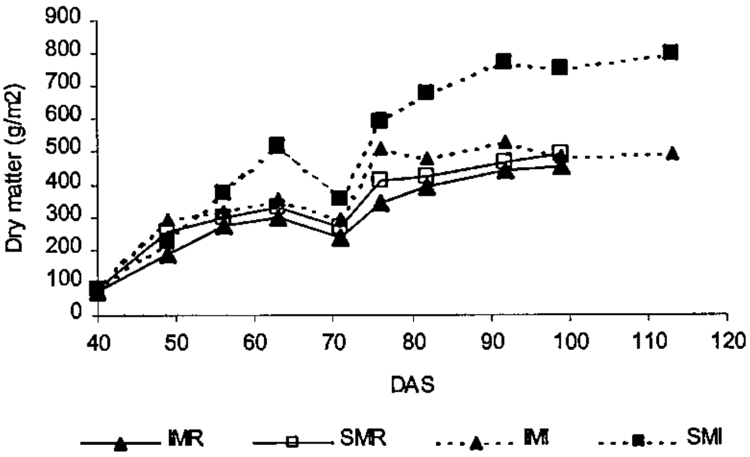

Figure 5.2: Maize intercrop and sole cropping dry matter accumulation trend under rainfed and irrigated conditions. (IMR, rainfed intercrop maize; SMR, rainfed sole maize; IMI, irrigated intercrop maize and SMI, irrigated sole maize).

5.4.2 Photosynthetic efficiency

Maize and bean plants differ in their efficiency to convert radiation absorbed by the plants into chemical energy during photosynthesis. Figures 5.3 and 5.4 show the photosynthetic efficiency trends during the growing season for maize and bean grown under intercrop and sole cropping conditions.

The results depicted in Figure 5.4 show that maize treatments had a better photosynthetic efficiency than the bean treatments. From the graph it is evident that rainfed sole maize (SMR) and irrigated intercrop maize (IMI) were almost the same and had better φ_{E_o} than all other treatments, throughout the season, which means that sufficient photons were transported and absorbed. Rainfed intercrop maize started at a very stressed situation but a good recovery was seen after the hail, as 51 mm of rainfall was received, and φ_{E_o} increased and then also dropped after day 101 as a severe stress condition was seen.

In bean plants, photosynthesis shows a negative response to rising temperatures (Masaya and White, 1991). According to Jones (1971) the optimum temperature for photosynthesis in bean leaves is 25 °C, showing decay with a continuous temperarure increase. In relation to photochemical efficiency, an increase in initial fluorescence (F_o) has been observed with rising temperatures. In some situations, F_o can be used as an indicator for irreversible damage in PSII (Pastenes and Horton, 1999), associated with LHCII dissociation II (Briantais *et al.*, 1996; Yamane *et al.*, 1997) and blocking of the electron transference in the reductant side of PSII.

φ_{Eo} gives an indication of photons transported per absorption. The actual photosynthetic values have been used to illustrate the photosynthetic trends throughout the season for different cropping systems and under water stress conditions. Figure 5.3 show the bean treatments and as can be seen the rainfed sole bean (SBR) perfomed the best compared to other treatments. It is also seen that photosynthetic efficiency was greatly affected after hail. The more photons absorbed the higher the photosynthetic efficiency. Irrigated intercrop bean (IBI) shows considerable better results than SBR and irrigated sole bean (SBI) shows a good photosynthetic trend. As the plants were still small the photosynthetic efficiency increased until it reached the maximum, then as the plants were drying out the photosynthetic rate dropped. However, SBR proved to be the most stressed treatment as SBI performed the best of them all.

The φ_{Eo} for maize is greater than the φ_{Eo} for beans as a result of differences in structure and physiological factors. Exposure to dry periods caused a significant decrease in φ_{Eo} and dry mass production (Menconi *et al.*, 1995). A consequence of drought induced limitation of photosynthesis is the exposure of plants to excess energy, which is not dissipated, and may be harmful to PSII because of over reduction of reaction centers and increased production of oxygen species in the chloroplast (Demming-Adams, 1992).

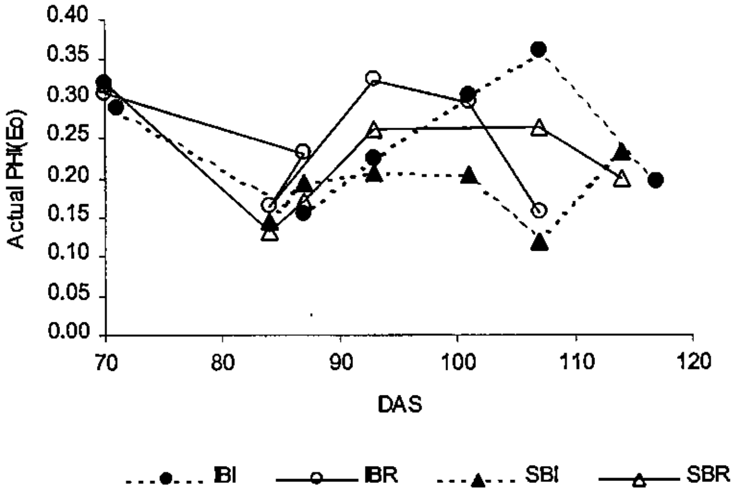

Figure 5.3: Bean actual photosynthetic efficiency φ_{Eo} values for intercrop and sole cropping systems under rainfed and irrigated condition.

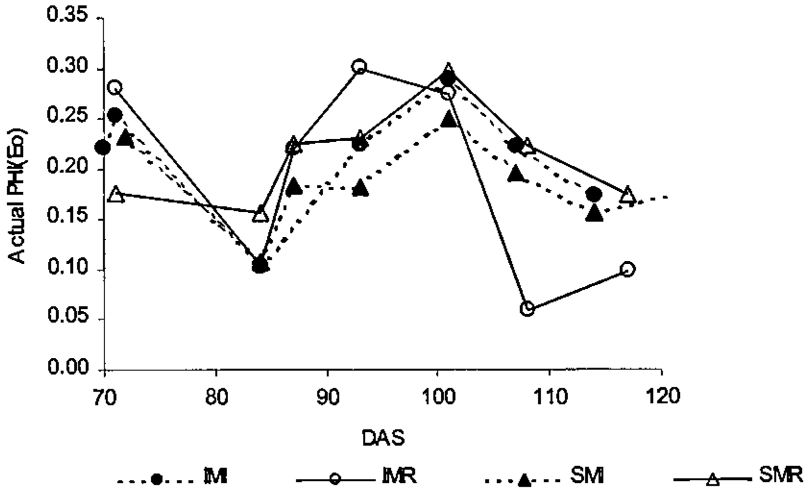

Figure 5.4: Maize actual photosynthetic efficiency φ_{Eo} values for intercrop and sole cropping systems under rainfed and irrigated condition.

Yield is determined not only by the amount of dry matter produced, but also by the pattern of partitioning of dry matter to different parts of the plant. Figures 5.5 and 5.6 show the relationship between photosynthetic efficiency and dry matter accumulation for intercrop and sole maize and bean under rainfed and irrigated conditions. In general, the higher the φ_{Eo} the larger the amount of dry matter in grams per square meter. For bean treatments, irrigated sole bean shows high dry matter accumulation throughout the season (Fig. 5.5). IBI and SBR are almost the same in terms of dry matter production and IBR was below 200 g/m^2, regardless of φ_{Eo} Figure 5.6 shows that the maize dry matter production for rainfed treatments were all below 500 g/m^2, while for irrigated treatments the highest amount was 748.9 g/m^2 at φ_{Eo} of 1.7. This graph shows the relationship between biomass and the quantum efficiency of electron transport.

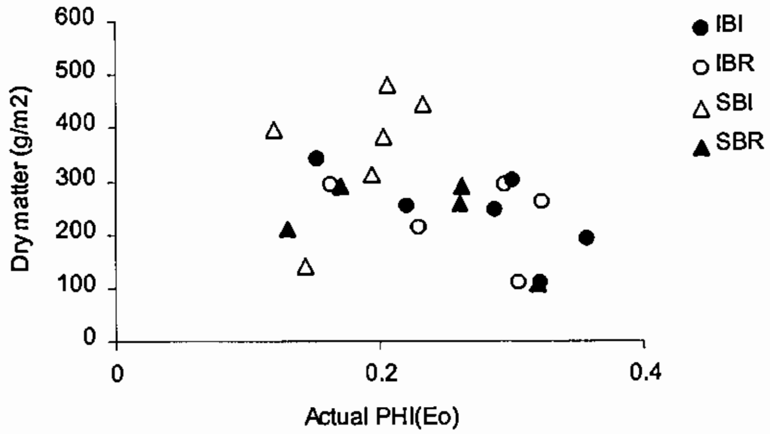

Figure 5.5: Bean photosynthetic efficiency φ_{Eo} against dry matter production throughout the growing season. (IBI, irrigated intercrop bean; IBR, rainfed intercrop bean; SBI, irrigated sole bean; SBR, rainfed sole bean).

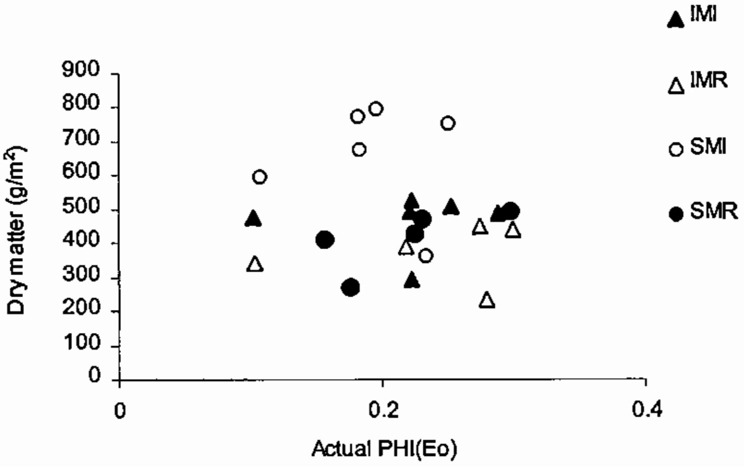

Figure 5.6: Maize photosynthetic efficiency φ_{Eo} against dry matter production throughout the growing season. (IMI, irrigated intercrop maize; IMR, rainfed intercrop maize, SMI, irrigated sole maize; SMR, rainfed sole maize).

5.5 Conclusion

Photosynthetic efficiency is the plant's effectiveness at converting the radiant energy of solar radiation into the chemical energy stored in the bonds of sugar molecules. Some variation in photosynthetic efficiency is genetically based and adapted to a particular climate. Some variation depends on factors that affect photosynthesis such as shading, carbon dioxide concentration, temperature, as well as water stress and adequate leaf area to intercept radiation.

Photosynthetic efficiency φ_{Eo} in this study was measured using the PEA., and the φ_{Eo} ranges between 0 and 1, with values drawn closer to 1 meaning the electron transport is good, and closer to 0 means poor φ_{Eo} (as explained in Chapter 2). The higher the $\varphi_{Eo,}$ the higher the dry mass accumulation (Figure 5.5 and 5.6).

Irrigated sole bean accumulated more dry matter than other treatments as it produced above 300 g/m$^{2;}$; rainfed intercropping bean produced below 200 g/m^2 ; rainfed sole bean produced better than irrigated intercrop bean. As the photosynthetic efficiency increases, the plant is able to produce more dry matter. Irrigated sole maize produced better than other treatments as it produced 500 g/m^2 and above. Other treatments produced an amount between 200 and 530 g/m^2.

In general, irrigated treatments are expected to do better than the rainfed ones as the biomass accumulation is expected to be higher than the rainfed ones due to less water deficit during the season. During the experimental period the rainfed sole maize (SMR) and rainfed sole bean (SBR) treatments showed better results in terms of biomass production and photosynthetic efficiency.

Chapter 6

GENERAL CONCLUSIONS

Overpopulation and poverty are threatening the food security of many developing countries in Africa. Maize and bean are among the most important crops that can produce sustainable yield and biomass and provide quality nutrients for people. These crops are usually grown under rainfed conditions and are a staple food in poor communities. Water deficit is one of the major constraints that lead to low yield in semi-arid areas. Rainfall determines the cropping potential of various areas, as water is an essential component for plant growth. Shortages of soil water cause water stress that affects the photosynthetic efficiency, resulting in low yield.

In this study soil water was the main limiting resource, especially for the rainfed treatments. Mild stress was experienced in the supplemental irrigated treatment. This resource formed the basis for comparison between the varying systems. Stress level comparisons were done using leaf water potential and soil water measurements. Photosynthetic efficiency measurements were used as a an indicator of the efficiency of dry matter accumulation and productivity under the cropping systems at the two stress levels. From this study it can be concluded that the irrigated treatment experienced less stress compared to rainfed treatment. This was confirmed by the higherLWP readings obtained for this treatment compared to the rainfed one.

Photosynthesis is a major biological energy source for life on the earth. The process of photosynthesis requires a variety of energy transducing protein complexes that transport electrons and pump protons, leading to the formation of ATP (adenosine triphosphate) and NADPH (reduced nicotinamide adenine dinucleotide phosphate). Photosystem II (PS II) is one of these protein complexes and it has been the focus of many studies. The complex traps PAR and uses it to reduce the Q_B plastoquinone and to synthesize molecular oxygen from water.

PSII is the membrane protein complex found in oxygenic photosynthetic organisms (higher plants, green algae and cyanobacteria), which harnesses radiant energy to split H_2O into O_2, protons and electrons. It drives one of the most oxidising reactions known to occur in nature and is responsible for the production of atmospheric oxygen, essential for aerobic life on this planet. In addition, by catalysing the first step of the photosynthetic electron transport chain, PSII is also involved in the production of a substantial proportion of the global biomass.

The chlorophyll fluorescence measurements and subsequent JIP-test proved to be a rapid method to measure photosynthetic parameters. This is interesting in view of the fact that photosynthesis is a good indicator of adaptation of plants to their environment and of how plants tolerate water stress.

The efficiency of photosynthesis of the whole plant is crucial to agriculture when it comes to analyzing productivity for food. The quality and quantity of incident photosynthetically active radiation (PAR), temperature and water stresses, availability and utilization of mineral nutrients, photorespiratory losses, are some of the factors, which affect plant productivity. The main aim of the study was to evaluate dry matter accumulation and assess the function of PSII for sole and intercropped maize and bean under rainfed and supplemental irrigation in the semi-arid area of South Africa.

The results are intended to confirm the hypothesis proposed in Chapter 1, that intercropping maize and beans use soil water more efficiently than sole crops. Intercropping may result in competition for resources such as soil water, nutrients, PAR, etc., although the competitiveness ranges according to the availability of these resources. However, intercropping has an advantage over sole cropping in terms of water conservation, since the latter consumes water more efficiently. Irrigated treatments would be less stressed than rainfed treatments as proposed in Chapter 3. However, the irrigated treatments did suffer some stress while the rainfed treatments only really became stressed on days 74 and 101. In semi-arid areas intercropping is recommended as a tool to alleviate poverty since many crops can be planted simultaneously on one field.

The purpose of Chapter 3 was to determine the leaf water potential of the whole plant and soil water trend for the growing season and to evaluate the final production. Figure 3.16 shows that leaf water potential status depends on the amount of soil water available to the plant. Interestingly, after hail damage the LWP increased for all treatments, as the values were lower negatives. Evapotranspiration was calculated and the findings were that irrigated treatments for maize and beans in terms of LWP were less stressed.

Furthermore, the study looked at the leaf height for leaf water potential and photosynthetic efficiency for both plants maize and bean. In the irrigated sole bean the top leaves had a higher energy dissipation, which resulted to lower photosynthetic efficiency. The top leaves for irrigated intercrop beans were less stressed since the performance index, driving force and photosynthetic efficiency values were above the control. This could be due to the fact that the intercrop bean plants were shaded by the taller maize plants and therefore experienced a modified microclimate resulting in reduced transpiration and lower soil surface evaporative water losses

Major differences in terms of water stress were noticed between irrigated and rainfed bean plants middle leaves for sole and intercrop beans as the season progressed. Intercrop bean middle leaves showed a high amount of energy dissipation, which highly affects the photosynthetic efficiency since most energy was lost instead of being used to improve the production. The lower leaves of the irrigated sole bean are not affected by stress and showed a sustainable photosynthetic efficiency until maturity was attained. However, rainfed sole bean lower leaves showed values lower than the control as a result of insufficient water.

The photosynthetic efficiency of the top leaves for irrigated intercrop maize was higher than for the rainfed intercrop maize. This was because of a high amount of energy dissipated. Irrigated sole maize top leaves exhibited less stress compared to rainfed sole maize. This was due to delay occurred for transport transferred to photosystem II.

Irrigated intercrop maize middle leaves show characteristics of well conditions for electron transported to the reaction center. For rainfed intercrop maize, middle leaves exhibited definite stress on all days with high energy dissipated and a little amount transported to the reaction center. Irrigated sole maize middle leaves performed considerably better as the season continued. This could be the fact that less energy dissipation occurred. Rainfed sole maize middle leaves also showed positive signs in terms of photosynthetic efficiency as less energy dissipation occurred.

Irrigated intercrop maize bottom leaves were severely stressed as the season progressed since major dissipation occurred this could be due to leaf aging. Rainfed intercrop maize bottom leaves resisted water stress, possibly because lower leaves are less exposed to the sunlight and therefore the transpiration rate is lowered accordingly. Irrigated sole maize bottom leaves suffered more severe stress than rainfed sole maize bottom leaves due to leaf aging, although irrigated treatments are expected to grow faster than rainfed treatments.

From the results pertaining to the leaf water potential and photosynthetic efficiency evaluation, it was clear that the rainfed sole beans were more stressed than the irrigated sole beans. Irrigated intercrop beans were also less stressed than the rainfed intercrop beans. However, the sole beans performed better than the intercrop beans, and sole and intercropped maize performed almost the same. The quantum efficiency of electron transport was higher under less stressed conditions.

The quantum efficiency of electron transport φ_{Eo} , performance index (PI(abs) and driving force were the backbone in this study for the purpose of analysing the PSII function. When assessing the functioning of PSII for the whole season, the criteria of performance were as follows for maize: IMI>SMI>IMR>SMR, and for beans: SBI>IBI>IBR>SBR, as discussed in Chapter 5.

Biomass accumulation relates to the capture and usage of resources and determines the competitive ability of the cropping system. The actual φ_{Eo} (quantum efficiency of electron transport) ranged from 0 to 0.2, denoting a larger number of transported electrons for functioning of PSII as the season progressed and the plant dry mass accumulated. However, during the period when the plants were approaching maturity the electron transport rate decreased due to plant aging. From the foregoing, it can be concluded that since stress influences rate of electron transport it also influences rate of biomass accumulation.

This study considered the relationship between LWP and soil water content. However, the relationship between electron transport and LWP was not investigated. It is therefore recommended that these relationships be further investigated for the cropping systems in future research. The other area of interest that was not studied is plant nutrient content and its relationship to all the other factors addressed in this research.

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Appendix

Table A.1 Bean leaf water potential (MPa) for intercrop and sole cropping at different heights of the canopy throughout the growing season under irrigated and rainfed conditions. SBI = irrigated sole bean, IBI = irrigated intercrop bean, SBR = rainfed sole bean, IBR = rainfed intercrop bean.

	SBI					IBI				
DAP	Bottom	middle	top	Plant average		DAP	Bottom	middle	top	Plant average
47	-0.3	-0.3	-0.3	-0.3		47	-0.6	-0.5	-0.6	-0.6
52	-0.2	-0.2	-0.2	-0.2		52	-0.2	-0.2	-0.2	-0.2
59	-0.3	-0.5	-0.4	-0.4		59	-0.2	-0.2	-0.3	-0.2
67	-1.1	-1.0	-0.9	-1.0		67	-0.5	-0.5	-0.5	-0.5
74	-0.4	-0.4	-0.3	-0.4		74	-0.2	-0.3	-0.3	-0.3
81	-0.2	-0.4	-0.4	-0.3		81	-0.2	-0.3	-0.4	-0.3
88	-0.9	-0.6	-0.3	-0.6		88	-0.5	-0.7	-0.9	-0.7
95	-0.2	-0.4	-0.1	-0.2		95	-0.6	-0.6	-0.6	-0.6
102	-0.4	-0.3	-0.2	-0.3		102	-0.4	-0.4	-0.4	-0.4
	SBR					IBR				
SBR	Bottom	Middle	Top	Plant average		IBR	Bottom	middle	top	Plant average
47	-1.3	-1.2	-1.2	-1.2		47	-0.8	-0.8	-0.7	-0.8
52	-0.5	-0.5	-0.4	-0.4		52	-0.2	-0.2	-0.2	-0.2
59	-0.6	-0.4	-0.6	-0.5		59	-0.2	-0.1	-0.1	-0.1
67	-0.6	-0.6	-0.7	-0.6		67	-1.1	-0.9	-0.8	-0.9
74	-0.5	-0.9	-1.0	-0.8		74	-0.7	-0.7	-0.7	-0.7
81	-0.3	-0.4	-0.6	-0.4		81	-0.2	-0.5	-0.6	-0.5
88	-0.8	-0.9	-0.5	-0.7		88	-0.2	-0.5	-0.3	-0.3
95	-0.2	-0.4	-0.1	-0.2		95	-0.6	-0.6	-0.6	-0.6
102	-0.8	-0.8	-0.8	-0.8		102	-1.1	-0.9	-1.0	-1.0

Table A.2: Maize leaf water potential (MPa) for intercrop and sole cropping at different heights of the canopy throughout the growing season under irrigated and rainfed conditions. IMI= irrigated intercrop maize, SMI = irrigated sole maize, IMR = rainfed intercrop maize, SMR = rainfed sole maize.

IMI						SMI				
DAP	Bottom	middle	top	Plant average		DAP	Bottom	middle	top	Plant average
47	-0.9	-0.9	-0.9	-0.9		47	-1.1	-1.05	-1.08	-1.1
52	-1.2	-1.3	-1.1	-1.2		52	-1.12	-1.03	-1.15	-1.1
59	-1.0	-0.9	-1.0	-0.9		59	-1.08	-0.9	-1	-1.0
67	-0.6	-0.6	-0.4	-0.5		67	-1	-0.7	-1.17	-1.0
74	-0.9	-0.7	-1.0	-0.9		74	-1.32	-1.27	-1.25	-1.3
81	-1.1	-0.9	-0.8	-0.9		81	-1.05	-0.65	-0.8	-0.8
88	-0.8	-0.7	-0.8	-0.8		88	-0.73	-0.72	-0.73	-0.7
95	-0.8	-1.0	-0.9	-0.9		95	-0.85	-1.15	-0.88	-1.0
102	-0.9	-0.8	-0.6	-0.8		102	-0.88	-1.05	-0.95	-1.0
IMR						SMR				
IMR	Bottom	Middle	Top	Plant average		SMR	Bottom	middle	top	Plant average
47	-0.7	-0.9	-1.0	-0.9		47	-1.0	-1.1	-1.0	-1.1
52	-0.9	-1.1	-1.0	-1.0		52	-1.1	-1.1	-1.3	-1.2
59	-1.0	-1.3	-1.2	-1.2		59	-0.9	-1.1	-1.0	-1.0
67	-1.0	-1.2	-1.6	-1.3		67	-1.7	-1.7	-1.5	-1.6
74	-1.8	-1.9	-1.8	-1.8		74	-1.9	-1.9	-1.8	-1.8
81	-0.6	-0.8	-0.8	-0.8		81	-1.0	-0.8	-0.9	-0.9
88	-0.7	-0.8	-0.6	-0.7		88	-0.9	-0.9	-0.9	-0.9
95	-0.9	-1.0	-1.0	-1.0		95	-0.9	-1.2	-0.9	-1.0
102	-1.0	-1.1	-1.3	-1.1		102	-1.0	-1.3	-1.4	-1.2

Table A.3: Soil water content measured with the neutron meter at a profile of 0-900 mm (rootzone) for irrigated intercrop maize/bean, irrigated sole maize and irrigated intercrop bean treatments under irrigation.

Irrigated	IMBI	SMI	SBI
DAS	0-900 mm	0-900 mm	0-900 mm
21	250.8	257.7	245.6
24	259.4	261.5	258.6
35	237.5	244.3	227.6
42	222.4	229.6	219.6
49	212.2	180.5	209.3
57	205.4	200.1	200.8
71	231.9	210.4	238.5
78	255.2	245.0	262.4
85	239.5	244.5	236.7
92	230.6	231.4	228.9
100	233.4	228.7	205.7
107	224.4	211.9	240.7
114	220.0	208.3	229.3
128	216.7	207.3	229.7
135	207.7	203.1	227.9

Table A.4: Soil water content at a rootzone 0-900 mm soil profile for IMBR, SMR and IBR treatments measured throughout the season. IMBR = rainfed intercrop maize and bean.

Rainfed	IMBR	SMR	SBR
DAS	0-900 mm	0-900 mm	0-900 mm
21	234.5	224.7	239.2
24	246.2	236.1	251.1
35	215.7	219.5	233.2
42	216.0	198.1	213.9
49	207.2	190.2	206.2
57	187.1	172.5	191.4
71	239.3	237.7	207.7
77	244.1	244.7	245.9
85	238.9	230.9	256.0
92	238.9	222.1	253.6
100	231.9	194.7	248.9
109	233.2	232.2	230.9
114	219.5	220.1	202.3
121	212.2	214.2	222.9
128	214.0	214.7	221.9
135	209.8	208.3	217.5

Table A.5 The biomass accumulation for maize/bean intercrop and sole cropping systems for IBR, IMR, and SBR showing the averages and the standard deviation under rainfed conditions.

RAINFED		IBR		IMR		SMR		SBR	
Date	DAP	Average	Stdev	Average	Stdev	Average	Stdev	Mean	Stdev
19-Jan	40	46.80	15.34	77.0	15.96	80.19	24.46	53.44	25.15
28-Jan	49	82.50	55.04	183.5	56.37	252.45	51.35	74.50	34.25
7-Mar	56	140.90	48.84	271.0	39.70	296.71	80.32	92.40	26.33
14-Mar	63	163.38	33.16	299.1	10.97	331.20	27.32	141.78	31.23
22-Mar	71	92.71	24.41	233.9	31.10	267.24	17.91	105.40	11.50
27-Mar	76	121.1	23.5	343.9	31.80	408.65	92.69	211.5	17.2
2-Apr	82	170.60	45.64	392.3	38.70	423.80	41.00	289.7	67.5
12-Apr	92	189.00	118.05	438.4	23.6	466.20	40.60	258.30	52.28
19-Apr	99	131.20	60.90	450.5	19.5	489.8	63.2	291.38	89.08

Table A.6: The biomass accumulation for maize/bean intercrop and sole cropping systems for IMI, SMR, and SBI showing the averages and the standard deviation under irrigated conditions.

	IBI		IMI		SMI		SBI	
DAP	Average	Stdev	Average	Stdev	Average	Stdev	Mean	Stdev
40	48.58	15.31	78.98	23.16	80.86	18.52	53.44	25.15
49	172.36	22.46	290.58	151.41	224.40	67.31	86.4	41.3976
56	197.78	56.98	317.00	28.82	372.00	93.11	169.51	90.70
63	174.84	43.43	355.11	33.0.	517.07	34.14	207.30	57.99
71	106.58	76.21	290.36	27.89	355.82	32.37	138.84	97.98
76	243.73	18.30	508.1	43.4	589.29	161.17	313.60	82.25
82	338.76	103.77	478.68	89.91	673.96	104.17	483.00	140.92
92	252.00	93.62	524.81	133.72	768.47	74.32	381.24	142.08
99	297.16	92.98	487.20	46.89	748.93	127.81	396.36	140.08
113	187.29	73.93	492.58	95.52	794.09	143.54	443.82	62.15

Table A.7: Intercrop bean normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under irrigation.

	Irrigated top leaves bean									
DAS	**Fo/Fm**	**Fv/Fo**	**PHI(Eo)**	**PHI(Do)**	**ABS/RC**	**TRo/RC**	**ETo/RC**	**DIo/RC**	**PI(abs)**	**D.F.**
70	1	1	1	1	1	1	1	1	1	1
84	2.1749	0.2573	0.3001	2.1749	1.3991	0.7827	0.4196	3.0429	0.0776	-0.5283
87	1.3847	0.6182	0.6158	1.3847	1.4061	1.2033	0.866	1.9471	0.2718	0.2215
93	1.0979	0.8774	0.9598	1.0979	1.0219	0.9844	0.9809	1.122	0.8539	0.9056
101	0.9417	1.0853	1.0294	0.9417	1.0856	1.1093	1.1174	1.0224	1.0115	1.0068
107	1.0587	0.9238	1.2889	1.0587	1.0398	1.0169	1.3401	1.1009	1.4388	1.2175
114	1.5083	0.5367	0.6642	1.5083	1.3105	1.0608	0.8703	1.9767	0.3041	0.2884
	Irrigated middle leaves bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	DIo/RC	PI(abs)	D.F.
70	1	1	1	1	1	1	1	1	1	1
84	1.704	0.4303	1.02	1.704	3.6105	2.6464	3.6822	6.1521	0.2653	0.3797
87	1.484	0.5503	0.4463	1.484	1.3176	1.0757	0.5879	1.9553	0.1591	0.1407
93	0.988	1.0169	0.6555	0.988	0.9848	0.9893	0.6454	0.973	0.5053	0.6809
101	0.8676	1.2109	0.7891	0.8676	0.8752	0.9191	0.6905	0.7594	0.8394	0.9181
107	0.9651	1.0502	0.8213	0.9651	1.0413	1.0551	0.8552	1.0049	0.6919	0.8278
114	1.4389	0.5794	0.5715	1.4389	1.254	1.0452	0.7167	1.8044	0.2435	0.3395
	Irrigated bottom leaves bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	DIo/RC	PI(abs)	D.F.
70	1	1	1	1	1	1	1	1	1	1
84	1.5718	0.5001	0.5049	1.5718	1.1191	0.8797	0.5651	1.759	0.2093	0.296
87	1.5215	0.5291	0.3646	1.5215	1.3939	1.122	0.5085	2.1208	0.1097	0.0051
93	1.069	0.9116	0.4744	1.069	1.0401	1.0132	0.4934	1.1119	0.2785	0.4245
101	0.8828	1.1823	0.9401	0.8828	0.8758	0.9142	0.8234	0.7732	1.1023	1.0439
107	0.9328	1.0993	1.0658	0.9328	1.1097	1.1376	1.1827	1.035	1.0742	1.0322
114	1.3647	0.633	0.538	1.3647	1.1091	0.9578	0.5966	1.5135	0.2555	0.3857
	The whole bean plan average									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	DIo/RC	PI(abs)	D.F.
70	1	1	1	1	1	1	1	1	1	1
84	1.8821	0.3678	0.6661	1.8821	1.5444	1.069	1.029	2.9066	0.2229	0.219
87	1.5419	0.5259	0.4776	1.5419	1.2751	1.034	0.6091	1.9662	0.185	0.1219
93	1.1098	0.8668	0.6895	1.1098	0.9459	0.9097	0.6523	1.0498	0.5405	0.6798
101	0.9664	1.0472	0.9392	0.9664	0.8479	0.8579	0.7964	0.8194	1.087	1.0434
107	1.0758	0.9049	1.115	1.0758	0.9407	0.9158	1.0489	1.012	1.2393	1.1116
114	1.5157	0.5413	0.6038	1.5157	1.1287	0.9256	0.6815	1.7107	0.2939	0.3627

Table A.8 Intercrop bean normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under rainfed.

	Rainfed intercrop top leaves for bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
84	1.92	0.36	0.60	1.92	1.38	0.96	0.82	0.21	0.18	2.65
87	1.54	0.53	0.84	1.54	1.33	1.09	1.12	0.41	0.54	2.06
93	1.13	0.85	1.21	1.13	1.27	1.22	1.53	0.99	0.99	1.44
101	1.05	0.94	1.13	1.05	1.08	1.06	1.22	1.09	1.04	1.13
108	1.22	0.76	0.49	1.22	1.12	1.04	0.54	0.28	0.34	1.36
117	1.16	0.82	0.76	1.16	1.10	1.04	0.83	0.53	0.67	1.27
	Rainfed intercrop middle leaves for bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1.00	1	1	1	1
84	2.2168	0.2848	0.5177	2.2168	1.4495	0.92	0.7506	0.1402	0.167	3.2132
87	1.6185	0.502	0.6102	1.6185	1.2979	1.05	0.7921	0.2408	0.3963	2.1004
93	1.1923	0.7898	0.9236	1.1923	1.2113	1.14	1.1189	0.6296	0.8038	1.4441
101	1.0757	0.908	0.8526	1.0757	0.9938	0.97	0.8475	0.7213	0.8615	1.0689
108	1.4013	0.6267	0.3387	1.4013	1.1529	1.01	0.3903	0.1387	0.1626	1.6155
117	1.3286	0.6776	0.4562	1.3286	1.1202	1.01	0.5111	0.2175	0.3532	1.4883
	Rainfed intercrop bottom leaves for bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1.000	1	1	1	1
84	2.1165	0.2622	0.4688	2.1165	1.255	0.697	0.5883	0.1591	-0.1066	2.6561
87	1.1386	0.8298	0.8235	1.1386	0.9969	0.942	0.8211	0.6658	0.7551	1.1351
93	1.106	0.8658	1.0808	1.106	1.0429	0.999	1.1272	1.0293	1.0174	1.1534
101	0.8719	1.2056	0.9443	0.8719	0.7837	0.824	0.7402	1.2905	1.1536	0.6833
108	1.0035	0.9951	0.6945	1.0035	0.8739	0.873	0.607	0.6528	0.7432	0.877
117	0.9793	1.0296	0.6938	0.9793	0.7998	0.806	0.555	0.7274	0.8084	0.7832
	The whole plant average for intercrop bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1.000	1	1	1	1
84	2.053	0.3118	0.5322	2.053	1.3465	0.862	0.7166	0.1724	0.1149	2.7643
87	1.4074	0.6118	0.7499	1.4074	1.201	1.034	0.9004	0.4072	0.5477	1.6903
93	1.1409	0.8343	1.0572	1.1409	1.1692	1.113	1.2362	0.8589	0.9234	1.3339
101	0.9929	1.01	0.9621	0.9929	0.9432	0.946	0.9075	0.9997	0.9998	0.9366
108	1.1907	0.7853	0.5064	1.1907	1.0424	0.974	0.5277	0.3092	0.4091	1.2413
117	1.1476	0.8275	0.6198	1.1476	0.9981	0.948	0.6186	0.4356	0.5816	1.1454

Table A.9: Sole bean normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under irrigated.

	Irrigated top leaves for sole bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
84	1.5898	0.4444	0.7187	1.5898	1.0685	0.7546	0.7679	0.4273	0.2201	1.6986
87	1	1	1	1	1	1	1	1	1	1
93	0.8689	1.2264	1.02	0.8689	0.8579	0.9139	0.8749	1.3378	1.267	0.7453
101	0.8626	1.2388	0.9749	0.8626	0.664	0.7095	0.6471	1.6242	1.4448	0.5728
107	1.0833	0.8849	0.5644	1.0833	0.9503	0.9109	0.5362	0.4482	0.264	1.0294
114	0.8947	1.1761	1.058	0.8947	0.9077	0.9553	0.9603	1.3059	1.2448	0.8122
	Irrigated middle leaves for sole bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
84	1.4665	0.4668	0.6474	1.4665	0.8752	0.5991	0.5665	0.4925	-0.5013	1.2835
87	1	1	1	1	1	1	1	1	1	1
93	0.7685	1.5052	1.1008	0.7685	0.7753	0.8967	0.853	1.8087	2.256	0.5958
101	0.6946	1.7374	1.043	0.6946	0.569	0.6865	0.5934	2.4915	2.9349	0.3952
107	0.8664	1.2584	0.7388	0.8664	0.8559	0.9333	0.6324	0.8733	0.7128	0.7415
114	0.7786	1.4769	1.1697	0.7786	0.7996	0.9193	0.935	1.8926	2.3523	0.6226
	Irrigated bottom leaves for sole bean									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
84	0.9402	1.1159	1.0684	0.9402	1.3814	1.4494	1.4758	0.8277	0.453	1.2988
87	1	1	1	1	1	1	1	1	1	1
93	0.6764	1.8722	1.2615	0.6764	1.0196	1.2909	1.2864	1.8278	2.7436	0.6896
101	0.6099	2.1652	1.3805	0.6099	0.7431	0.9814	1.0261	3.0961	4.2671	0.4532
107	0.7345	1.6587	0.6808	0.7345	1.2029	1.4655	0.8191	0.6681	-0.1662	0.8836
114	0.6802	1.8573	1.6483	0.6802	1.107	1.3981	1.8254	2.4517	3.5924	0.753
	The whole plant average leaves sole bean irrigated									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
84	1.3479	0.5826	0.7415	1.3479	0.8725	0.6851	0.6471	0.6151	0.2391	1.1761
87	1	1	1	1	1	1	1	1	1	1
93	0.7883	1.4341	1.0645	0.7883	0.7962	0.9003	0.8477	1.6515	1.7857	0.6277
101	0.7354	1.5822	1.0495	0.7354	0.5915	0.6881	0.6209	2.3103	2.3111	0.435
107	0.9062	1.1672	0.6182	0.9062	0.9033	0.9556	0.5582	0.6343	0.2875	0.8186
114	0.8006	1.403	1.1976	0.8006	0.8424	0.9461	1.0091	1.8321	1.948	0.6745

Table A.10: Sole bean normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under rainfed.

	Rainfed sole bean top leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	2.7225	0.1643	0.3993	2.7225	2.0136	0.9008	0.8043	0.068	-0.2742	5.4819
87	1.6851	0.4631	0.5473	1.6851	1.4425	1.1255	0.7897	0.1881	0.208	2.4307
93	1.1029	0.8768	1.0192	1.1029	1.3031	1.2601	1.3282	0.7354	0.8543	1.4371
101	1.2083	0.7725	1.0222	1.2083	1.1717	1.0935	1.1981	0.7711	0.8768	1.4157
108	1.2083	0.7725	1.0222	1.2083	1.1717	1.0935	1.1981	0.7711	0.8768	1.4157
117	1.7587	0.4302	0.61	1.7587	1.6504	1.2487	1.0069	0.1863	0.2035	2.9026
	Rainfed sole bean middle leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	2.4205	0.2141	0.6279	2.4205	1.6412	0.8504	1.0307	0.1872	0.1781	3.9724
87	1.7572	0.423	0.5395	1.7572	1.3714	1.0191	0.7398	0.1865	0.1764	2.4098
93	1.2432	0.7381	0.7873	1.2432	1.2044	1.105	0.9484	0.4766	0.6365	1.4972
101	1.12	0.8568	0.9011	1.12	1.0273	0.9855	0.9258	0.7502	0.859	1.1506
108	1.12	0.8568	0.9011	1.12	1.0273	0.9855	0.9258	0.7502	0.859	1.1506
117	1.4343	0.5947	0.5746	1.4343	1.2625	1.0765	0.7255	0.2563	0.3322	1.8107
	Rainfed sole bean bottom leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	2.5992	0.1627	0.224	2.5992	1.7223	0.7282	0.3856	0.0354	-0.6629	4.4765
87	1.313	0.6756	0.5106	1.313	1.0995	0.9753	0.5617	0.2581	0.3256	1.4436
93	1.1252	0.8487	0.6579	1.1252	1.0758	1.0272	0.708	0.4275	0.5769	1.2104
101	1.0875	0.8906	0.7994	1.0875	0.8833	0.8554	0.7061	0.7221	0.8379	0.9606
108	1.2432	0.7338	0.5451	1.2432	1.0484	0.9564	0.5716	0.3095	0.416	1.3034
117	1.3997	0.6115	0.3287	1.3997	1.1694	1.0007	0.3845	0.1306	-0.0135	1.6368
	The whole plant average for sole bean leaves rainfed									
DAS	PI(abs)	D.F.	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	0.0812	-0.2222	2.5798	0.1795	0.4096	2.5798	1.7988	0.8327	0.7365	4.6404
87	0.2106	0.2416	1.5542	0.5222	0.5341	1.5542	1.2989	1.0542	0.6935	2.0187
93	0.5363	0.6967	1.1545	0.8206	0.8176	1.1545	1.1975	1.1346	0.9791	1.3825
101	0.7478	0.8579	1.1386	0.83997	0.90757	1.1386	1.02743	0.97813	0.94333	1.1756
108	0.5854	0.7394	1.1853	0.7904	0.822	1.1853	1.0839	1.0157	0.8907	1.2847
117	0.1867	0.183	1.5148	0.5446	0.4941	1.5148	1.3425	1.1076	0.6631	2.0335

Table A.11: Intercrop maize normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under irrigation.

	Irrigated intercrop maize top leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
71	1.3004	0.675	0.8349	1.3004	1.2365	1.0858	1.0322	0.5063	0.4691	1.608
72	1	1	1	1	1	1	1	1	1	1
84	1.6784	0.4317	0.4465	1.6784	1.0964	0.7946	0.4896	0.2031	-0.2432	1.8401
93	0.9823	1.0252	0.8194	0.9823	0.8754	0.8817	0.7171	0.8703	0.8916	0.8598
101	0.9813	1.0266	1.1459	0.9813	0.8337	0.84	0.9553	1.5048	1.3188	0.8181
107	0.9872	1.018	1.2471	0.9872	0.7152	0.7189	0.8919	2.011	1.5449	0.706
114	1.1968	0.7687	0.7015	1.1968	0.9113	0.8385	0.639	0.5737	0.5666	1.0907
	Irrigated intercrop maize middle leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
71	1.2983	0.6703	0.959	1.2983	1.3613	1.1845	1.3058	0.5744	0.5803	1.7674
72	1	1	1	1	1	1	1	1	1	1
84	1.5297	0.5029	0.3993	1.5297	1.0796	0.8305	0.4312	0.1921	-0.2486	1.6513
93	0.9061	1.1491	0.7981	0.9061	0.9589	0.9982	0.7654	0.8163	0.8464	0.8688
101	0.9321	1.1049	1.3767	0.9321	0.8956	0.9221	1.2333	2.0155	1.5304	0.8348
107	0.9855	1.0213	0.7907	0.9855	0.6961	0.7005	0.5505	1.0339	1.0252	0.6859
114	1.0485	0.9337	0.76	1.0485	0.8833	0.8647	0.6714	0.7326	0.7645	0.9261
	Irrigated intercrop maize bottom leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
71	1.3071	0.6693	0.8576	1.3071	1.2644	1.106	1.084	0.5126	0.5523	1.6527
72	1	1	1	1	1	1	1	1	1	1
84	0.9055	1.1474	1.0231	0.9055	0.9061	0.941	0.9268	1.2356	1.1418	0.8204
93	1.0262	0.964	0.9247	1.0262	0.8848	0.8753	0.8181	0.9784	0.9854	0.908
101	0.9969	1.0045	0.6336	0.9969	0.7448	0.7457	0.4718	0.6947	0.7559	0.7424
107	1.1777	0.7875	0.5885	1.1777	0.9113	0.8452	0.5361	0.4464	0.4597	1.0733
	The whole plant average intercrop maize leaves irrigated									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
71	1.3019	0.6717	0.8806	1.3019	1.2846	1.1232	1.131	0.5286	0.5335	1.6724
72	1	1	1	1	1	1	1	1	1	1
84	1.6154	0.4606	0.4036	1.6154	1.1063	0.823	0.4462	0.18	-0.2546	1.7872
93	0.9312	1.1046	0.8845	0.9312	0.9117	0.9378	0.8062	0.9661	0.9748	0.849
101	0.9803	1.0289	1.1425	0.9803	0.8707	0.8779	0.9946	1.4456	1.2696	0.8536
107	0.9884	1.0166	0.875	0.9884	0.7185	0.7219	0.6287	1.1498	1.1021	0.7102
114	1.1382	0.8282	0.6821	1.1382	0.9006	0.8489	0.6144	0.5771	0.5978	1.0251

Table A.12: Intercrop maize normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under rainfed.

	Rainfed intercrop maize top leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.5727	0.4496	0.534	1.5727	1.0707	0.7573	0.5719	0.2741	-0.1093	1.6839
87	1.1283	0.8279	1	1.1283	1.1489	1.0735	1.1491	0.8078	0.8171	1.2963
93	0.8253	1.3197	1.1418	0.8253	0.7707	0.8395	0.8802	1.8526	1.5284	0.636
101	0.8782	1.2096	1.0054	0.8782	0.8651	0.919	0.8699	1.2797	1.2113	0.7597
108	0.984	1.0244	0.3192	0.984	0.7767	0.7831	0.248	0.2903	-0.06	0.7642
117	1.0494	0.9287	0.4069	1.0494	0.7938	0.7738	0.3232	0.3557	0.1142	0.833
	Rainfed intercrop maize middle leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.996	0.2909	0.3097	1.996	1.3446	0.7808	0.4165	0.0855	-0.5115	2.6837
87	1.2366	0.7282	0.6435	1.2366	1.2603	1.1347	0.8109	0.3402	0.3372	1.5584
93	0.8981	1.1617	0.9505	0.8981	0.7871	0.8209	0.7482	1.2617	1.1429	0.7068
101	0.9588	1.0611	0.9247	0.9588	0.9276	0.9437	0.8575	0.9729	0.9831	0.8893
108	1.1606	0.8035	0.2181	1.1606	0.8517	0.7941	0.1857	0.1401	-0.2081	0.9885
117	1.0621	0.9172	0.3438	1.0621	0.7927	0.772	0.2726	0.2751	0.2068	0.8419
	Rainfed intercrop maize bottom leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.6327	0.4137	0.311	1.6327	1.1848	0.8003	0.3688	0.1162	-0.7331	1.9343
87	1.1156	0.8431	0.7569	1.1156	1.1135	1.0474	0.8429	0.5348	0.4962	1.2422
93	0.7416	1.527	1.1421	0.7416	0.6775	0.7673	0.7738	2.2863	1.6658	0.5024
101	0.9032	1.162	1.0262	0.9032	0.8287	0.8698	0.8506	1.3499	1.2416	0.7485
108	0.9714	1.0446	0.1032	0.9714	0.717	0.7276	0.0741	0.0905	-0.9344	0.6965
117	0.9971	1.0046	0.307	0.9971	0.7472	0.7484	0.2294	0.2758	-0.037	0.745
	The whole plant average intercrop maize leaves rainfed									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.7272	0.3777	0.3715	1.7272	1.2051	0.7864	0.4478	0.1369	-0.462	2.0815
87	1.1605	0.7956	0.7798	1.1605	1.1775	1.0872	0.9184	0.5144	0.5112	1.3666
93	0.8203	1.3234	1.0697	0.8203	0.7463	0.8104	0.7985	1.7292	1.4026	0.6122
101	0.9134	1.1403	0.98	0.9134	0.8763	0.9125	0.8587	1.1756	1.119	0.8004
108	1.0356	0.9489	0.2084	1.0356	0.7816	0.7683	0.163	0.1656	-0.322	0.8094
117	1.0359	0.9486	0.3497	1.0359	0.7779	0.7645	0.2721	0.2986	0.1114	0.8058

Table A.13: Sole maize normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under irrigated. Irrigation.

	Irrigated sole maize top leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
72	1	1	1	1	1	1	1	1	1	1
84	1.4066	0.5895	0.5434	1.4066	1.2243	1.0149	0.6652	0.2703	-0.011	1.7222
87	1.3161	0.6588	0.7181	1.3161	1.1593	1.0051	0.8321	0.4342	0.3552	1.5257
93	0.9696	1.0447	0.8914	0.9696	0.8408	0.8515	0.7495	1.0334	1.0254	0.8152
101	0.9872	1.0187	1.2919	0.9872	0.9011	0.906	1.1638	1.6853	1.4034	0.8896
107	1.1185	0.8494	0.6885	1.1185	0.951	0.9036	0.6546	0.5707	0.5664	1.0636
114	1.306	0.6672	0.619	1.306	0.9746	0.8491	0.6031	0.4262	0.3408	1.2727
129	1.1618	0.8021	0.7172	1.1618	1.016	0.9469	0.7286	0.5463	0.5328	1.1803
	Irrigated sole maize middle leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
72	1	1	1	1	1	1	1	1	1	1
84	1.3272	0.6264	0.5318	1.3272	1.2292	1.0216	0.6538	0.2845	-0.479	1.6313
87	1.1974	0.7504	1.0599	1.1974	0.164	0.1473	0.1739	5.8245	3.0731	0.1964
93	0.8167	1.3405	0.9543	0.8167	0.7374	0.8072	0.7038	1.5064	1.4821	0.6023
101	1.4364	0.5394	1.1739	1.4364	0.3624	0.2808	0.4255	2.851	2.2326	0.5205
107	0.8396	1.2897	1.1466	0.8396	0.8152	0.8827	0.9347	1.7163	1.6355	0.6844
114	1.1081	0.8524	0.7704	1.1081	0.9201	0.8687	0.7086	0.7032	0.5858	1.0195
129	0.899	1.1706	1.031	0.899	0.8995	0.9465	0.9272	1.2641	1.2758	0.8086
	Irrigated sole maize bottom leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
72	1	1	1	1	1	1	1	1	1	1
84	1.6577	0.4476	0.3567	1.6577	1.3873	1.0297	0.495	0.1185	-0.327	2.2998
87	1.2702	0.7038	0.7198	1.2702	1.2246	1.0948	0.8813	0.4147	0.4521	1.5556
93	0.9901	1.014	0.5903	0.9901	0.8076	0.8107	0.4768	0.5933	0.675	0.7996
101	1.1541	0.814	0.9041	1.1541	1.0296	0.9674	0.9307	0.744	0.816	1.1884
107	1.0004	0.9995	0.7769	1.0004	0.9376	0.9374	0.7286	0.7316	0.8055	0.9381
114	1.1048	0.8679	0.6545	1.1048	0.852	0.817	0.5576	0.5849	0.6662	0.9413
129	1.065	0.915	0.8228	1.065	0.9407	0.9167	0.7741	0.7519	0.8226	1.0019
	The whole plant average sole maize leaves irrigated									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
72	1	1	1	1	1	1	1	1	1	1
84	1.3497	0.6133	0.4609	1.3497	1.6775	1.3889	0.7736	0.1648	-0.206	2.264
87	1.0961	0.869	0.7884	1.0961	1.4734	1.4037	1.1619	0.4471	0.4617	1.615
93	0.8532	1.2568	0.7781	0.8532	1.04	1.1151	0.8093	0.7653	0.8211	0.8873
101	1.1659	0.7876	1.0747	1.1659	1.0681	0.981	1.1478	0.9487	0.9648	1.2453
107	0.9054	1.1556	0.8395	0.9054	1.1773	1.2322	0.9883	0.7122	0.773	1.0658
114	1.0792	0.8906	0.6678	1.0792	1.1881	1.1419	0.7934	0.4479	0.463	1.2821
129	0.9621	1.0584	0.8288	0.9621	1.2457	1.269	1.0325	0.6288	0.6897	1.1985

Table A.14: Sole maize normalised fluorescence values for selected parameters measured top, middle and bottom and the whole plant averages calculated using the JIP-test for the whole growing season under rainfed.

	Rainfed sole maize top leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.5793	0.4693	0.6598	1.5793	1.1994	0.8889	0.7915	0.3256	0.1808	1.8943
87	1.3863	0.5967	0.5043	1.3863	1.2882	1.0658	0.6498	0.2259	-0.086	1.7859
93	0.9343	1.1015	0.7631	0.9343	0.7315	0.753	0.5582	0.9574	0.9682	0.6834
101	0.977	1.0341	1.057	0.977	0.892	0.9012	0.9432	1.2507	1.1633	0.8715
108	1.0463	0.936	0.9622	1.0463	0.9279	0.9087	0.8931	0.9807	0.9858	0.9709
117	1.0978	0.8709	0.6653	1.0978	0.9134	0.8735	0.6077	0.555	0.5701	1.0028
	Rainfed sole maize middle leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.0763	0.8749	0.9133	1.0763	0.9244	0.8707	0.8445	0.9075	-0.605	0.995
87	0.8923	1.2127	1.4254	0.8923	0.9119	0.9867	1.2999	1.9935	12.403	0.8136
93	0.665	1.8876	1.5797	0.665	0.5508	0.6914	0.8701	4.7839	26.873	0.3663
101	0.6717	1.8607	1.9828	0.6717	0.6558	0.8199	1.3003	5.796	30.045	0.4405
108	0.7683	1.5312	1.3221	0.7683	0.7507	0.8832	0.9922	2.4045	15.503	0.5768
117	0.7746	1.5124	1.2379	0.7746	0.7199	0.8436	0.8912	2.2679	14.536	0.5577
	Rainfed sole maize bottom leaves									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.3493	0.5643	0.6464	1.3493	1.049	0.7986	0.6779	0.4159	-0.16	1.4154
87	1.0623	0.9012	0.755	1.0623	1.0622	1.017	0.8021	0.5884	0.2991	1.1284
93	0.7692	1.505	1.0261	0.7692	0.6532	0.7562	0.6702	1.9017	1.8495	0.5023
101	0.7494	1.5628	1.2621	0.7494	0.7159	0.8385	0.9035	2.4767	2.1985	0.5365
108	0.8751	1.2401	0.8675	0.8751	0.832	0.903	0.7216	1.0537	1.0691	0.7281
117	0.8881	1.2119	0.6216	0.8881	0.8229	0.8858	0.5114	0.6673	0.4653	0.7309
	The whole plant average sole maize top leaves rainfed									
DAS	Fo/Fm	Fv/Fo	PHI(Eo)	PHI(Do)	ABS/RC	TRo/RC	ETo/RC	PI(abs)	D.F.	DIo/RC
70	1	1	1	1	1	1	1	1	1	1
84	1.1772	0.7395	0.8896	1.1772	0.9651	0.8402	0.8584	0.7902	0.0869	1.1362
87	0.8837	1.228	1.2829	0.8837	0.9012	0.9778	1.156	1.7502	3.1702	0.7964
93	0.7005	1.74	1.313	0.7005	0.588	0.7166	0.772	3.2993	5.6285	0.4119
101	0.7081	1.7132	1.6938	0.7081	0.6886	0.8355	1.1663	4.199	6.5634	0.4876
108	0.7982	1.4379	1.2732	0.7982	0.766	0.8789	0.9751	2.1874	4.0349	0.6114
117	0.8159	1.3903	0.9852	0.8159	0.7487	0.8494	0.7374	1.5242	2.6344	0.6108