FIELD MEASUREMENT OF TEMPERATURE AND LEAF GROWTH ON MAIZE/BEAN INTER-CROP

BY

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DECLARATION

I declare that the thesis hereby submitted by me for the Master of Science in Agriculture degree at the University of the Free State is my own independent work and has not previously been submitted by me to another University/faculty. I further cede copyright of the thesis in favour of the University of the Free State.

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SUMMARY

FIELD MEASUREMENT OF TEMPERATURE AND LEAF GROWTH ON MAIZE/BEAN INTER-CROP

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Notwithstanding the emphasis of research on the intensification of sole-crop systems, the practice of inter-cropping remains widespread. Evidence is accumulating that indicates that under many situations it may represent a more efficient use of natural resources. Much of the basic information on the response of leaf growth to a single environmental factor was obtained during the 1960s when controlled environment facilities became available, yet it proved difficult to extrapolate results obtained in a controlled environment to the field situation. From this background emerged the notion that temperature constitutes one of the main environmental factors influencing leaf growth at the field level for both monocotyledonous and dicotyledonous crops.

Sole- and inter-crop maize (*Zea mays* L.) and dry beans (*Phaseolus vulgaris* L.) were grown in order to examine the mechanisms by which temperature influences leaf growth during the early growth stage using of three consecutive planting dates in summer. For daily measurements of leaf growth 15 individual plant samples were measured from each replicated plot. Temperature variations were observed during the three planting dates, namely in November, January and March, from the automatic weather station at the experimental site. Generally the temperature increased gradually from the first planting in November until late January during the second planting and thereafter decreased from the beginning of February to reach the lowest temperature in May. Due to the difference in temperature at the consecutive planting dates the seedling emergence in the third planting showed took longer.

From daily leaf length measurements of sole and inter-crop maize the leaf length proved to be almost linear with time (days after planting). During the first planting, the leaf growth was more rapid and the largest leaf size was recorded. In the case of the third planting it took a longer time to reach the same length due to low temperatures, while in the second

planting heat stress caused the maize crop to grow at a slower rate and reach a smaller size compared to the other planting dates. For sole and inter-crop beans during the first planting, the leaf growth displayed some form of sigmoid curve, whereas in the second planting due to the high temperatures the growth appeared to have two sigmoidal cycles during the growing period.

For simplicity in the analysis, the mean leaf growth rate, and the slope (rate) of a linear regression was applied for each leaf length. In maize, both approaches showed an increase in its rate with increasing leaf number with the exception of leaf 11 in first planting, whereas in the third planting the leaf growth was lower and fewer leaves resulted. In beans, these two approaches showed some differences during the growth period for all planting dates but they followed the same general trend of growth rate. Comparing the two approaches, the slope of the linear regression could render a more representative rate provided the leaf growth was linear with time.

On the other hand, the behaviour of leaf growth as a function of temperature was recorded by searching for the most appropriate thermal responses by curve fitting, using the Richards function model. This gave the highest correlation of maize leaf growth with thermal time. Generally, in all planting dates and cropping systems there was a significant correlation between the leaf growth variables and thermal time after emergence when using 10°C and 30°C as T_{base} and extreme temperatures respectively. In contrast, for the bean crop the estimates displayed a weak correlation and it became important to consider other environmental factors along with the temperature variations.

The study also assessed the field measurements of hourly leaf extension rate versus leaf temperature for sole- and inter-cropped maize plants. On each cropping system 6 auxanometers were installed to measure hourly leaf extension rate along with leaf temperatures for three days during warm and cool periods. It was shown that the leaf extension rate (LER) is one of the first components of plant growth to be affected by short period changes in temperature. Its importance led to the measurement of hourly growth rate in conjunction with leaf temperature. In this study the LER of maize as an average for three hours was used during both warm and cool periods. The measured rate was higher during the warm period, yet declined sharply above 29.5°C. Nonetheless, most of the data concentrated on temperatures up to 24°C with very few measurements in the range of 29-29.5°C of temperatures. These values were used as common values for both fitting lines.

The combination of data from both periods produced two linear regression equation. LER reached a maximum (3.2 mm h^{-1}) at 27.8°C and was expected to be zero at the lower temperature of 6.2°C and the higher temperature of 35.3°C.

These measurements of leaf growth and temperature show how temperature variations during the early growth stage of sole- and inter-crop maize/bean influence the leaves' subsequent expansion to final size. It was also observed that temperature greatly influences the rate of leaf expansion in chronological time, particularly for leaves in the field. It is difficult to resolve leaf growth data without recourse to thermal time analysis. From the study it was seemed that accurate estimation of T_{base} and T_{max} as well as the method of calculating the thermal time play a great role in assessment of possible variation of leaf growth in different planting dates.

Key words: Planting date, Thermal time, Richards function, Leaf length, Leaf number, Optimum temperature, Leaf growth curves, Leaf extension rate (LER), Auxanometer, Leaf temperature.

OPSOMMING

VELDMETING VAN BLAARGROEI EN TEMPERATUUR OP MIELIES/BONE TUSSENBOU-STELSELS

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Ongeag die klem wat navorsing op die verskerping van enkelbou-stelsels plaas, bly die beoefening van interbou-stelsels baie algemeen. Toenemende getuienis dui daarop dat dit sigself in vele toepassings tot 'n doeltreffender benutting van natuurlike hulpbronne mag leen. Baie van die basiese inligting oor die reaksie van blaargroei op 'n enkele omgewingsfaktor is gedurende die 1960's ingewin toe beheerde omgewingsgeriewe beskikbaar geword het: tog het dit moelik geblyk te wees om uitslae wat in 'n beheerde omgewing verkry is, tot die veldsituasie uit te brei. Vanuit hierdie agtergrond het die denke ontstaan dat temperatuur een van die hoof omgewingsfaktore is wat blaargroei in die veld, beide op monocotyledoneuse en dicotyledoneuse gewasse, beinvloed.

Enkel- en tussenverboude mielies (*Zea mays* L.) sowel as bone (*Phaseolus vulgris* L.) is gekweek met die doel om die meganismes waardeur temperatuur blaargroei beinvloed te ondersoek tydens hul vroeë groeistadium gedurende drie opeenvolgende planttye in die somer. Vyftien individuel plante is daagliks op drie ewebeeldige persele vir blaargroei gemeet. Temperatuurwisselings is tydens die drie plantdatums deur die nabygeleë outomatiese weerstasie aangeteken en wel in November, Januarie en Maart. Oor die algemeen het die temperatuur geleidelik toegeneem vanaf die eerste planting in November tot laat Januarie van die tweede planting en daarna gedaal van die begin van Februarie tot sy laagste vlak in Mei. Vanweë die temperatuurverskille vir die opeenvolgende plantdatums het die saadopkoms oor die derde planting langer gevat.

Daaglikse bepalings van blaarlengte van enkel- en tussenverboude mielies het feitlik 'n reglynige verband met tyd (dae na planting) getoon. Gedurende die eerste planting was die blaargroei vinnig en is die grootste blaargrootte aangeteken. In die geval van die derde planting het bereiking van dieselfde grootte langer geneem weens lae temperature, terwyl

hittespanning in die tweede planting stadiger groei en 'n kleiner finale grootte as in die ander gevalle veroorsaak het. Vir enkel- en tussenverboude bone met die eerste planting het blaargroei 'n tipe sigmoidale kurwe vertoon, terwyl dit vanweë die hoë temperature in die tweede planting twee sigmoidale siklusse tydens die groeiperiode gevolg het.

Vie Eenvoudigheidshalwe van in die ontleding is gemiddelde blaargroei en die helling van 'n lineêre regressiekurwe gebruik gemaak. Vir mielies het beide benaderings 'n toename in die groeitempo met toename in blaartelling getoon, met die uitsondering van blaar 11 van die eerste planting, terwyl beide die blaartal en groei met die derde planting afgeneem het. Vir bone het die twee benaderings sommige verskille tydens groei getoon oor en die plantdatums, hoewel hulle dieselfde algemene verloop van groeikoers gehad het. 'n Vergelyking tussen die twee benaderings dui aan dat die helling van lineêre regressie moontlik 'n meer verteenwoordigende koers kan lewer mits die blaargroei lineêr met tyd is

Daarteenoor is die gedrag van blaargroei as 'n funksie van temperatuur aangeteken deur met behulp van kurwepassing die toepaslikste termiese reaksies deur middel van die Richards funksiemodel na te spoor. Dit het die beste korrelasie van mielieblaargroei met termiese tydindek gelewer. Dit dui op 'n beter sigmoidale kurwe vir mielieblaargroei deur die tydsduur van elke temperatuurvlak te gebruik. Oor die algemeen was daar vir al die plantdatums en verbousisteme aansienlike korrelasie tussen die blaargroeiveranderlikes en termiese tyd na opkoms mits 10°C en 30°C as T_{base} gebruik word. In teenstelling hiermee het die ramings vir die bone 'n swak korrelasie gelewer en het dit belangrik begin lyk om ander omgewingsfaktore saam met die temperatuurvariasies te oorweeg.

Die studie het ook die veldmetings van uurlikse blaarverlengingskoers teen blaartemperatuur vasgestel vir enkel- en tussenverboude mielieplante. Op elke verboustelsel is 6 auxanometers ingebou om uurlikse blaarverlengingskoers saam met blaartemperatuur oor drie dae tydens warm en koel tydperke te meet. Dit is aangetoon dat die blaarverlengingskoers (LER) een van die eerste komponente van plantgroei is wat deur kortduur temperatuurveranderinge geraak word. Die belangrikheid hiervan het gelei tot die meting van uurlikse groeitempo in samehang met temperatuur. In hierdie studie is die LER van mielies as 'n gemiddelde oor drie uur tydens beide warm en koel periodes gebruik. Die gemete koers was hoër gedurende die warm tydperk, maar het tog skerp gedaal bo 29.5°C. Meeste van die data was egter toegespits op temperature net tot 24°C, met min temperature in die 29-29.5°C interval. Hierdie waardes is as gemeenskaplike waardes vir

beide paslyne gebruik. Die kombinering van data vir beide periodes het twee lineêre regressievergelyking gegee. LER het 'n maksimum (3.2mm h^{-1}) teen 27.8°C bereik en het op 'n verwagte nullesing by die laer temperatuur van 6.2 °C en die hoer temperatuur van 35.3 °C gedui.

Hierdie metings van blaargroei en temperatuur toon aan hoe temperatuurwisselings tydens die vroeë groeistadium van enkel- en tussenverboude mielises/boontjies die blare se uitsetting tot finale grootte beinvloed. Daar is ook waargeneem dat temperatuur die tempo van blaarvergroting in chronologiese tyd aansienlik beinvloed, veral in blare op die akker. Dit is moeilik om blaargroeidata te verwerk sonder toevlug na termiese data-ontleding. Uit die studie is die gevolgtrekking gemaak dat akkurate beraming van Tbase en Tmax en, sowel as die metode van berekening van termiese tyd 'n groot rol speel in die bepaling van moontlike variasie in blaargroei vir veskillende plantdatums.

Skeutelwoorde: Plantdatum, Termiese tyd, Richards funksie, Blaarlengte, Blaartal of-telling, Optimum temperatuur, Blaargroeikurwes, Blaarverlengingskoers (LER), Auxanometer, Blaartemperatuur.

CHAPTER 1

INTRODUCTION

Associated cropping of maize (*Zea mays L.*) and beans (*Phaseolus vulgaris L.*) is one of the most common cropping systems used by small-scale farmers. It is estimated that 80% of beans and 60% of maize in Latin America is produced by small-scale farmers, mostly in associated cropping (Francis, Flor and Proger, 1978). The usual explanation offered for the advantage of using such a system is that the cereal and legume species make partial complementary use of resources in either time or space, thus utilizing resources more efficiently.

In the tropical and sub-tropical regions the cereal component is usually maize, sorghum or millet and to a lesser extent rice and the legume is usually cowpea, groundnut, soybean, chickpea, beans or pigeonpea (Ofori and Stern, 1987b). Both early and late maturing crops are combined to ensure efficient utilization of resources during the whole growing season (Baker, 1979). In high rainfall areas of West Africa a common crop combination is maize and cowpea (Okigbo and Greenland, 1976), whereas in South and Central America and in some countries in Africa maize and different types of beans dominate (Francis, Flor and Temple, 1976).

Although many tropical crops are grown where rainfall is the main restraint on productivity, yields are by no means insensitive to geographical and seasonal differences in other climatic factors. In particular temperature is the main factor determining the period from sowing to maturity for an annual crop. The availability of radiation within the growing season sets an upper limit to the amount of dry matter that the crop can accumulate when water is abundant (Ong and Monteith, 1985). Ong and Monteith (1985) concluded that temperature exerts a major influence on the rate at which crop plants develop and on processes of expansion and extension, and that radiation determines the rate of growth (i.e. dry matter production) at any stage of development. However, there is an important interaction as development can be slowed down by low radiation and growth can be retarded when the temperature is not within the optimal range.

Ong and Monteith (1985) provide a framework for the review of the experimental evidence, when stage of development is influenced by radiation and temperature. When a crop is sown, the time, which elapses before germination, and emergence of seedlings is strongly dependent on temperature as well as on soil water content of the seedbed. The initiation primordial in the seedling is the first stage in development of leaves and roots and the rate at which these organs appear and subdivide depends strongly on the temperature of the appropriate meristem tissue (Ong and Monteith, 1985).

Temperature also interacts with radiation and water supply to control the assimilation of carbon by green leaves and the rate at which individual organs grow. Nevertheless, despite uncertainty over base temperatures, thermal time is still the most useful and meaningful method of analysis to assess the effect of temperature on leaf growth in the field. For example, Gallagher and his co-workers have shown that the production of leaf and spikelet primordial, leaf appearance, lamina expansion and the duration of leaf growth of field grown wheat and barley can all be described in terms of thermal time (Gallagher, 1979; Baker and Gallagher, 1983).

Temperature greatly influences the rate of leaf expansion in chronological time, especially for the leaves in the field, therefore it is hard to resolve leaf growth data without recourse to thermal time analysis. Much of the recent crop phenology research has involved estimation and comparison of crop growth curves as a function of thermal time (Hunt, 1982). In this study, an alternative method of leaf growth curve analysis is accomplished by fitting a Richards' function regression of individual leaf length in terms of thermal time with the form of sigmoidal curve to both maize/bean crops.

The measurement of leaf length, using a ruler, was only done once per day and there was no distinction between hourly or day and night growth rate and temperature variations. However, some workers have successfully related leaf length measurements using a ruler, to weather variations on a daily basis (Bull, 1963; Peacock, 1975). But this method has two disadvantages: firstly, it is difficult to accurately describe the response of leaf growth to temperature because of the diurnal variation in temperature in the field. This is particularly important at low temperature when leaves grow very slowly; secondly, it is impossible to detect decrease in leaf growth rate caused by transient periods of plant water stress lasting for only a few hours. Therefore, for detail studies of the effects of environment, particularly temperature, on leaf growth, a technique is needed which detects responses over a shorter time period, at least within an hour (Biscoe and Gallagher, 1976).

Recently, Inman-Bamber (1995) used a semi-automatic growth transducer (auxanometer) with sufficient accuracy for hourly plant extension measurement in relation to temperature and soil water of sugar cane. This technique will be used for monitoring leaf extension rate for sole- and inter-crop maize at the field level during warm and cool planting dates in this project.

There have been an increasing number of studies to quantify the effect of weather on crop growth, development and yields. Generally, the goals of such research have been to assist in the interpretation of agronomic experiments, encouraging more efficient use of valuable climatic resources (Coelho and Dale, 1980). For such studies and in crop modeling, temperature is one of the most important weather variables, which has to be considered as it limits plant growth. In the field study, the effect of temperature on leaf growth was verified by measuring leaf length, elongation rate and other plant variables describing growth during the early growth stage of maize and bean inter-crop systems at three different planting dates in summer.

Overall Objectives

From different studies, it is clear that a prime objective of the crop physiologists in studying leaf growth must be to understand the way in which internal and external factors interact in controlling the rate and duration of leaf growth. The environmental factors certainly have a major influence on leaf growth. Therefore, this study primarily assesses a series of field studies of leaf growth of maize/bean inter-crop under a wide range of temperatures. The behaviour and distribution of leaf growth as a function of temperature was described and the most appropriate thermal time response sought. The secondary aim was to assess the relationship between hourly rate of leaf extension and leaf temperature of the maize crop, using the auxanometer. The main aim includes the following objectives:

i) To quantify the relationship between temperature and measurements of leaf growth during the early growth stages of the maize sole- and inter-cropped with beans (Chapter 4) and beans sole- and inter-cropped with maize (Chapter 5).

ii) To assess the suitability and difficulties of field measurements of leaf growth as influenced by temperature and to compare different methods of leaf growth analysis (Chapter 4, 5 and 6).

iii) To use field measurement methods to measure leaf extension rate at hourly intervals with reasonable precision (Chapter 6).

iv) To investigate the daytime temperature and leaf extension rate variation in warm and cool seasons with different planting dates through the summer time (Chapter 6).

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

Generally, knowledge of how temperature affects leaf growth is important for several main reasons:

- Firstly, the importance of the leaf area in determining the growth rate of crops. The leaf area influences the growth via the amount of radiation obserbed and photosynthate available for further potential leaf growth (Biscoe and Gallagher, 1976). In some studies the leaf length measurements were used to investigate the leaf dimension and to interrelate with temperature instead of using radiation interception on the leaf area that causes growth, since the amount of radiation exposure could define the magnitude of the temperature.

- Secondly, the introduction of new crops to different climatic regions is largely determined by consideration of the influence of temperatures (Bunting, 1976).

- Finally according to Ong and Baker (1985) even in a region where low rainfall is the main restraint to productivity, temperature is still an important factor determining leaf growth because water deficit and heat stress are often closely linked.

Therefore, the focus of this review is on several responses of leaf growth to a wide range of temperatures in some common cereal and legume inter-cropping systems and in particular to maize/bean inter-cropping systems. The concept of thermal time will also be assessed for its usefulness, and some difficulties of examining leaf growth in the field will be highlighted. Hence the literature review will be mainly concerned with leaf length and extension rate as influenced by various temperatures. The effects of temperature on other aspects of leaf phenology or development such as leaf number, leaf area, plant height and biomass accumulation will also be reviewed.

2.2 Advantages of Inter-cropping Systems

Inter-cropping is the traditional form of agriculture in many developing countries, especially those with tropical climates (Austin and Marais, 1987). Inter-cropping is practiced in many African countries including South Africa, with different crop combinations *inter alia* maize and groundnut (Liphadzi, Thomas and Hammes, 1997; Ayisi and Poswall, 1997); maize and cowpea (Watiki, Fukai, Banda and Keating, 1993); pearl millet and groundnut (Reddy and Willey, 1981); sorghum and beans (Osiru and Willey, 1972); mustard and chickpea (Kushwahu and De, 1987); sorghum and pigeonpea (Natarajan and Willey, 1980a, b); and maize and beans (Mukhala, 1998; Tsubo, 2000). Mixed cropping of two or more species is the most common form of production in areas where subsistence agriculture is the norm. Such systems are complex and frequently include legumes and cereals (Hamblin and Zimmermann, 1986).

Various advantages of inter-cropping have been claimed; for example, total yield is often higher than the sole crop yield since a mixture may utilise environmental resources more efficiently; it is a form of insurance against crop failure; disease and pests spread less rapidly; weeds may be suppressed and a mixture supplies a better food quality (Beets, 1982). Inter-cropping systems have a great influence on yield components of maize, component combination of ½:½ (maize: beans) was most effective for all yield components of maize. Intraspecific competition appears to be more intense than interspecific competition in both crops (Olijaca, Cvetkovic, Kovacevic, Vasic and Momirovic, 2000).

Inter-cropping systems are regularly reported as more productive than sole cropping systems grown on the same area of land (Pilbeam, Okalebo, Simmonds and Guthua, 1994; Davis, Amezquita and Munoz, 1981; Francis, Prager and Tejada, 1982; Harris, Natarajan and Willey; 1987). Pilbeam *et al.* (1994) mentioned that common beans and maize have different durations of growth so that when grown together, beans utilise resources earlier than maize. Yield components of bean were more sensitive to the water regime of the site than the planting pattern in an inter-crop. Irrigation increased all yield components of beans (especially pod number) (Olijaca *et al.*, 2000).

Common bean (*Phaseolus vulgaris* L.) is an important legume for direct human consumption and in traditional agriculture such as in the north-west of Spain it is mostly grown inter-cropped with maize (*Zea mays* L.) rather than as a sole-crop (Moreno, Martinez and Cubero, 1985). In the same way, maize is widely serving many people as their stable diet. In Northern Zambia, Siame, Willey and Morse (1998) state that as maize constitutes the more important crop, farmers are likely to assess the comparison between inter-cropping beans with maize and growing maize on its own.

On the other hand, inter-cropping beans with maize has resulted in improved utilisation of resources (Willey and Osiru, 1972) and higher yield per unit land area (leaf extension rate; LER >1) (Fisher, 1977; Crookston, Treharne, Ludford and Ozbun, 1975; Edje, 1995; Francis *et al.,* 1976), though bean seed yields are reduced substantially when bean plants are grown in association with maize (Agboola and Fayemi, 1972; Aidar and Viera, 1976; Francis *et al.,* 1978). Reports indicated that bean yield in a maize / bean inter-crop was reduced due to fewer racemes per plant and lower pod and stem weight per plant than grown alone beans (Francis *et al.,* 1976).

According to Zeilitch (1971), shading resulting from the rapid crop growth rate and height advantages of the maize appeared to represent the main competitiveness of maize over beans. Various indices have been proposed for examining the benefit of inter-crops. Broadly, they fall into two categories: either they describe the overall advantages of the inter-crop relative to the sole crop (Mead and Willey, 1980; Azam-Ali, Matthews, Williams and Peacock, 1990) or they assess the relative performance of the components of the mixture in relation to their performance as a sole crop (McGilchrist and Trenbath, 1971). Therefore, by measuring the crop performance through growth rate during the active growing period, one can assess the degree of shading imposed by associated inter-crops. However, most agricultural research has focused on sole-crop farming systems, and there has been a lack of in-depth research in mixed cropping (Santalla, De Ron and Escribano, 1994). Probably the most frequent justification for this is that cropping mixtures become more difficult to manage when mechanisation is introduced.

Other advantages of mixtures could be to produce higher yields than when the component crops are grown separately because of more efficient utilisation of environmental resources (Willey and Osiru, 1972). It must also be appreciated that there can sometimes be disadvantages of inter-cropping such as yield decrease due to adverse competitive effects (Willey, 1979). In most cases researchers found that in the association of maize and bean, both species are affected by the inter-cropping. Maize yields are however, generally affected much less than those of beans (Francis *et al.,* 1978).

As reviewed by Francis, Ofori and Stern (1987), the small-scale farmer has, for a number of complex historical, nutritional, biological and economic reasons, preserved with the inter-cropping system to minimize risk and maintain a balanced and stable diet for the family. Mukhala, De Jager, Van Rensberg and Walker (1999) reported that there was an advantage in maize/bean inter-cropping over sole cropping in South African semi-arid regions. Fisher (1977) and Pilbeam *et al.* (1994) also reported that inter-cropping was advantageous in the semi-arid areas of Kenya during the extended rain season. However, a disadvantage is recorded for inter-cropping in the short rain seasons, indicating that little benefit from inter-cropping can be expected under conditions of severe shortage of water. Similarly, in Zambia Siame *et al.* (1998) described that for any level of nitrogen applied, returns on the cost of nitrogen and the overall net returns were greater from inter-cropping than from the sole maize.

All these advantages of inter-cropping systems are highly influenced by environmental factors, such as temperature, radiation, carbon dioxide, water and nutrient availability. These factors ultimately determine how a crop system performs and the success of any particular production method, whether based on a single or combination of species, depends on how effectively these resources are shared between the component plants (Baker, 1979). However, unlike water and nutrients, temperature is a resource that cannot be stored for later use. If the plant leaves or other green parts do not receive the optimum temperature during the right time period, the opportunity is effectively missed. Therefore, the knowledge of the effect of temperature on leaf growth in inter-cropping systems is important for increased understanding of the nature of phenological activities in the associated crops.

2.3 Importance of Planting Date

The microclimate (environment near the crop surface) can be altered in many ways, such as, site selection, tillage, irrigation, drainage, fertilization, pest control and numerous other cultural strategies e.g., planting date (Gardner, Pearce and Mitchell, 1985). Growth rate may depend on environmental conditions during the early stage of plant development (Villalobos and Ritchie, 1992). For instance, the response of leaf appearance to temperature is also influenced by location and planting date (Baker, Gallagher and Monteith, 1981; Cao and Moss, 1989), thus, amongst other things, making a general plant development model difficult to develop unless the microclimate is described in detail.

Planting date is one variable in tropical inter-cropping systems which is under direct control of the farmer. The farmer's decision each season as to which crops, cropping systems, planting dates and levels of technology to use, depends upon past agronomic experience and economic variables. To solve some of these problems they can control date of planting and choice of cultivar. With simultaneous or near simultaneous planting of two or more inter-crops there is opportunity to give one species an initial advantage over the other (Francis *et al.*, 1978).

The effects of different planting dates on most growth variables are highly significant throughout the season. These effects due to differences in planting date can be attributed to a better growth environment characterized by higher solar radiation, higher temperature and more regular timely rainfall (Wells, 1991). Influences of sowing date on the growth and yield of bambara-groundnut land races in Tanzania showed differences in dry matter production between planting date and seasons (Sibuga, Tarimo and Azam-Ali, 2000). These were attributed mainly to differences in the quantity and distribution of rainfall and to declining temperature towards the end of the season. However, partitioning to pods was remarkably consistent across planting dates.

According to Swanson and Wilhelm (1996) maize growth has been shown to be affected by planting date and amount of residue on the soil surface. Planting maize before or after the optimum date resulted in reduced leaf area index, leaf area duration, total dry matter production and grain yield. Yield declined with early or late season planting dates and also declined more rapidly when planting was delayed than when planting was advanced. On the other hand, Nanda, Bhargava and Rawson (1995) reported planting date having a significant effect on the time span to the appearance of the first leaf, with the range being from first sowing to 22 days after first sowing, which is equivalent to a delay of 1.35 days for each 1°C reduction in mean temperature. It was also mentioned that planting date had no effect on the rate of appearance of subsequent leaves, which ranged between 2.68 (first planting date) and 2.84 days per leaf (third planting date) with an average equivalent to 0.37 +/-0.003 leaves per day.

Selection of planting date by small-scale farmers is usually dependent on the amount of rainfall expected for that particular growing season, but it is important to account for the temperature variation effects on plant growth, especially in inter-cropping systems. The accumulated temperature as a thermal time is also closely influenced determined by the planting date, which is an important factor in influencing the physiological growth and growth duration for the plant. Therefore, in making decisions for planting date it is wise to include temperature as one of the climatic factors could contributes much for crop production and in minimizing crop risk. This could be practical when it is excluding other factors limiting leaf growth.

2.4 Plant Growth

2.4.1 Definition

A common view of the senses in which expressions of "plant growth" and "plant development" are used, must first be established in order to define the scope of the study.

- 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 the cell wall and accumulation of the solutes (Boyer, 1985). While some define plant growth as a process of cell division and elongation, agronomists generally define it as an increase in dry matter (Fussell, Pearson and Norman, 1980). This includes the diurnal reversible changes due to temperature, radiation and leaf water potential.
- In the case of plant development, leaf expansion is considered to be a physiological process about the stages of anatomical development, which a

leaf passes through during its growth from primordium to maturity (Digby and Frin, 1985). It must, however, also be noted that monocotyledonous and dicotyledonous leaves are different in several respects with regard to their development. Gardner *et al.* (1985) concluded that plant growth and development is a combination of a host of complex processes of growth and differentiation that lead to the accumulation of dry matter.

According to Fournier and Andrieu (2000) the kinetics of elongation was found to be composed of four phases. The rate of elongation rises exponentially during phase I, and then increases sharply during a short period (phase II), followed by a major period of constant growth rate (phase III) followed by a period of decline (phase IV). During phase I elongation appears to be integrated at the level of the whole apical cone. From phase II onward elongation becomes determined at the level of phytomer (Fournier and Andrieu, 2000).

2.4.2 Physical aspects and interaction with environment

Plant growth and development are essential processes of the life and propagation of a species. They 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). Empirically, plant growth can be expressed as a function of genotype X environment = *f* (internal growth X external growth factors). In modern crop production the object is to maximize growth rate and yield through both genetic and environmental manipulation.

Evans (1972) mentioned that a plant body grows gradually, tissues maturing progressively and being added to those matured earlier; and that, 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. For better understanding Hunt (1982) explained that it appeared to be necessary to record in detail the plant growth in a natural environment at any particular time and to interpret the result of the past environments, which have contributed to its make-up.

Regarding climatic factors, the effect of temperature treatments initiated at various stages of plant growth have been widely reported. Other environmental factors such as vapour pressure deficit (VPD) are also known to influence leaf growth together with temperature (Clifton-Brown and Jones, 1997). Interaction between temperature and VPD were evident during the plant extension measurement, as a consequence of the drop in VPD as the temperature stepped downwards. The response of plant extension rate to temperature and VPD is best discussed within the framework of the Lockhart model (Lockhart, 1965), which is written:

$$G = m(P - Y) \tag{2.1}$$

where G is the cell growth (plant extension), described in terms of the capacity of the cell wall to expand irreversibly (plastic extensibility, m) and the effective turgor for growth $(P\text{-}Y)$, where P is the pressure potential of the cell and Y is the threshold turgor for growth.

In a review, Passioura (1994) stated that the response of leaf expansion rate to environment has been analysed in terms of a change in mechanical properties of cell wall, which affects the ability of plant cells to deform in response to turgor pressure. However, several reports in the literature suggested the change in cell number in a leaf with unchanged final cell size (Mac Adams, Sharp and Nelson, 1992). This is the case in fescue leaves experiencing low nitrogen availability (Gastal and Nelson, 1994) and pea leaves subjected to water deficit during the first days of leaf development (Lecoeur, Wery, Turc and Tardieu, 1995). Cell division rate therefore plays a role in the control of leaf expansion rate in spite of the fact that cell division *per se* cannot affect leaf expansion. In the following sections a review of physical characteristics of growth is attempted to describe cell growth in terms of physical processes for a better understanding of leaf growth.

2.4.3 Plant growth rate

As the leaf is the photosynthate factory of the plant, the amount of photosynthate available for biomass production is related both to the current leaf area and photosynthesis rate of the leaves. Crop growth generally can be measured by biomass accumulation and increase of leaf area index during the growing season (Walker, 1988). Hunt (1982) described crop growth rate as the weight gain of a community of plants on a unit of land in a unit of time, and this concept is used extensively in growth analysis of field crops. According to Hunt (1982) the growth rate, G, may be defined as

$$G = \frac{dW}{dt} \tag{2.2}$$

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.

The relative growth rate (RGR) expresses the dry mass increase in a time interval in relation to the initial mass (Gardner *et al.*, 1985). In practical situations, the mean relative growth rate (RGR) is calculated from measurements taken at times t_1 and t_2. The equation for calculating the RGR is derived from the standard compound interest equation (Blackman, 1919). Therefore, according to Gardner *et al.* (1985) the relative growth rate over the instantaneous value was given as

$$RGR = \frac{1}{W} \bullet \frac{dW}{dt} \tag{2.3}$$

where W is the initial dry mass for change in dry mass, dW, and change in time, dt.

Plants vary widely in their relative growth rates (RGR), but are dependent on environmental conditions or due to genetic background (Bultynck, Fiorani and Lambers, 1999). Variations in RGR tended to correlate with that in the leaf growth rate (LGR). It is also mentioned that when different species are compared under identical growing conditions, variation in growth rate may or may not correlate with that in RGR depending on the comparison, since RGR was described by an exponential equation, whereas leaf growth rate was mainly a linear process. Then they conclude that any correlation between RGR and LGR must be fortuitous. That is, exponential growth must be due to increase with time in plant traits such as leaf dry mass per unit leaf length invested per unit time and/or the total leaf elongation rate of all growing leaves at a point in time.

However, the leaf growth rate and RGR in monocots are different in nature from the leaf blades of dicots. This means in monocots the zone of cell division is very small and the zone of elongation is also small; e.g. cell elongation in maize is restricted to a small zone near to a ligule (Boyer, 1985). Boyer (1985) has shown that although the zone of elongation remains at constant width with time, the speed at which the cell passes through the elongation zone decreases with time. On the contrary the leaf expansion in dicots is produced by division of the marginal meristems (Baker and Gallagher, 1983). Therefore it is known that for several dicotyledonous species the growth of leaves assumes a further degree of complexity when the timing and duration of events are considered.

2.5 Plant Variables Used to Describe Growth

2.5.1 Leaf number

The number of leaves formed on a determinate plant species, such as maize, is dependent on the developmental processes. Firstly, it is determined by the rate of leaf production at the apical meristem and secondly by the time lapse between sowing and floral (tassel) initiation. Both of these processes are in turn influenced by environmental factors such as temperature and photoperiod (Warrington and Kanemasu, 1983a & b).

For maize the increase in number of visible leaves was linear with time in the 10°C - 30°C range of temperatures, with the rate of increase being greater at a higher temperature (Thiagarajah and Hunt, 1982). This is similar to other observations made for maize (Brouwer, Kleinendorst and Locker 1973) as well as other grasses (Jewiss, 1966). While the rate of appearance of leaves varies with the environmental conditions, it remains constant for any given set of conditions and was not affected by a switch to the reproductive phase. On the other hand, Bos, Vos, Tijanieniola and Struik (2000b) measured a lower maize leaf appearance rate at higher plant densities and under shade conditions. These effects were not caused by small differences in canopy temperature observed but were closely associated with reduction in the growth rate per individual plant. Leaves growing in the shade were larger than in full sunlight, the effects of plant density on leaf length were inconsistent, while leaf elongation rate and leaf elongation duration were longer at higher plant densities (Bos *et al.*, 2000b).

The effect of temperature at the early stage of maize leaf growth for successive leaves showed that the number of visible and actively growing leaves increased from two at 25/20°C to seven at 30/20°C (Thiagarajah and Hunt, 1982). According to Tollenaar, Daynard and Hunter (1979) the total number of leaves per maize plant increased at a rate of approximately 0.2 leaf per °C in the range from 15 to 35°C, with a mean number of leaves of 16, 17, 18, 19, and 20 leaves at 15, 20, 25, 33, and 35°C respectively. Similarly others including Duncan and Hesketh (1968) and Hesketh, Chase and Nanda (1969) have reported an increase in leaf number with increasing temperature.

Therefore at different planting dates, it is expected that the leaf number may vary according to the temperature experienced during the growing period. The change in accumulated thermal time will also have an influence on the number of leaves appeared during the growing period. This also varies according to the quantity of thermal time accumulated in a specific growing period.

2.5.2 Plant height

Height and maturity of maize are highly proportional to leaf number (Cross and Zuber, 1972) and the relative plant height of different crops grown together in an associated inter-crop system is important. Profiles of radiation intensity and leaf area in crop canopies indicated that the taller crop has an advantage over its shorter crop companions (Trenbath, 1974). Both legumes grown with the tallest sorghum yielded less than those with shorter sorghums (Vorasoot, Patanothai, Wongpichet, Chintavate and Boontop, 1976). They concluded that optimum yield of sorghum and the legume occurred when the sorghum was less than 1.7m tall. In the contrary sorghum plant height differences were also studied in association with soybean (Wahua and Miller, 1978a & b). Sorghum cultivars of two heights, 1.3 m (short) and 2.09 m (long) were inter-cropped with soybean in alternate rows, and their yields were decreased 74 and 14% respectively by inter-cropping with soybean as opposed to sole-crop sorghum.

Mukhala (1998) reported a small variation in the effect of plant density on both maize and beans inter-cropping under irrigation. But generally it was observed that both maize and beans at the highest plant density were taller than maize and beans in low and medium densities. During the early growth period the plant height differences among the cropping systems were minimal. Watiki, Fukai, Banda and Keating (1993) mentioned that the difference was sole- and inter-crop maize with cowpea increased rapidly from 43 days after planting.

2.6 Biomass and Leaf Area

The 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. Roberts, Long, Tieszen and Beadle (1993) indicated that net primary production is the total amount of organic matter assimilated, less that lost due to respiration. As cited by Beadle (1993), Blackman (1919) defined "production in terms of compound interest law". If the rate of assimilation per unit area of leaf surface and the rate of respiration remain constant, and the size of leaf of the system bears a relation to the dry mass of the whole plant, then the rate of production of new material as measured by dry mass increase, will follow the compound interest law.

Increase in total dry matter is associated with the interception of more radiation and more efficient use of radiation in a number of inter-crops such as for millet (*Pennisetum typhoides* S. H.) and groundnut (*Arachis hypogaea* L.); by Marshall and Willey (1983) for sorghum (*Sorghum bicolor* L.) and peaonpea *(Cajanus cajan* L.); by Willey and Natarajan (1980) for sorghum and groundnut by Harris *et al.,* (1987) and for maize and bean inter-crop by Mukhala (1998) and Tsubo (2000). However, far less attention has been paid to the importance of determining canopy temperature and water status in relation to dry matter, despite several theoretical reviews (Allen, Sinclair and Lemon, 1976; Trenbath, 1974). Since rates of plant development are governed by temperature and water status, changes in these variables as a result of inter-cropping could account for the differences in allocation of dry matter (Ong, 1984; Harris *et al.,* 1987). Enyi (1973) reported a reduction of about 50% in maize grain yield when it was inter-cropped with cowpea, but the reduction in grain yield in sorghum was only 23%. Likewise the legume may also suffer from the competition when grown with maize. Similar results were obtained in maize/bean inter-crop systems in semi-arid areas (Tsubo, 2000; Mukhala, 1998).

According to Wakiti *et al.* (1993) in sole crop maize total dry matter production was promoted by high density during early stages of growth and the difference was then maintained through to maturity. While inter-cropping maize with a legume resulted in total dry matter production being small at high and medium density of maize, but total dry matter production maize was affected greatly by inter-cropping at low maize density. To assess such differences in plant growth, it is better to consider the whole plant growth and by partitioning the plant organs according to their function.

2.6.1 Biomass production at early growing stage

Seasonal above-ground biomass accumulation follows a typical nearly sigmoidal growth curve through the growing season (Salisbury and Ross, 1985; Gardner *et al.*, 1985). This can be conveniently divided into three main phases: a) ground cover limiting, b) radiation limiting (linear phase) and c) senescence.

As cited by Walker (1988) the biomass accumulation was described by Blackman (1919) by the "compound interest law" with the initial phase early in the season recognized as the exponential growth phase (Salisbury and Ross, 1985), when the canopy was incomplete. The form of equation used was as follows:

$$m = m_o \, exp[K \, (t - t_o)] \qquad (2.4)$$

where m is biomass (g m^2) at a given time (t), m_o represents the initial biomass at time t_o, K the relative growth rate. Hunt (1982) gives a detailed explanation of how the analogy to the compound interest rate applies to the plant growth when considering an increase in biomass. Many workers have calculated relative growth rate of crops from biomass accumulation through the season, for maize (Allison, 1969) for Brome grass (Engel, Moser, Stubbendieck and Lowry, 1987) and for soybean (Hunt, 1982; Shibles and Weber, 1965). The question remains, as to whether this exponential growth law still holds true for each component of crop growing in an inter-cropping situation.

Tollenaar (1989) described the response of crop dry matter accumulation to temperature and analyzed it in terms of the temperature response of the processes underlying crop growth. Since dry matter partitioning is closely associated with crop growth (Potter and Jones, 1977), 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. However, the response of dry matter partitioning to temperature is not well documented, as it is difficult to determine.

In maize, the rate of development and leaf photosynthesis show a curvilinear response to temperature with a maximum at approximately 31°C (Duncan and Hesketh, 1968; Tollenaar *et al.*, 1979). It has also been reported that the root/shoot ratio tends to decline, whereas partitioning of photosynthesis into new leaf area increases with an increase in temperature during the vegetative phase (Boote, 1977; Potter and Jones, 1977). Using wheat (*Triticum aestivum* L.), Rawson and Turner (1982) reported no differences in dry matter partitioning as the rate of dry matter accumulation at different temperature regimes showed similar results by varying temperature and incident radiation. However, substantial changes in dry matter distribution, in particular during the early phase of development, have been reported for maize (Hunter, Tollenaar and Breur, 1977). Generally, the effect of maize dry matter accumulation is particularly large during the early phase of development, when mutual shading of leaves within the canopy is relatively small (Tollenaar, 1989). So to demonstrate the effect of temperature in inter-cropping it is important to take readings at frequent intervals during the early growth stage.

2.6.2 Leaf area during the early growth stage

Some studies showed that the leaf area expansion rate positively correlated with temperature (Bull, 1963; Monis and Murata, 1970), whereas others show a negative correlation (Gregory, 1983). To increase the understanding of the mechanism involved in leaf area expansion, Bos, Vos and Struik (2000a) investigated effects of environmental factors on leaf growth of maize species in a growth chamber including different combinations of day and night temperatures (13/8, 18/13, 23/18, and 28/23°C). At 13/8°C a large proportion of the plants died due to prolonged exposure to cold stress. High temperatures at 28/23°C increased leaf appearance rate and showed that maximum leaf width at intermediate temperature was strongly related to specific leaf weight. On the other hand leaf elongation rate increased and leaf elongation duration decreased with temperature, the resultant being a maximum final leaf length at 23/18°C.

The effects of other environmental factors have not been consistently detected. Due to the use of destructive harvests, small day to day changes in leaf area are not possible to measure (Gallagher, Biscoe and Saffell, 1976). Monteith and Elston (1985) suggested a simple model for increase in crop leaf area, where the relative growth rate (of area) was a function of temperature (Bull, 1963). The use of such a model, even when it is accurate was restricted to the early portion (phase I) of the growth curve, when the relative leaf growth rate may be assumed constant in the linear phase under constant conditions. Therefore, the three main leaf growth phases can be distinguished as the exponential phase, linear and senescence phase. This is clearly illustrated in the following diagram by describing leaf growth against time (Figure 2.1).

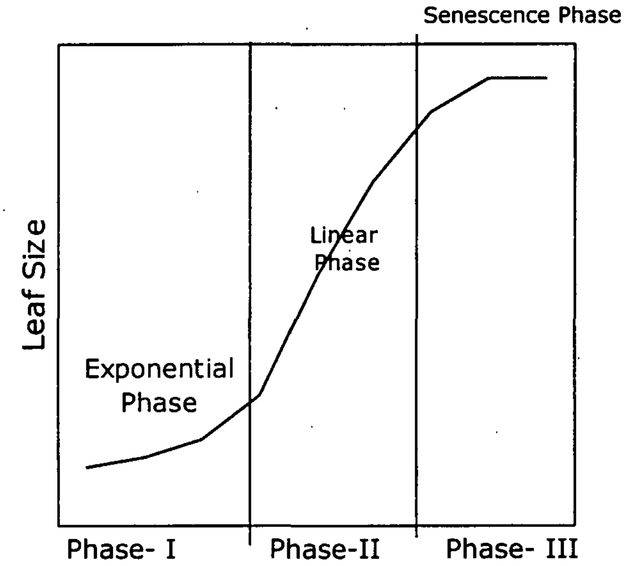


Figure 2.1 The three main leaf growth rate phases: The exponential phase, the linear fast growth phase and the leaf senescence phase.

2.7 The Richards Function Growth Equation

The use of a growth function is largely empirical: the form of the function, *f,* will sometimes be chosen by simply looking at the data and deriving the best-fit equation. However, it is preferable to try to select or construct a function that has some biological plausibility, and contains parameters that may be meaningful (Hunt, 1982). The Richards function is viewed as an empirical equation; it has a generality that may sometimes be an advantage for particular values of an additional parameter *n;* it encompasses the three previouly known parameters (Causton, 1978; Richards, 1959). The form of the function and the fitting procedure used for leaf area were described by Dennett, Auld and Elston (1978). The equation is:

$$a = \frac{A}{\left[1 + \exp - \frac{(\lambda + \kappa t)}{\theta}\right]^{\theta}} \tag{2.5}$$

where a is the area of the leaf with maximum leaf area estimation A at time t and κ, λ, θ are fitted parameters.

Since the shape of the growth curve is important when we consider the physiological process of leaf growth, this function can adequately describe the changes in shape of leaves growing under different temperature regimes. Eskridge and Stevens (1987) described an alternative method of growth curve analysis using the estimation and comparison of crop growth as a function of thermal time. Therefore, in any growth analysis to assess the relationship between leaf growth and temperature, the application of the fitting model can be important in determining the growth curve. The temperature responses to leaf growth are also commonly described using the accumulated thermal time rather than the temperatures of the growing period.

2.8 Temperature Effect on Growth

Since temperature affects many plant processes including nutrient uptake, water absorption, photosynthesis, respiration, and translocation of photosynthate, it is not surprising that temperature is considered the most important environmental factor governing plant development (Berbecel and Eftimescu, 1972; Coelho and Dale, 1980).

The effect of temperature on plant growth including germination, establishment and early vegetative growth of pearl millet (*Pennisetum amercanum*) was well documented by Fussell *et al.* (1980). The experiment showed that the percentage of seedling germination was independent of temperature between 33/28 and 15/10°C (day/night), but the rate of germination was faster at the higher temperature (Pearson, 1975). Percentage final emergence, rate of emergence and seedling survival and growth usually increase with temperature up to 33°C (Pearson, 1975). The processes involved in the response to temperature in the vegetative phase include reduction in leaf photosynthetic rates, especially below 24°C (Pearson and Derrick, 1977). They also mentioned the increase in percentage of photosynthate in source leaves when the temperature declines from 33/28 to 18/13°C. Therefore it is important to recognize the cardinal temperatures for crop growth, at which the growth reaches a maximum.

In growth chamber experiments, bean (cultivar *Bush Blue Lake 274*), maize (cultivar *Bellringer*, chilling sensitive species) and peas (cultivar *Olympia*) and spinach (cultivar *Packer*, chilling tolerant) were grown in 28/18°C (warm) or 18/12°C (cool) day and night temperatures. Emergence was delayed approximately 4 and 2 days in chilling sensitive and tolerant species respectively, at the 18/12°C regime (Wolfe, 1991). In particular in maize and bean relative growth rate decreased at 18/12°C by 10% as compared to 28/18°C. From the research it is understood that both maize and beans showed lower RGR at lower temperatures but the sensitivity to low temperatures may vary for these two crops. In some literature maize plants are more sensitive to low temperatures than bean plants.

From the above two ideas of Fussell *et al.* (1980) for pearl millet and Wolfe (1991) for beans, maize and peas, the increase in rate of growth in higher temperatures is clearly illustrated, although the range of optimum temperatures varies according to different crops and cultivars.

This poses a problem in analysing field measurements of leaf growth under the wide range of temperatures experienced during the growing season, as temperature is known to affect cereal leaf growth and appearance rates (Friend, Helson and Fisher, 1962; Watts, 1972a). In particular, the growth of wheat occurred over a wide daily and weekly mean temperature range (Gregory and Squire, 1978). For barley crop, the mean weekly temperature during leaf growth ranged only between 7.9 and 11.7°C and leaf appearance rate increased linearly with time (Gallagher, 1979). The temperature during leaf appearance was 9.5°C and the corresponding appearance rate was 0.12 (± .003) leaves per day, as opposed to the value of 0.09 obtained for the wheat normalized to 10°C. Kirby (1974) reported a leaf appearance rate of 0.18 (± 0.004) per day for the leaves sown at the end of March. But none of these studies describe the diurnal variations of temperature of weather data to differentiate the effect of day and night temperatures on leaf extension rate.

An understanding of the way crop plants react to different temperatures was of considerable importance in developing varieties for a specific thermal environment.

Leaf growth characteristics provide meaningful parameters for the study of temperature - plant development relationships and the effect of temperature on leaf growth has been documented for a number of crop species (Thiagarajah and Hunt, 1982). Milthorpe (1959) showed that the rate of cucumber leaf expansion increased between 12 and 24°C, and that the rate of production of new leaves also increased with temperature. Subsequently Friend *et al.* (1962) noted that the rate of wheat leaf emergence, lamina expansion and leaf senescence increased with temperature to an optimum at about 25°C although dry mass per leaf area was higher at low temperatures.

Ong (1983a) described the relation between environmental and meristem temperature during the development of the canopy. Temperature has a strong influence on factors that determine radiation interception in pearl millet (Pearson, 1975; Ong, 1983a; Squire and Ong, 1983) and in other species (Gallagher and Biscoe, 1979). Milford and Riley (1980) stated that an increase in temperature accelerates germination and leaf expansion and so shortens the duration from germination to maturity. In contrast, at a different level of organization this was difficult to demonstrate as the growth rates of complete canopies are influenced predominately by irradiance and much less by temperature, except near the extremes of the temperature ranges for a species (Monteith and Scott, 1982).

Ong (1983b) reviewed temperature as being the major environmental factor governing the rate of leaf extension, but unlike many developmental processes the rate was also sensitive to irradiance for the first few leaves and possibly to saturation deficit above about 3.0 kPa. The Ong study has confirmed the linearity of the growth rate / temperature relation for leaf extension in millet, up to an optimum of about 30°C, when water is not limiting, consistent with the finding for other cereals. For instance, field studies consistently demonstrate a linear relationship between leaf extension rate and meristem temperature up to about 25-30°C when water is not the limiting factor for barley (Gallagher and Biscoe, 1979; Keating and Evenson, 1979); and for perennial ryegrass (Keating and Evenson, 1979); (Stewart, Dwyer and Carrigan, 1998). The importance of leaf extension rate in controlling dry matter production is well established (Thomas and Norris, 1977; Biscoe and Gallagher, 1976). During the main growth period of many crops, the rate of dry matter production is directly related to the radiation intercepted by the foliage and is a function of environmental factors such as temperature, which govern the expansion of leaves and rate of photosynthesis.

2.9 Thermal Time Concepts and Applications

2.9.1 Responses of plant growth using the cardinal temperatures

Thermal time, known elsewhere as "cumulated temperature" or heat units, is not the amount of heat which is transferred from the environment to the plant, but a time scale as perceived by the plant as a function of temperature (Ong and Monteith, 1985). It is generally used to predict or analyse the rate of plant development such as time to flowering or crop maturity (Cross and Zuber, 1972; Robertson, 1973) and has been widely used for analysing the influence of the climatic factors in relation to leaf growth (Gallagher, 1979; Baker *et al.,* 1981; Ong, 1983a; Squire and Ong, 1983).

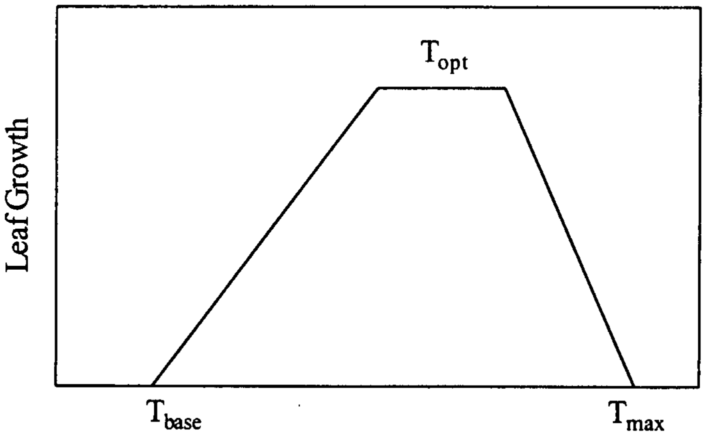


Figure 2.2 General relationships between temperature and leaf growth. Base, optimum and maximum temperatures are T_{base}, T_{opt} and T_{max} respectively (adapted from Monteith, 1979).

The effect of temperature on development rate has been described using thermal time concepts, such as the growing degree-days. It assumes that phenological development is constant per degree of temperature between the base temperature and maximum temperature, below and above which the development rate is zero (Stewart, Dwyer and Carrigan, 1998). Figure 2.2 illustrates the way of describing the response for leaf expansion over a range of temperatures, namely the three sharply defined points – the so called cardinal temperatures: base (T_{base}), optimum (T_{opt}) and maximum (T_{max}).

According to Yan and wallace (1998) the nature of the response to temperature between the cardinal temperatures within the limited range concludes that the rate of development is a linear function. Therefore the linear model is convenient and effective when the temperature does not approach or exceed the optimum, T_{opt} (Summerfield and Roberts, 1985). However, under natural conditions temperature frequently approaches and exceeds T_{opt}, a situation that strongly challenges the linear approach (Shaykewich, 1995). Various non-linear models have been developed to describe the temperature response of developmental processes. For instance, Bonhomme, Derieu and Edmeades (1994) and Ellis, Summerfield, Edmeades and Roberts (1992) developed non-linear temperature response functions to fit measured maize development during the vegetative periods.

2.9.2 Thermal time equation and calculation

As quoted by McMaster and Wilhelm (1997), since 1730 when Reaumur introduced the concept of heat units or thermal time, many methods of calculating heat units have been used successfully in agricultural science. Particularly in the areas of crop phenology and development, the concept of heat units, measured in growing degree-days (GDD °C day), has vastly improved description and prediction of phenological events compared to other approaches such as time of the year or number of days after planting or emergence (Cross and Zuber, 1972; Klepper, Belford and Rickman, 1984; McMaster, 1993; McMaster and Smika, 1988).

The calculation of thermal time is based on the linear relationship between rate and temperature between T_{base} and T_{opt} , although it can be easily modified to take into account temperature above T_{opt} (Garcia-Huidobro, Monteith and Sugre, 1982). Thermal time summation is calculated with different formulas but the common one applied is:

$$GDD = \sum \left[\frac{(T_{mx} + T_{mn})}{2} \right] - T_{base} \bullet \Delta t \qquad (2.6)$$

where T_{mx} is the daily maximum air temperature, T_{mn} is the daily minimum air temperature and T_{base} is the temperature below which the plant process of interest does not progress. GDD represents the accumulation of thermal time during the growth period.

The intent of equation 2.6 is to describe the heat energy received by the crop over a given time period (i.e. integration of the area under the diurnal temperature curve). It is the summation of the daily heat energy over an interval of time and it is then used to relate the accumulation of heat energy to progress in development or growth processes.

A number of scientists have tested the accuracy of various forms of the basic thermal time equation 2.6 in predicting various growth and development processes in several species. For example, Perry, Siddiique and Wallace (1987) noted variations of calculations of accumulated thermal time for cucumber, Cross and Zuber (1972) discussed different methods of thermal time; and Gilmore and Rogers (1958) examined methods of calculating thermal time for maize. The use of heat summation methods for determining the responses of flowering time and grain maturity to temperature in maize has been examined extensively (Bunting, 1976; Tollenaar *et al.*, 1979; Coelho and Dale, 1980). These methods were developed largely to overcome the inadequacies of calendar days for predicting crop developmental events.

McMaster and Wilhelm (1997) noted the two types of implementations for calculating accumulated thermal time. The first method was where $[(T_{max} + T_{min})/2] < T_{base}$, then $[(T_{max} + T_{min})/2]=T_{base}$. This method seems to be the most widespread method used for calculating thermal time, particularly in simulation models (e.g., Davidson and Campbell, 1983; Kirby, 1995). The second method implemented was where if $T_{max}<T_{base}$, then $T_{max}=T_{base}$, and if $T_{min}<T_{base}$, then $T_{min}=T_{base}$. This is the most commonly used method in calculating thermal time for maize, but is used for other crops as well (e.g. Baker and Gallagher, 1983; Swanson and Wilhelm, 1996). Occasionally a combination of the two methods is used (Baker and Gallagher, 1983). This kind of systematic calculation of thermal time is important in comparing the effect of temperatures on leaf growth on different planting dates. The temperatures during summer might be higher than optimum, in which case the crop becomes stressed. During summer time in the tropics it is rare for T_{min} to become less than T_{base}.

In different sources of literature there is still some uncertainty concerning the choice of T_{base} and T_{opt}, because of various crop adaptations and widespread varieties. For instance the base temperature used for winter wheat was 0°C (McMaster and Smika, 1988) and for maize 10°C (Cross and Zuber, 1972). Upper threshold temperatures used also vary, being 25°C and 30°C respectively.

In a field experiment of maize hybrids based on general thermal index (GTI), different locations were divided into four groups based on thermal time requirement (Stewart *et al.,* 1998). One of the methods used to evaluate the GTI employed the coefficient of variance (CV). The reliability of the thermal index was determined by its consistency across years and locations but not across hybrids, since the index is used to characterize the thermal requirement of individual hybrids (Table 2.1).

Table 2.1 Characterizations of four hybrid groups of maize numbered from highest to lowest GDD for relative maturity rating (after Stewart *et al.*, 1998)

Hybrid groups	Locations (code)	Mean Thermal Time	
		Vegetative (GDD)	Reproductive (GDD)
1	146	748	669
2	115	710	631
3	69	651	588
4	109	595	525

NB: *Growing degree-days with threshold limits of 30 °C (maximum) and 10°C* T_{base}

For the vegetative period the response function used for the four hybrids grown was the sigmoid curve similar to those measured by (Ellis *et al.*, 1992) on maize hybrids under controlled environmental conditions.

One must determine the thermal unit requirement for different growth stages for dry beans since it is used differently in the literature. Various models gave satisfactory estimates of the thermal response of field and greenhouse grown beans, comprising varieties which were examined over a wide temperature range. Angus, Mackenzei, Morton and Schafer (1981) concluded that the generalization of the estimates raises the question whether this approach displays ecological generalization as well as being merely statistically convenient. From different reviews, the distribution of values of base temperature and maximum temperature for some species of beans is presented in table 2.2. The distribution of threshold values suggested was a discrete group of temperate adapted species with a base temperature below 7°C and less defined groups of sub-tropical and tropical adapted species with most values of base temperature between 7 - 10.8°C. In the same way the maximum temperatures for most species ranged between 25 - 30°C. In controlled environments relative growth rates of various varieties of green bean leaves decline sharply between 20°C and 14°C with an optimum of approximately 20 - 25°C (Jones, 1971).

Table 2.2 Estimates of the threshold temperatures and the number of degree-days for the different growing seasons of some species of bean crop collected from different literature.

Growing Months	Bean Variety	*Base Temp* (T_b)	*Maximum Temp.* (T_{max})	*Therm. time °C d*	Crop stage	References
May-Sep	Navy Bean	10	20-25	718-1000	Emerge to mature	Hardwick, 1988
Jan-Apr	Runner-Bean	4.5	30	-	Sowing to Harvest	Mauromicale, Cosentino and Copani,1988
May-Oct	Bush- bean	10	30	-		
May-Sep	Navy- bean	10	28	2069	Sowing to Harvest	Dodd, 1991
		10	30			Hardwick and Andrews, 1980
Nov-Feb	Pinto- bean	7	25-30	974		Dapaah, Mckenzie and Hill, 1999
Apr-June	Common bean	5.05	-	757.5	50%-Emer to 50%-anthesis	Scully and Waines, 1988
		4.37	-	686.7		
		6.4	-	615.9		
		6.17	-	445.1		
	Tepary-bean	7.2	-	679.2		
		8.4	-	580.1		
		7.89	-	579.1		
Apr-Jun	Dry bean	10-19.5	26.8-31.9	-		Wallace and Enriqueze, 1980
May-Sep	Common bean	-	27.9 29.8	-		Yan and Wallace, 1998
Apr-June	Navy -bean	10.6	-	525	For emerge	Angus *et al.*, 1981
May-Sep	Mung-bean	10.8	-	49.6		
Dec-Mar	Adzuk-bean	9.9	-	69.9		

Therefore the evidence suggested that estimates of T_{base} and T_{max} as well as the method of calculating the thermal time have a great role in assessing the possible variation in planting dates and the required thermal time units. On the other hand, for bean species different researchers used different values but as it is common in tropical areas it is preferable to use similar cardinal values as for maize crop. However, it is impossible in the field to consider the sensitivity of the variety to low and high temperatures and the nature of response to temperatures between the cardinal points, when calculating the phenology, adaptation and yield of the crops.

2.10 Methods of Measurements of Leaf Growth

For dicotyledonous and monocotyledonous plants different methods have been used for the measurement of leaf growth, due to the different form of the leaves. Monocotyledonous leaf length is typically measured, since the predominant growth is in one direction from the intercalary meristem (Walker, 1988). Simple leaf elongation measurements have often been made using a ruler from some fixed reference pointed to the leaf tip (Acevedo, Hsiao and Henderson, 1971; Peacock, 1975; Gallagher, 1979; Eastham, Oosterhuis and Walker, 1984; King and Bush, 1985). Such leaf extension may include not only laminar extension but also that of the associated sheath and all internodes of the stem if the length measurement is from the soil surface.

Some workers have successfully related ruler measurement of leaf dimension to weather variables on a daily basis (Bull, 1963; Peacock, 1975). In the experiment of pearl millet, the ruler measurement of daily extension rate showed substantial differences between the air temperatures (19, 25 and 31°C treatments). The value of the extension rate per unit thermal time on a daily basis showed the influence of ontogenetic position in all different temperatures (Ong, 1983a). This result showed that extension rate per thermal time increased markedly from leaf 3-5 but remained relatively constant for leaves 6-9. Therefore most of the differences in daily extension rate between treatments can be accounted for by the difference in daily mean temperature. However, this method had two disadvantages. Firstly, it is difficult to accurately describe the response of leaf growth to temperature because of diurnal variations in temperature in the field (Gallagher, Biscoe and Saffell, 1976). This was practically important at low or minimum temperature when leaves grow very slowly or cease to grow for some hours in a day. Secondly, it is impossible to detect a decrease in leaf growth rate caused by transient periods of plant water stress when measuring over intervals of merely a few hours. Therefore, for detailed studies of the effect of the environment on leaf growth, a technique detecting responses within an hour or less is necessary (Biscoe and Gallagher, 1976).

Leaf growth in grasses consists predominantly of extension of leaf lamina length and can be conveniently studied using simple mechanical auxanometers. These measurements were generally taken as being related to cell extension (Kleinendorst and Brouwer, 1975; Hsiao, Acevedo, Fereres and Henderson, 1976) since, during leaf appearance, laminar and sheath extension were caused mainly by cell extension (Williams, 1975). The interpretation of differences of leaf extension in terms of cell extension was therefore, probably justified for Graminaceous leaf growth until stem extension begins. Recent studies by Prat and Paresys (1995) of plant growth using this measurement technique revealed apparent irregularities in the growth rate, but it was unclear whether or not these were of biological or measurement instrument origin. To determine what factors limit the expansion of leaves on a crop plant, it is important to work in the field, but as weather varies it is difficult to uncouple the response of leaf extension to temperature and that of other factors (Gallagher and Biscoe, 1979). Therefore auxanometers registering hourly rates of leaf extension on maize may provide a practical solution to integrated leaf growth over 24 hours or shorter time periods, such as day light hours. According to Ong (1983b) the significance of maximum and minimum temperature (for day and night temperature) for leaf growth was easily settled by using sensitive auxanometers to measure hourly extension rates. Similarly Salah and Tardieu (1995) used the auxanometer to measure leaf extension rate of maize leaf number 6 and related the growth to diurnal change in meristem temperature.

2.11 Rationale for the Study

From the literature review, it became evident that the effect on leaf growth lies mainly in the importance of temperature variations in determining the expansion rate in different cropping systems. Although several factors have been implicated as influencing plant growth, temperature is considered a major limiting factor for leaf growth, as evident from null-hypothesis research. Therefore this study focused on the field measurement of leaf growth as influenced by temperature using different planting dates in an attempt to provide measurements at a wider range of temperatures at different times of the year.

Subsequently, thermal time concepts and applications were reviewed broadly to assess the response of plant growth using the cardinal temperatures, from emergence of the crops to the early growth stages. Therefore, this overview of literature concerned itself with leaf length, leaf number, leaf area, plant height, biomass production and methods of field measurements for leaf growth versus temperatures.

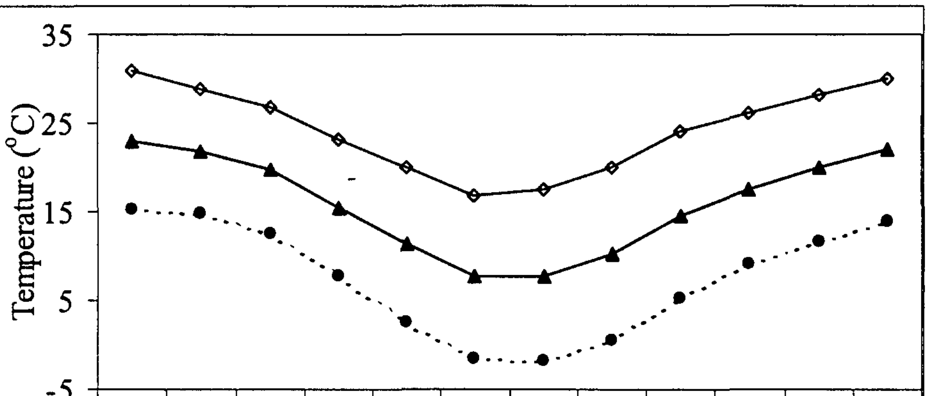
CHAPTER 3

MATERIALS AND METHODS

3.1 Study Site

Three consecutive field experiments were carried out during the 2000/2001 summer growing season at the Agrometeorological Experimental Site located on the western side of the campus of the University of the Free State, {Latitude 29° 06'S, Longitude 26° 11'E, Altitude of campus 1410 m above mean sea level}. According to the soil classification for South Africa by the Soil Classification working Group (1991), the soil is a fine sandy loam Bloemdal Verede (3100) soil. The soil characteristics of a specific area are directly and indirectly influenced by the annual, seasonal and extreme thermal patterns (Oliver and Fairbridge, 1987). The soil in the top 300 mm has a high sand content (63.5%) with clay and silt contents of 20% and 9.4% respectively, and a pH of 6.3 (Soil Classification working Group, 1991).

3.2. Climate



	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
—◇— Max	30.8	28.8	26.9	23.1	20.1	16.8	17.4	20.0	24.0	26.1	28.1	30.1
—▲— Mean	23.0	21.8	19.7	15.4	11.3	7.7	7.7	10.3	14.6	17.6	19.9	22.0
···●··· Min	15.3	14.7	12.4	7.7	2.5	-1.5	-1.9	0.5	5.2	9.1	11.7	13.8

Figure 3.1 Long-term mean monthly temperature at Bloemfontein Airport, South Africa (latitude 29°06'S, longitude 26°18'E, altitude 1351m above mean sea level; 30 years from 1961-1990).

As reviewed in Koppen climate classification, the climate of the study area (Bloemfontein, Free State, South Africa) belongs to a Bsk [arid (steppe) cold and dry climate, with mean annual temperature below 18°C] and according to the Thornthwaite climate classification; it is categorized as a semi-arid warm climate (Schulze and Mc Gee, 1987). The seasonal rainfall of the experimental area is in the range of 350-600mm year^{-1}.

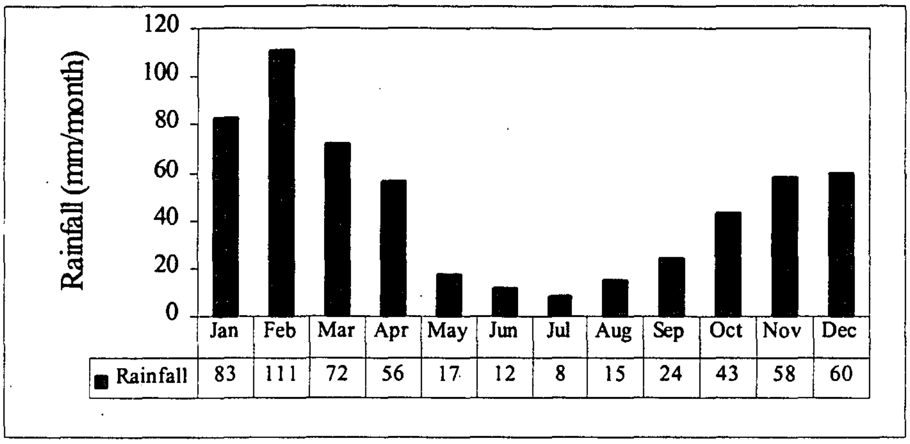


Figure 3.2 Long-term mean monthly rainfall at Bloemfontein Airport, South Africa (latitude 29°06'S, longitude 20°18'E, altitude 1351m above mean sea level; 30 years from 1961-1990).

As reported by the South African Weather Service (SAWS), the long-term (30 years from 1961 to 1990) mean monthly temperature and rainfall in the study area (Bloemfontein Airport, South Africa) are shown in figures 3.1 and 3.2 respectively. Long-term average monthly maximum temperature of the experimental site is in the range of 16.8°C to 30.8°C, while average monthly minimum temperature varied between -1.9°C and 15.3°C.

3.3 Weather Parameters

Weather parameters were collected throughout the growing season from an automatic weather station situated at the experimental site. The main weather variables during the early vegetative growth periods in all three trials (Nov-Dec, Jan-Feb and Mar-Apr) are listed in table 3.1. Mean monthly temperatures of the early growing period for the three trials; (Dec, Feb and Apr) were recorded as 22.2, 22.4 and 16.6°C respectively.

Table 3.1 Mean daily weather data for each month of the three consecutive growing periods from automatic weather station at the site. Eo (Pme) calculated using Penman Monteith equation.

Planting	Growing	RAD	TEMP	TEMP	TEMP	WIND	RF+Irr		Eo (Pme)
Dates	Months	Mean	Min	Max	Mean	Mean	RF	Irr	Total
		W/m2	°C	°C	°C	m/s	mm	mm	mm
First Planting	Nov	317.7	12.1	25.3	18.7	2.1	6.8	6.0	155.7
	Dec	320.4	15.4	29.0	22.2	2.2	74.6	8.2	226.9
Second Planting	Jan	328.2	15.8	30.4	23.1	2.2	32.8	47.2	246.8
	Feb	294.1	15.9	28.9	22.4	2.1	54.1	25	174.0
Third Planting	Mar	234.2	15.6	27.5	21.6	1.7	68.6	-	154.0
	Apr	159.2	11.0	21.0	16.5	1.4	99	-	78.0

Temperature and solar radiation are two weather variables that have direct and significant effect on crop development (Muchow and Coates, 1990). Temperature also affects the duration of crop growth (Allison and Daynard, 1979) and consequently the maximum time that the incident radiation can be intercepted. The highest amount of radiation intercepted was during the month of January and it was 328.2Wm^{-2}. Monthly mean maximum temperatures for January were higher than for February and April by 1.5 and 9.4°C respectively. In April the maximum and minimum temperatures were much lower compared to the previous months. Similarly, daily mean value of solar radiation reaching the canopy surface during April was only 159.2 Wm^{-2}, significantly lower than the December and February figures of 320 and 294 Wm^{-2} respectively. In general, the weather data shows that the third planting period was cooler than the first two trials though the minimum temperatures from December - March were more or less similar, in the range of 15.4°C - 15.9°C.

3.4 Agronomic Information

Seedbed preparation was completed during the dry season, well ahead of planting time, with minimal tillage. A compound fertilizer was applied at planting at a rate of 800kg ha^{-1} 3:2:1 (25) NPK and 550 kg ha^{-1} LAN (Limestone ammonium nitrate) (28) giving a total of 254 kg N ha^{-1}, 67kg P ha^{-1}and 33kg K ha^{-1}. No topdressing was applied during the growing season. All the rows were orientated SW-NE.

For all three planting dates sowing was done by hand. Regular weeding was carried out by hand or hand hoe, keeping the plots virtually weed-free throughout the growing period. On the first two trials, during the early seedling stages a bird problem became apparent, so to prevent further damage every plot was covered with a shade net. On the second planting date insecticides were applied to control aphids on the bean crop. Rainfall was not evenly distributed during crop growth, so occasionally additional supplementary irrigation was given. A central pivot irrigation system was used to apply irrigation water.

3.5 Plant Material

The maize cultivar used was an early maturing hybrid PAN 6804. It is suited to high plant population, with mainly a single ears and with physiological maturity at approximately 105 days after planting. In the case of dry beans the cultivar sown was PAN 148, having intermediate growth habit and rapines very evenly. The time required to reach maturity was 100-120 days from planting.

Dutu (1996) reviewed the influence of the weather conditions during germination and the vegetative period, and showed that air temperature plays a big role. To ensure seed viability before planting in the field a simple germination test was performed at room temperature. The maize and bean seeds showed 98% and 83% germination percentages respectively.

3.6 Experimental Layout

In the main part of the experiment, there were three planting dates (Nov, Jan and Mar). In the first two planting dates plots were arranged in a randomized complete block design with three different treatments (sole-crop maize, sole-crop beans and inter-crop maize/bean) in each of three replicates, giving a total of 9 experimental plots. The effective plot size was 12X18 m with an area of 216m^2. In the third planting, plots were designed without replicates in small plot sizes of 7X7 m for each treatment. However, measurements were still done on replicate plants in each treatment.

Row spacing of maize was 1.0m, and inter-row spacing between maize plants was 0.50m in order to produce designated maize densities in both sole- and inter-cropping. In inter-cropping the experimental plot was made up of two rows of beans with a spacing of 0.40m between the maize rows and 0.50 m between plants (Figure 3.3). With beans alone the same pattern was used. At all planting dates two seeds were sown per hole and were thinned to a single plant per spot later.

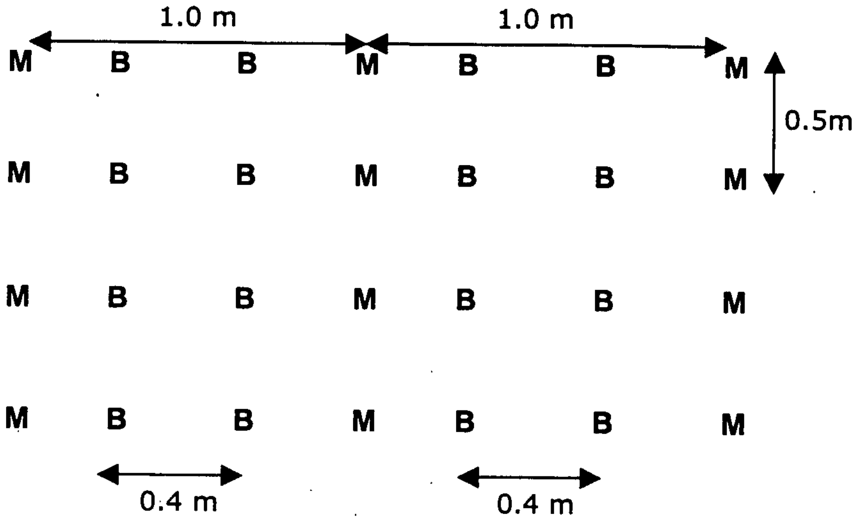


Figure 3.3 Field crop arrangement of inter-cropped maize and beans with inter-row distance of 1.0 m for maize and 0.4 m for beans, where "**M**"= maize and "**B**"= beans.

3.7 First Planting Date (Experiment 1)

The seeds were sown on 20th Nov, 2000. The emergence of seedlings started 4 days after planting and after 10 days more than 85% of the seedlings had emerged fully. The growth measurements on selected sample plants were only taken during the early vegetative growth stages from 2nd until 28th of Dec., (39 days after sowing). Air temperature was recorded hourly at the nearby automatic weather station. During the early growing season (December, 2000) the range of maximum temperature was 25.4°C to 33.0°C with a minimum temperature range from 11.9°C to 18.4°C.

3.8 Second Planting Date (Experiment 2)

Seeds were sown on 13th January 2001. All the necessary measurements were taken in a way similar to the first planting date. During the early growing season (in February) the maximum temperature range was 19.9°C to 33.3°C with minimum temperatures 12.6°C to 19.4°C.

Prior to the second planting date the field was severely infested with weeds due to early ploughing. Therefore, before planting the field was cleared by applying Round-up herbicide. The seedlings started to emerge 5-6 days after planting. The seedling coverage in percentile was less than that of the first planting date and resulted in an estimated less than 75% coverage. This was due to poor tillage and seedbed formation and some part of the soil was compacted enough to limit emergence of seedlings.

All the necessary measurements were taken from 30th January 2001 until 3rd March 2001. The experiment ended 50 days after sowing. In this experiment in addition to ruler measurement, leaf growth rate was also measured using auxanometers for about 3 days, during the active growing period (18-20 Feb, 2001).

3.9 Third Planting Date (Experiment 3)

Seeds were sown on 13th March 2001. In April mean air temperature ranged from 13.1°C to 18.1°C. The plot size of this experiment was small and was arranged without replicate plots due to those on previous tillage problems. However, all the measurements were similar to the previous planting dates. In addition hourly leaf lengths were measured by auxanometers for about 10 days. The measurements were started on the 4th April and ended 3rd May, 2001 (53 days after planting). All the crops were killed by severe frosts on 5th-7th May 2001.

3.10 Field Measurements

3.10.1 Leaf length

Measurements were taken on five randomly selected plants per plot in each treatment plot. In the maize crop, the length was measured from a reference brick fixed in the ground at the base of each plant to the apex of individual leaves vertically extended (Meyer and Green, 1980; Eastham *et al.*, 1984; Walker, 1988). Thus some stem internodal elongation was included in the measured leaf length, though this error should be small during the early vegetative growth. As has already been mentioned by Gardner *et al.* (1985), maize remains stemless until reaching a height of about 40cm and developing eight fully expanded leaves, which sprout from the pseudo stem (a vegetative shoot). Therefore, at the beginning of the growing season this length represented the length of lamina and sheath, but later the length of the internode was included (Walker, 1988). For simplicity, this length is referred to as a leaf length. In the case of bean plants the leaf length was measured by stretching the ruler from the end of the petiole vertically to the leaf tip across the leaf blade. Due to the trifoliate nature of the legume leaves the representative selected leaflet for measurement was the central one.

3.10.2 Leaf number and plant height

Leaves similar to those measured for length were sampled for leaf number, plant height and leaf inclinations. Plant height was measured from the ground to the top of the leaves on that particular plant, as the leaves were in their natural positions in the canopy. The leaf number was estimated by counting the number of visible fully expanded leaves every three days. In maize, a leaf was considered to be fully expanded when the ligule at the base of the lamina was visible above the enclosing sheath of the preceding leaf (Muchow and Carberry, 1989). In beans the leaf number was counted when it had expanded to at least 2-3 cm of length from the petiole.

3.10.3 Leaf area and biomass production

Leaf area and biomass samples were taken at 10-15 day intervals during the early vegetative growth stage. Four sample plants were cut at the soil surface above the ground from every replication. Leaf area measurements were made with a LI 3000 portable leaf area meter (Lambda Inst. Corp). Then, after the fresh weight was determined separately, the samples were dried in an oven at 70°C to determine dry matter.

All the measurements were done in the early morning for three reasons. Firstly to minimize possible effects of diurnal variation. Second the wind speed was insignificant during the measurements. Thirdly, the evaporative demand was low, and thus the leaves were not affected by possible water stress (Drouet and Moulia, 1997).

3.10.4. Auxanometer measurements

Hourly plant extension rate of maize (in sole and inter-crop systems) were measured using 12 auxanometers made from linearly variable displacement transducers with a stroke length of 100 mm. These instruments were constructed at the University of the Free State in the Faculty of Natural and Agricultural Science Instrumentation Division in collaboration with the Electronics Division. The auxanometer and its installation at field level is illustrated in figure 3.4.

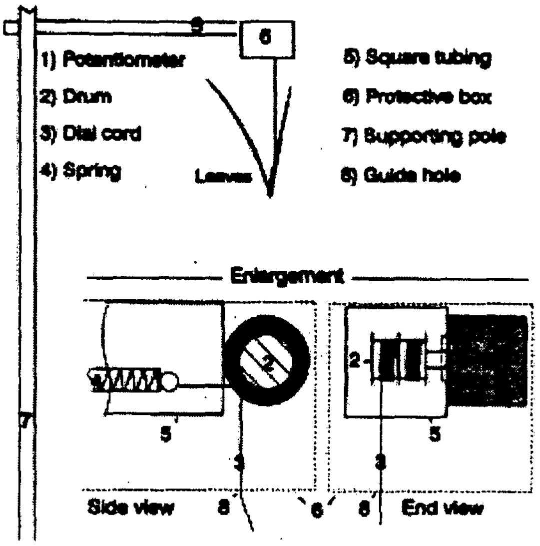


Figure 3.4 A simple sketch of the auxanometer from a side view and end view and its installation in the field (after Inman-Bamber, 1995).

Details of the construction and its manufacturing specification were similar to those described by Gallagher *et al.* (1976) and Inman-Bamber (1995). The auxanometer or linear variable differential transducer (LVDT) has also been described by Gallagher (1979), Walker (1988) and Clifton-Brown and Jones (1997).

The output signals per unit displacement (in mV) were large enough and recorded at the end of each hour by a Campbell datalogger (type CR 10). The data was downloaded to a computer for analysis every other day. Each auxanometer was reset about once a day. The initial calibration had shown a linear change in output signal with displacement. Based on the calibration factor (mm mV^{-1}) each hourly rate of leaf extension was calculated in mm per hour. This leaf extension may again include not only lamina extension but also that of the associated sheath and stem internode.

3.10.5 Leaf temperature measurements

Leaf temperature was measured continuously on two selected inter-crop plants and on three selected sole-crop plants using copper-constantan thermocouples (80 μm wire diameter). The junction of the thermocouple was attached to the abaxial (bottom) leaf surface with a hair clip. The thermocouples were connected in parallel to a datalogger to enable mean hourly leaf temperature readings.

The thermocouples were calibrated in a temperature-controlled waterbath with a resolution of 1°C. Measurements were made at different temperatures on each thermocouple in the range of 0 to 40°C. The thermocouples were attached in the plant canopy at least at the 4th - 6th leaf. They were moved upwards as the crop grew.

3.11 Statistical Data Analysis

Results were subjected to analysis of variance as appropriate. The effect of different planting dates (as a function of various temperatures) and cropping system on the regression slope and the intercept of line for either maize or beans was investigated by fitting to the data set. The common approach used for analysis of leaf growth was to relate it to accumulated thermal time. These models were compared using the T test in the accumulated analysis of variance. At first Richards' function model was fitted to all data from both crops to form a sigmoid curve of leaf growth as a function of chronological and thermal time series by using a comprehensive computer model (Curve Expert 1.3 for Windows).

Therefore, the statistical package used for the relationship between various variables of leaf growth was Mstat-C (1991 version) and the regression lines were presented graphically using Microsoft Excel graphics (Excel, 1997). Data transformations were also used to examine interactions and linear relationships. A similar analysis approach was described by Pilbeam (1996) to determine the effect of different seasons and crop management practices on the slope and intercept of the maize/bean inter-crop systems.

CHAPTER 4

FIELD MEASUREMENTS OF LEAF GROWTH FOR SOLE- AND INTER-CROP MAIZE IN RELATION TO TEMPERATURE

4.1 Introduction

Leaf growth characteristics provide meaningful parameters for the description of leaves. The study of the temperature-plant development relationship and the effect of temperature on leaf growth has been documented for a number of crop species (Thiagarajah and Hunt, 1982). In this study the effect of temperature on certain leaf growth characteristics is described for sole- and inter-crop maize. The shape of the growth curve is important when considering the physiological processes of leaf growth. In the analysis different shapes of growth curve resulted from changes in climatic factors. As one of these climatic factors, air temperature, appears to be decisive for growth and development, its effect on the leaf was incorporated by using thermal time.

In this study the weather, in particular the temperature, and leaf growth relationships were analyzed using different methods with planting date variations and cropping systems. This experiment includes daily weather and leaf growth measurements made for three planting dates on maize crops. To estimate the effect of temperature in terms of thermal time on leaf growth the growth curve fitting method (Richards function model) was applied to individual leaves.

The principal objective of this study was to develop a temperature function and incorporate it with leaf growth during the early growth stage of maize alone and maize inter-cropped with beans.

4.2 Experimental Procedures

Measurements of leaf growth were made in terms of individual leaf length, leaf number, plant height, leaf area and biomass production for sole maize and inter-crop maize during the early growth stage of the three planting dates. For measuring leaf length of monocotyledonous (maize) using the ruler the soil surface was used as reference point in view of differing form of leaf growth (see Chapter 3).

The leaf growth rate was calculated from the daily leaf length measurements by using the slope of the linear regression through the data in the exponential growth phase. Synchronized mean growth rates of individual leaves are also presented for discussion. Relative growth rate was also calculated from the daily leaf length measurements. All measurements were made under a range of environmental variations at different planting dates. The Richards function, unlike the straight-line model, attempts to fit some form of sigmoid curves to the measurements of individual leaves. Statistically, regressions fitted to the measurements provide an estimated correlation between the leaf length and accumulated thermal units since emergence.

4.3 Results and Discussion

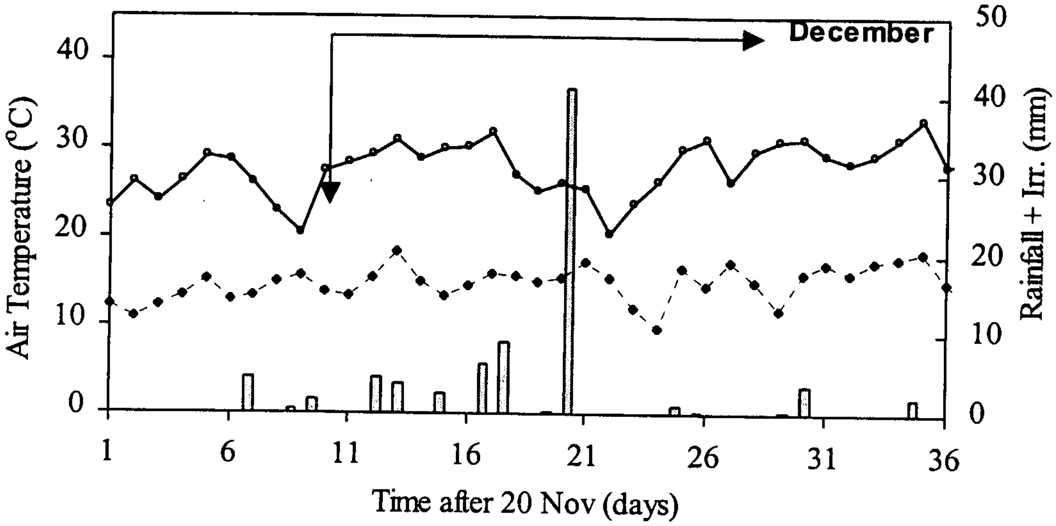
4.3.1 Weather and early plant growth stage

4.3.1.1 Weather variables during experimental period

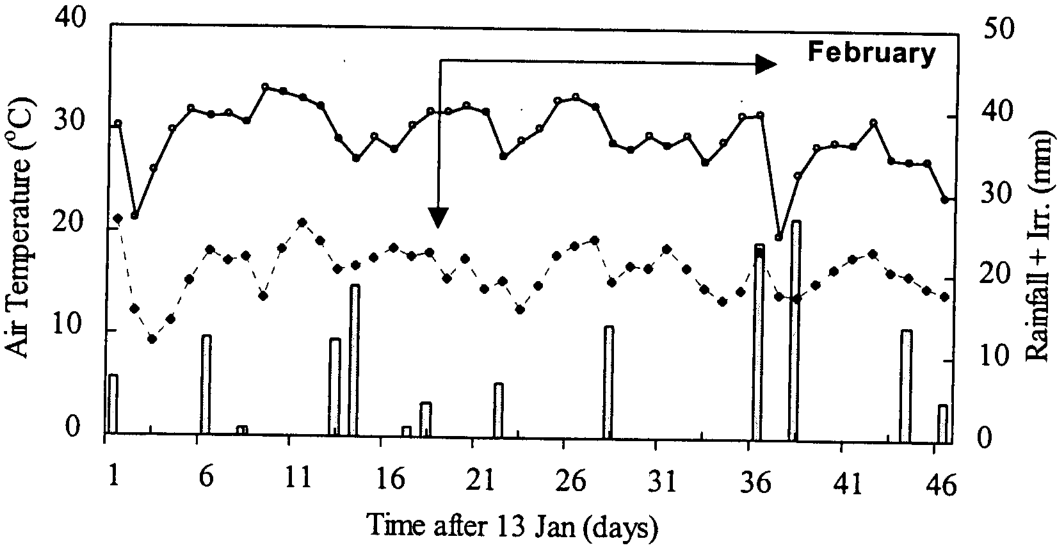
The weather conditions, particularly the temperature, solar radiation and precipitation during the early growth stages of the three planting dates are shown in figure 4.1. The maximum and minimum temperatures were uniformly higher during the November and January plantings than that of the third planting date (March planting). On the other hand, the temperature of the second planting date (January planting) was also slightly higher than that of the first planting. The highest temperature recorded was during January; with a maximum and minimum mean daily temperature of 30.4 and 15.8°C respectively. During the first planting date, initially both maximum and minimum temperature was relatively low but increased later in the experiment; mean daily temperatures were 18.9 and 22.2°C in November and December respectively (Figure 4.1a).

In the third planting, the temperature was higher at the beginning of the growth stage and declined throughout the growth period and remained low; thereafter the mean maximum/minimum temperature in April and May were 21.0°C/11.1°C and 19.2°C/3.8°C respectively (Figure 4.1c). Therefore, generally the temperature gradually increased from November until late January and decreased thereafter from the beginning of February to reach low temperatures in May. During the three consecutive experiments the months of December, February and April corresponded to the early growth stages of the crops. Due to that fact, the mean maximum and minimum temperatures of first and second planting were similar. The growing periods after emergence are indicated in figure 4.1 by arrows.

a) First planting date



b) Second planting date



c) Third planting date

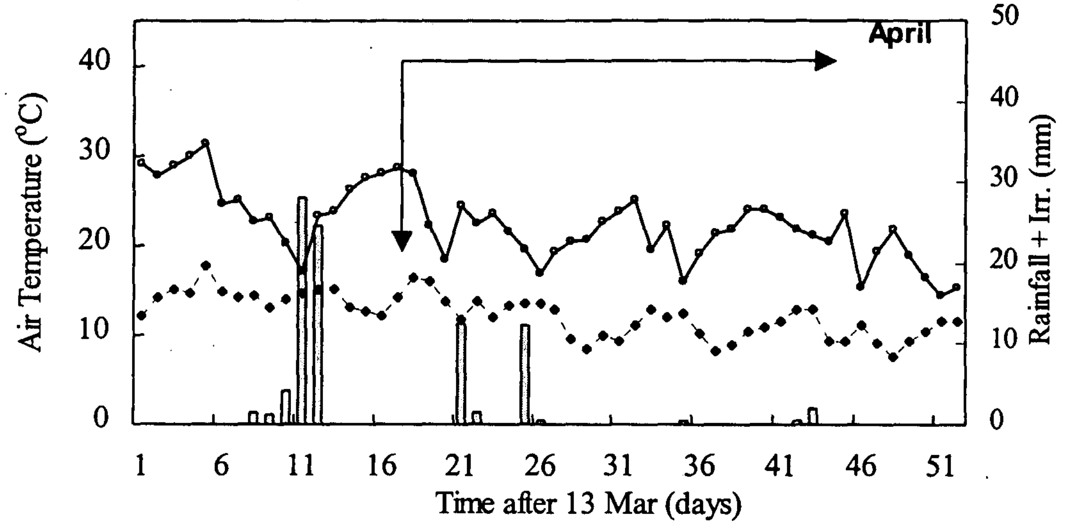


Figure 4.1 Daily mean maximum (circles & solid line) and minimum (diamond & broken line) temperatures and rainfall + Irrigation (bar graph) for planting on (a) Nov. 20, 2000; (b) Jan. 13, 2001; and (c) Mar. 13, 2001.

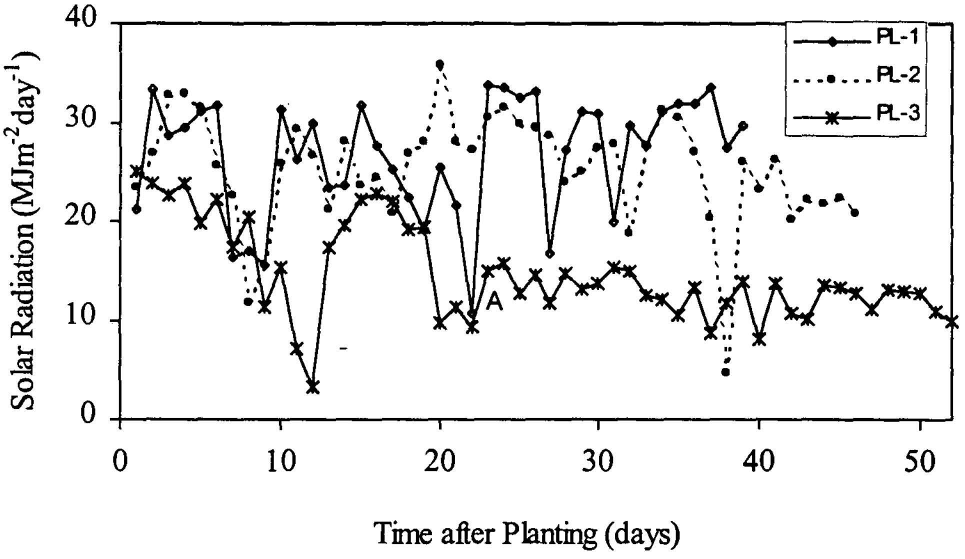


Figure 4.2 Solar radiation during the three planting dates from time of planting until early growth stages. PL-1, PL-2 and PL-3 represent for the three planting dates sown on Nov. 20, Jan. 13 and Mar. 13 respectively.

The rainfall was generally unevenly distributed. There was only a small amount of rainfall during the first planting and for sometime the crops showed signs of water stress, although there was much more rain during the second and third planting dates (Figure 4.1) The unique occurrence in the third planting date was that the soil was fully saturated (11 and 12 days after planting), and due to decreasing in temperature it remained wet for a long time. The emergence and development of the crop was much slower in comparison with the other two planting dates.

The solar radiation was high (average 26.8 and 25.4MJm^{-2}day^{-1}) during the early growth of November and January planting dates, but steadily declined during the third planting date, which averaged 14.7 MJm^{-2}day^{-1} (Figure 4.2). Therefore the difference between the temperatures during series planting dates was caused by the amount of radiation intercepted. With regard to response of pearl millet trial to radiation and temperature, Ong and Monteith (1985) confirmed that the difference between the 22°C and 28/29°C treatments in two consecutive years was due to the difference in the amount of radiation.

4.3.1.2 Seedling emergence in relation to temperature

Air temperature during the experimental period from the sowing time was depicted in figure 4.1. The soil temperature was not measured regularly during the experimental period, but for the purpose of checking some rough estimate of soil temperature was made around midday at a depth of 5-10 cm during the emergence period. It was found to be 1-6°C higher than daily maximum air temperature. However, according to Buckle and Grant (1974) average soil temperature at 5cm was usually similar to air temperature while daily maximum was 1-2°C lower and daily minima 1-3°C higher in the soil than in the air. The difference in temperature depends on the soil albedo, soil texture, colour, water content and other factors.

The effect of temperature on the number of emerged plants and time to emergence showed some differences for both maize and beans crops during the different planting dates. From table 4.1, the time to emergence in planting date one was more similar to time to emergence for the second planting date. Probably due to a common factor being involved, which is largely independent of temperature, as the average maximum and minimum temperatures were shown to increase from the first five days after planting to the next five days after planting. However, there were large differences with the third planting time due to lower temperatures during that period.

Table 4.1 Time to emergence, estimation of final emergence (%) and the first 15 days maximum and minimum temperatures for an average of five-day intervals on three planting dates for maize and bean crops.

Planting Date	Average 5 days temperature after sowing (^{0}C)						DAP Emerge. started	DAP Emerge. completed	Estimation of final emerge. (%)
	First 5 days		Second 5 days		Third 5 days				
	Min	Max	Min	Max	Min	Max			
Nov. 20	12.9	25.1	14.3	26.9	14.7	25.7			
Maize							4-5	10	85%
Beans							6-7	12	85%
Jan. 13	13.1	28.0	17.6	32.5	17.6	29.1.			
Maize							5-6	12	75%
Beans							7-9	14	70%
Mar. 13	11.1	19.5	10.9	22.8	10.3	19.8			
Maize							12-13	18	85%
Beans							15-16	21	80%

DAP: days after planting

Some information on grasses and cereal explained that the soil and air temperatures have a major influence on leaf growth during the early vegetative phase, because the seedling meristem, the site of temperature perception is situated below or close to the soil surface (Ong, 1983b; Peacock, 1975). Average temperatures during the growth period were lower for the later third sowing date and therefore directly affected germination and delaying emergence.

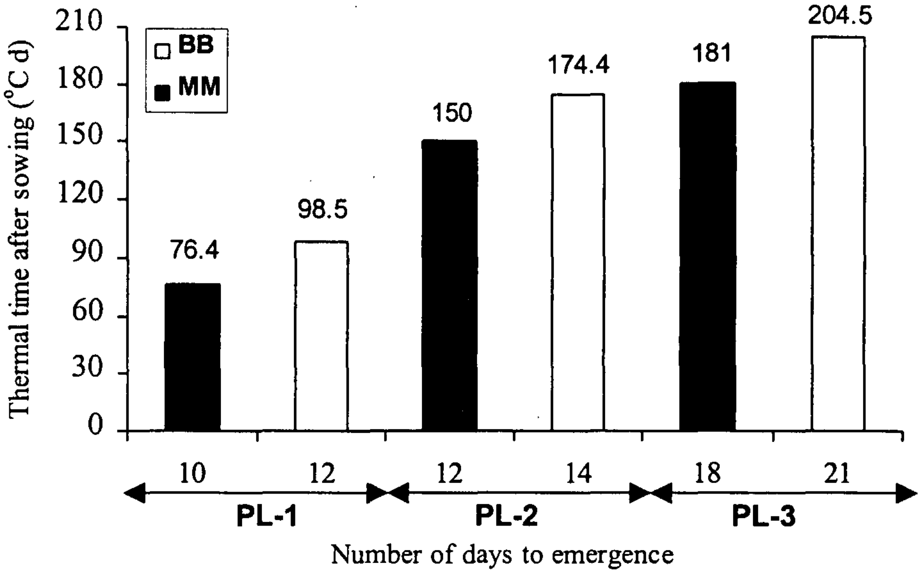


Figure 4.3 The relationship between the time to emergence and accumulated thermal time for three planting dates (PL-1, PL-2 and PL-3) for both cropping systems. BB and MM represent for beans and maize crops respectively.

The time from sowing to emergence increased from 10 -12 days in the first planting and 12 -14 days in the second planting to 18 –21 days for the third planting date as a result of a decrease in temperature (Table 4.1). Warrington and Kanemasu (1983a) found that the response of maize seedling emergence to mean temperature was strongly curvilinear under cool temperature conditions (16/6°C), taking 16 days to emerge while those under high temperature conditions (up to 30°C) took only 3 days. The number of days to emergence was also related to the thermal time accumulated after days of sowing for three planting dates.

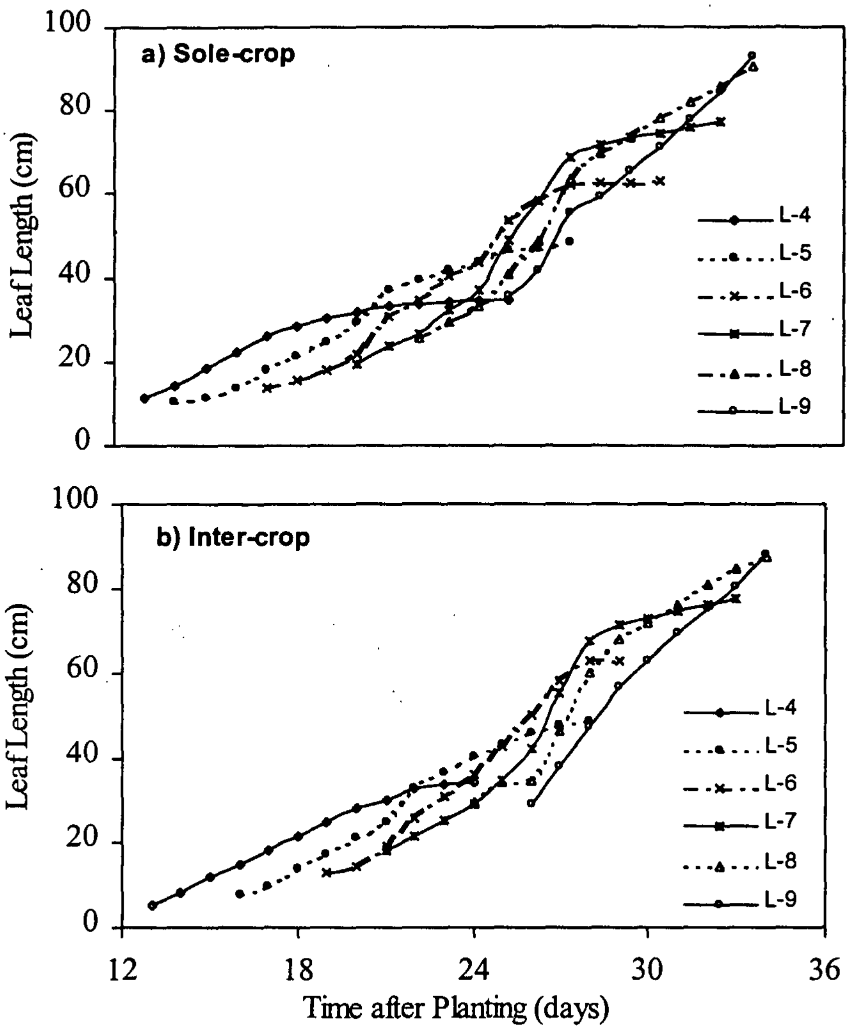
The effect of temperature as thermal time function on the time to emergence is presented in Figure 4.3 for three planting dates as, PL-1, PL-2 and PL-3 for maize and bean crops. The thermal time accumulation was higher during the lower temperature periods due to the crops taking a longer time to emerge. The highest accumulation was during the third planting date, which was about 181 and 204°C d for maize and beans respectively. The lower accumulation recorded during the first planting when the temperature was higher compared to the third planting. In the second planting there was only 2 days difference in time to emergence in comparison with the first planting date, but the accumulation of the degree-days was relatively higher due to high temperatures during the growing period.

On the other hand, despite higher temperatures in the January planting, the date of emergence was slightly delayed due to poor soil tilling conditions. For the same reason the percentage of fully emerged plants was also lower at 70-75% for both crops, while in the rest of the trials the percentage of emerged plants was more than 80-85% of all seeds sown.

4.3.2. Maize leaf growth for sole and inter-cropping systems

4.3.2.1. Maize leaf length

The mean values of 15 plants from each cropping system during the first planting date are presented in figure 4.4. In most parts of the growth period, growth was nearly linear and some of the leaves at the beginning showed typical exponential growth with time after planting as it is usually observed (for maize, Acevedo *et al.*, 1971; and for sorghum, Walker, 1988).



**The range of standard deviation (Std) for each leaf (leaf 4-9) in the above figure.

Leaf No.	4	5	6	7	8	9
a) Sole-crop	±2.4-±3.8	±2.4-±4.9	±2.1-±7.5	±2.3-±7.7	±2.8-±7.7	±3.5-±8.8
b) Inter-crop	±1.5-±3.8	±1.5-±4.9	±2.4-±6.0	±2.5-±7.4	±4.6-±7.6	±6.4-±7.6

Figure 4.4 Length of maize leaves 4-9 as measured with ruler from the soil surface reference point for (a) sole-crop and (b) inter-crop systems for the Nov. planting date (Planting date-I). The mean of n=15 with Std range in the above table **.

From the visual observations the maize leaf continues growth until the ligule appears out of the enclosing sheaths of the older leaves, whereafter the growth probably declines to zero or the length remains constant. To determine the overall pattern of leaf growth, it is desirable to establish the time course for a standard leaf length of maize according to the leaf position. In the analysis, in order to compare the growth of different leaf ages, it has been separated into lower (4 & 5 leaves), middle (6 & 7 leaves) and upper (8 & 9 leaves), as representative leaves. The experimental values for leaf length and the chronological time of the measurements are listed in Table 4.2 according to the above three levels of leaf stages.

Table 4.2 Leaf length – time relations for representative lower, middle and upper leaves during the early growth stage of sole and inter-crop maize plants. The data gives measurement range from initial length to the final length measurements (n=15).

Leaf No.	First Planting				Second planting				Third Planting			
	MM	DAP	IM	DAP	MM	DAP	IM	DAP	MM	DAP	IM	DAP
4	11.2 34.6	13 25	10.4 34.3	13 24	27.7 38.5	18 27	24.4 38.0	18 31	19.6 38.3	23 39	15.2 38.0	23 39
5	15.4 48.3	14 27	7.7 48.8	16 28	25.1 44.5	18 31	21.9 50.3	18 33	16.8 53.6	23 41	17.8 49.3	27 41
6	13.9 63.1	13 26	12.9 63.1	19 29	22.7 57.1	18 34	19.8 56.9	17 38	18.7 65.8	27 47	24.9 62.9	32 47
7	19.3 77.0	16 28	17.8 78	21 33	17.5 66.6	18 38	22 68.7	21 38	31.6 65.5	34 47	29.1 65.0	36 47
8	25.5 90.0	22 33	29.4 87.7	23 33	26.1 76	22 38	23.2 77.9	22 38	34.3 65.5	38 47	37.7 58.6	39 47
9	35.5 93.7	25 33	28.8 88.2	25 33	27.2 82.4	24 38	34.1 82.4	25 38	42.2 58.9	41 47	41.9 47.6	43 47

DAP: days after planting, MM: Sole crop maize, IM Inter-crop maize. The upper value for each column indicates the initial length measurements and the lower indicates the final length measurements

From table 4.2 it is clear that in planting one in both sole and inter-cropping systems the exponential growth of the leaves extended from day 13 to day 33 from a length of 11.2 to 34.6 cm and from 35.5 to 93.7 cm for leaf 4 and leaf 9 respectively. Similarly in the January planting to attain a maximum length of about 38 or 82 cm for leaf 4 and 9 respectively, it required 31 - 38 days. While in the third planting, as the temperature declined sharply, the leaf growth was delayed and only reached a maximum of 38 cm for leaf 4 on day 39 after planting and leaf 9 only attained its greatest lengths of 58.9 and 47.6 cm for sole and inter-cropped plants until the last measurements just prior to frost at day 47 after planting.

In contrast there were no visible differences observed in leaf length and growth duration among the cropping systems within each planting date. This can be examplified well enough with the January planting (Figure 4.5), where leaf 6-9 grew in the same pattern to a maximum length of 57.1/56.9, 66.6/68.7, 76/77.9 and 82.4/82.4 cm at the plant age of 34/38, 38/38, 38/38 and 38/38 days after planting for sole/inter-crop respectively. Therefore the data showed the similarities in leaf length and duration attained the maximum size of the leaf in sole and inter-crop maize in between planting dates.

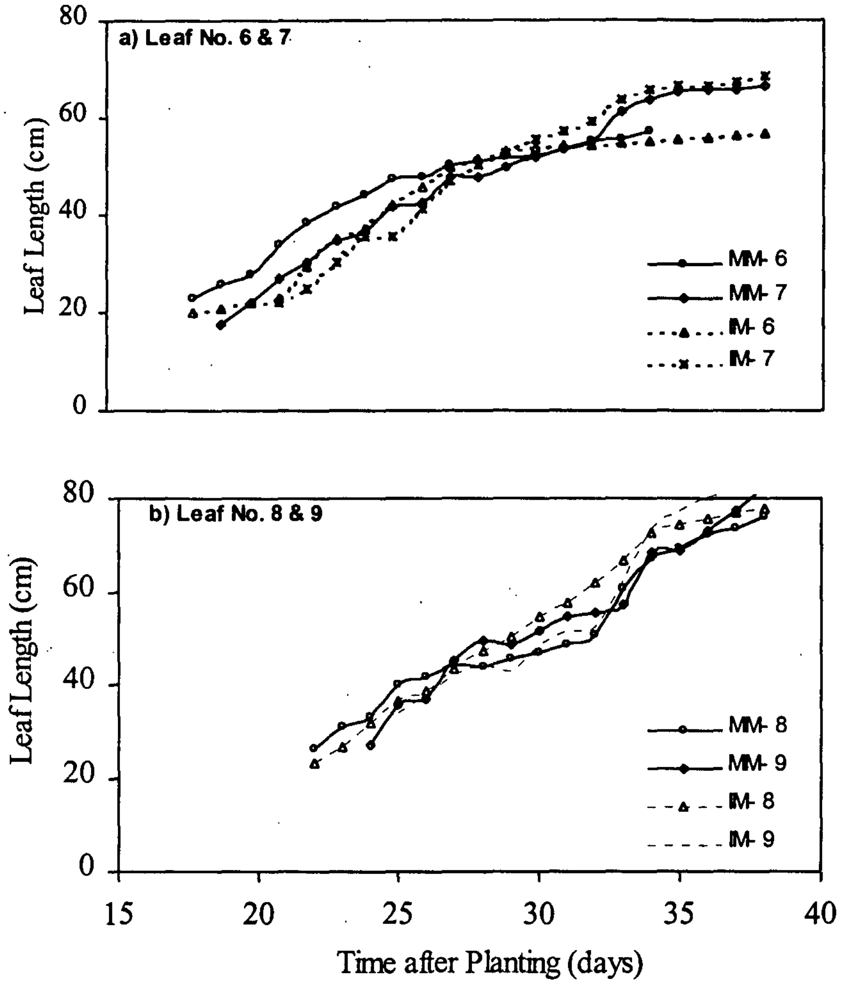


Figure 4.5 Leaf length measurements for sole- (MM) and inter-crop (IM) maize with respect to chronological course time in January planting time: a) upper for leaf 6 & 7 for sole (MM) and inter-crop (IM); b) below for leaf 8 & 9 for sole (MM) and inter-crop (IM). The data is mean of n=15.

4.3.2.2 Leaf length comparison between planting dates

When comparing the period of exponential growth for the three planting dates, representative leaves from the middle canopy level leaf 6 and from upper level leaf 8 were selected for analysis for both sole and inter-crop systems. Similar to the result given in table 4.2 the leaf length in the first planting one sole-crop of leaf 6 grew to a maximum of 63.1 cm after 13 days but in the case of the third planting date it took 20 days to reach about the same length. However, in inter-crop maize in the first planting leaf elongation started later but still reached the same length as the sole-crop (Figure 4.6).

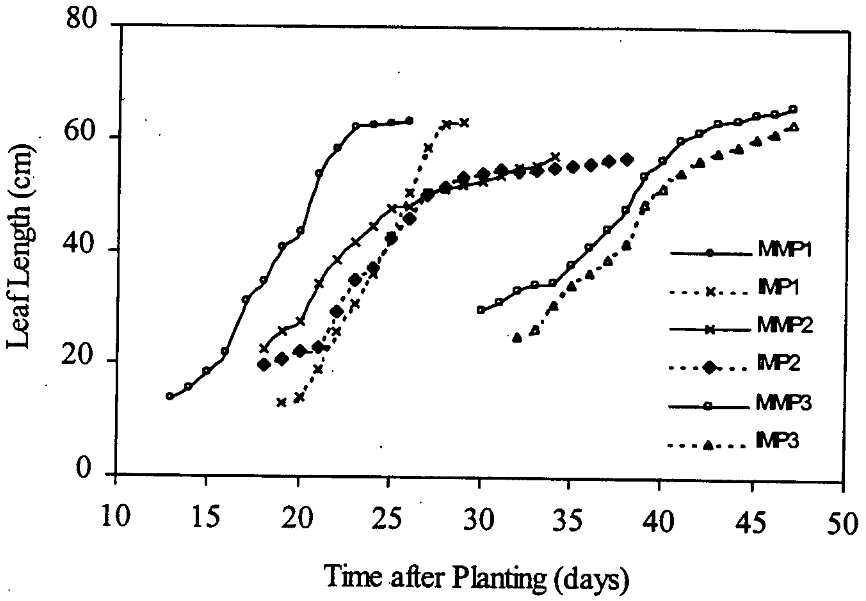


Figure 4.6 Comparison of average leaf length for leaf-6 in sole and inter-cropping systems versus their corresponding days after sowing to each planting dates. MMP1, MMP2 and MMP3 belong to Sole-crop Planting I, II and III. IMP1, IMP2 and IMP3 also indicated for inter-cropping systems for three planting dates.

In the second planting (January planting) the maximum leaf length of leaf 6 was less than that attained at other planting dates. It only reached about 57 cm after 16 days growth. This was due to the effect of heat stress on the crops, where the maximum temperature during that period reached 32°C and the leaf length growth almost ceased with a little growth to about 51-57cm within a week. Squire and Ong (1983) have shown that at a maximum temperature of 36°C the leaf growth of maize will be inhibited and Thiagarajan and Hunt (1982) showed the largest final leaf areas at 30/25°C.

In the third planting the leaf length increment decreased when the temperature declined to a monthly mean of 16^0C. During the last week of leaf growth, the length was only extended to 60-66 and 53-62 cm in sole and inter-crop respectively. This result agrees well with Fortin and Pierce (1996), whose results showed that a maize plant exposed to 21.3°C had a developmental delay of 7.7 calendar days relative to maize exposed to 24.8°C. Pearson and Derrick (1977) also confirmed that the growth rate of maize is expected to decline sharply below 19°C because photosynthetic rates are reduced. Based on the observation for the middle level leaf of the canopy, the leaf length of maize plants declined at low temperature and also during heat stress periods when the temperature exceeded the optimum level. The upper leaves in the maize canopy during the vegetative stage are responsible for most of the radiation interception and also the major contributors of photosynthates to the ear during grain filling periods (Simmons and Jones, 1985).

4.3.2.3 Leaf growth rate analysis

The final size of monocotyledonous leaves can be described in terms of their mean rate and duration of expansion. That is an expression, which can be evaluated at a point, or infinitesimally small increments, in leaf surface. For simplicity such an expression is an important factor in analysis of final leaf size for both rate and duration of elongation. In this study the leaf length data were analyzed in terms of mean growth rate and by using the slope of the linear regression of each leaf length.

Analysis using mean leaf growth rate

The mean values of the actively growing leaves were calculated by taking only those leaves that are synchronized together for each possible leaf number Since at the field level measurements appeared over a wide range of differences due to various emergence dates and the way of exposure of individual plants and leaves.

The mean leaf growth rate during the measurement period plotted against successive leaf numbers in three planting dates is given in figure 4.7. From the ruler measurements of leaf extension rate for different wheat cultivars, Gallagher (1979) used the same method to calculate leaf growth rate. These results for the mean leaf growth rate were not consistent for different planting dates, and there were little variations between the sole and inter-cropping systems.

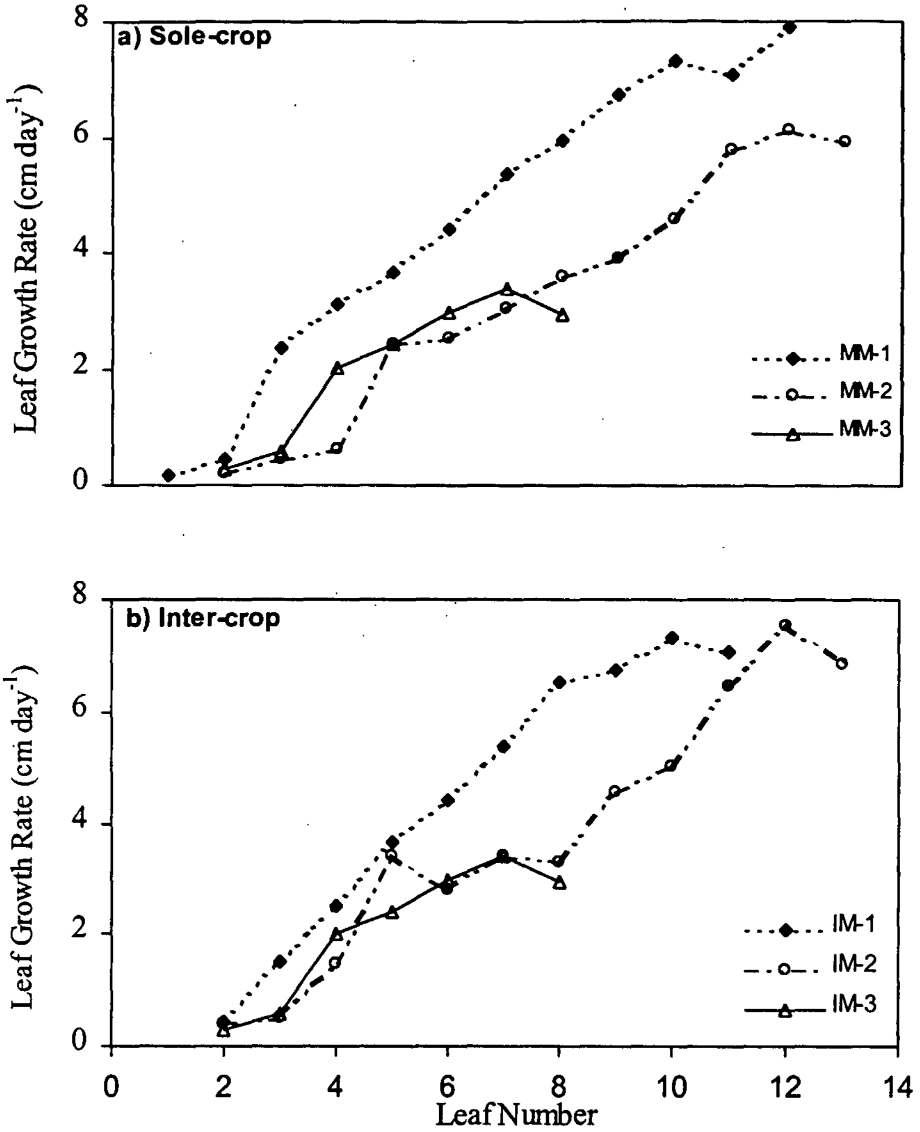


Figure 4.7 Mean leaf growth rate per day (cm day^{-1}) for three planting dates for individual leaves versus leaf number: (a) Sole-crop and (b) for inter-crop. Each point is the mean of daily observations of 15 sample plants.

In the first and second plantings the growth rate generally increased rapidly with leaf number and when it reached leaf 12-13 it started to decrease in rate, whereas in the third planting, though the growth increased initially with leaf number, it started to decline sooner when it reached leaf 7 (Figure 4.7). Using this analysis, the rate was higher for the first planting date, ranging from 0.4 cm day^{-1} for leaf 2 to about 7.0 cm day^{-1} for leaf 11 and in the second planting leaf growth rate was 0.3 - 6.0 cm day^{-1}. In the third planting the leaf growth rate never exceeded 3.0 cm day^{-1}. In all planting dates the increased leaf growth rate with increasing leaf number contributed to the larger leaves later in the season. Similar results for sorghum are described by Hamdi, Harris and Clark (1987) and Walker (1988) as the increased leaf growth rate increased with increasing leaf number but varied under different planting dates.

Analysis using linear regression slope

The duration and slope (rate) of the exponential and linear growth of the leaf is often described by using the slope of the linear regression portion of each curve. In this analysis the mean growth rate for each leaf number is calculated as the slope of the linear regression of the fast growing linear portion of each curve (Figure 4.8.) The regressions had r^2 values in the range of 0.90 to 0.99.

Earlier in the growing season in the second and third planting dates the first few leaves showed little differences in leaf growth rate between the cropping systems. But in the case of the first planting until leaf number 4 the inter-crop leaf growth rate was higher than the sole-crop and later, after leaf 7, the inter-crop showed slower growth rates. In the same way in the second planting after the tenth leaf the sole and inter-crop showed a big variation in the growth rate that was a maximum of 3.5 and 5.5 cm day^{-1} respectively.

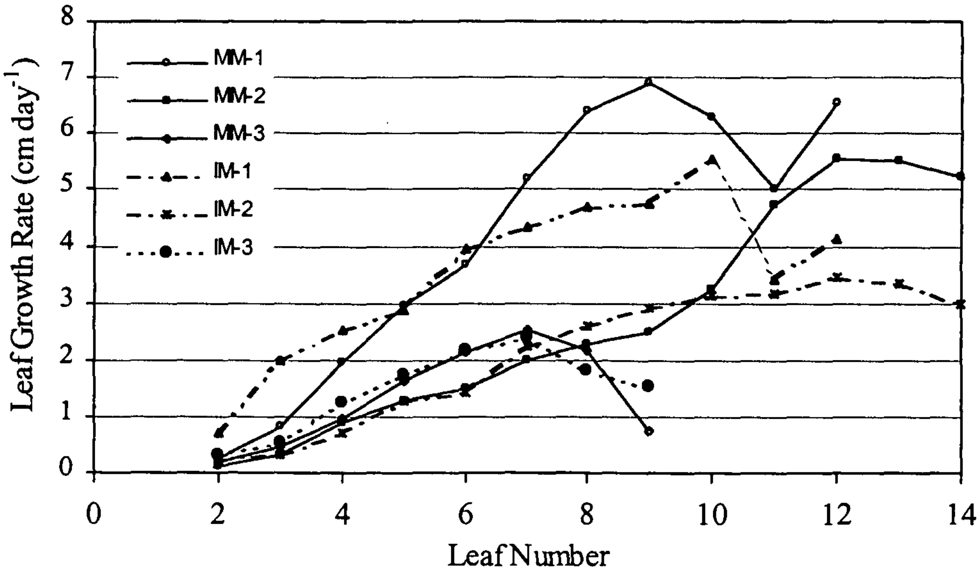


Figure 4.8 Leaf growth rates for sole and inter-cropping systems, in three planting dates, calculated from the slope of the linear regression of leaf length versus leaf number. For the given figure, MM- 1, 2 & 3 rep

resent for sole-crop maize in planting I, II & III and IM-1, 2 & 3 also for inter-crop of the respective planting dates.

On the contrary, in the first planting the growth rate was higher from the beginning of the leaf growth and stretched to a maximum of about 7 cm day^{-1} for sole-crop and 5.5 cm day^{-1} for inter-cropping. In the first planting the growth rate was different in leaf 11 in that the rate decreased in sole-crop 6.3 - 5.0 cm day^{-1} and in inter-crop 5.5 - 3.5 cm day^{-1}. In the third planting the leaf growth rate started to decrease sooner at leaf seven. This was due to a sharp decline in temperature. At leaf 9 it showed a rate near to zero and the crop had totally ceased growth, when the temperature decreased to an average minimum temperature of 3.8°C.

From the above two approaches (Figures 4.7 and 4.8) all planting dates showed some similarities of expressing the leaf growth rate during the early growing stage. The leaf growth rate also normally increased with increasing leaf number with the exception of leaf 11 in the first planting, which decreased in both approaches. This may be probably due to compacted nodes nature to form an internode. Gardner *et al.* (1985) mentioned that maize remains stemless until it develops 8 fully expanded leaves. The third planting also showed lower leaf growth rate with fewer numbers of leaves due to a decrease in the temperatures.

Individual leaf growth rate

The growth rates of leaves 7 and 8 were plotted against days after planting in figure 4.9. It shows a decline from maximum rate at earliest measurement stage to nearly zero, until the leaf finally ceases growing.

The change in the rate for individual leaves showed some fluctuating (up and down) responses as temperature changes often and over a wide range in the field, the rate of increase being greater at higher temperatures in both sole and inter-cropping systems. This agrees with observations made for maize by Brouwer *et al.* (1973) as well as on other grasses (Jewiss, 1966) indicating that there was a substantial increase in rate with increase in temperature under controlled temperature conditions.

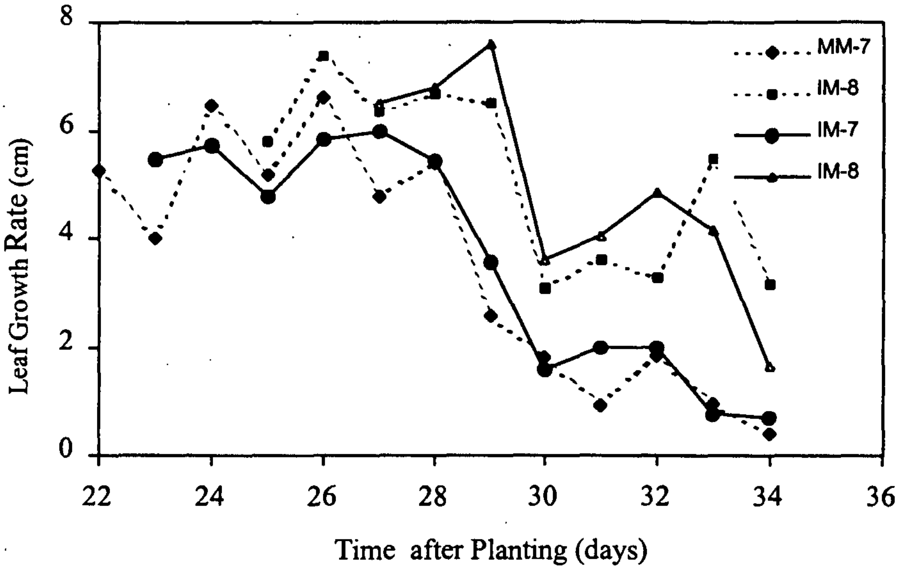


Figure 4.9 Individual leaf growth rates during the first planting for leaf 7 and 8 from 22-34 days after planting. MM represents sole-crop and IM represents inter-crop maize plants.

However, in this study leaf length was measured on a daily basis, thereby integrating changes in the growth rate between the dark and light periods. Volenec and Nelson (1982) and Schnyder and Nelson (1988) observed that leaf growth rate is higher during the night period. But later in the experiment, the temperature was not held constant, being lower at night. In contrast, previous studies showed that growth rate was lower in the dark period than in the light period (Gallagher and Biscoe, 1979). As a solution Ong (1983b) suggested that the significance of day and night temperature for leaf growth is only easily settled by using sensitive auxanometers to measure at hourly intervals in order to calculate the actual rate against variation of temperature. These types of measurements are discussed in detail in Chapter 6.

Leaf length in maize seems to follow a sigmoid curve (Figure 4.10) with final leaf length attained 27 days after planting. Based on leaf 5 in first planting, the leaf elongation was maximal and approximately constant from 16 days after planting until 24 days after planting.

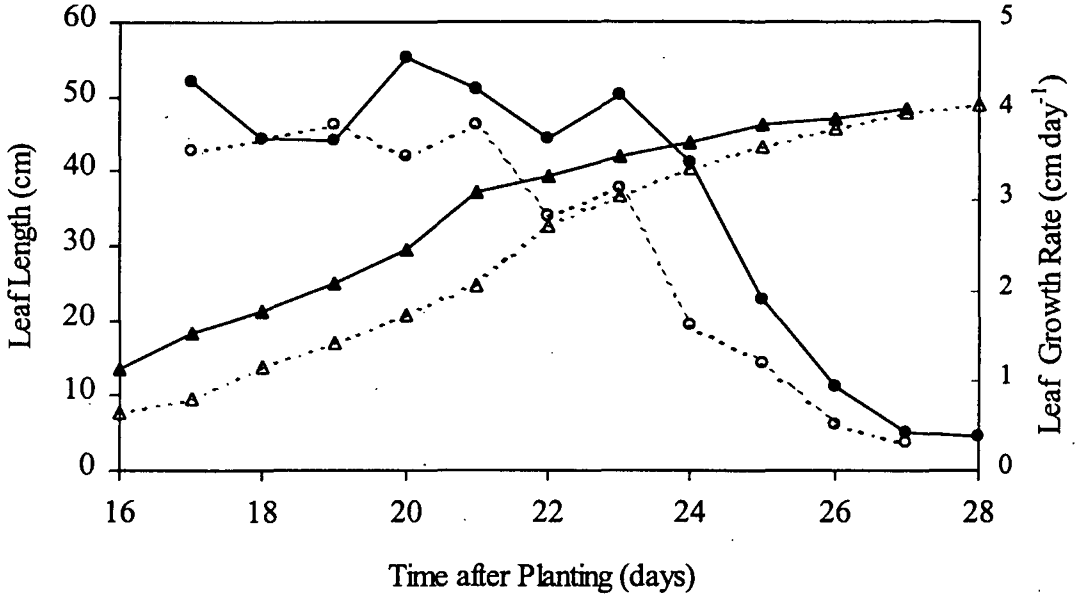


Figure 4.10 Time series of leaf length (△ & ▲) and growth rate (o & ●) of the fifth leaf for sole-crop (solid line) and inter-crop (broken line). Each point represents the mean of 15 plants in planting - I.

Leaf growth rate of leaf 5 was initially at about 3.5 - 4.5 cm day^{-1} for a period of 5-6 days. From 23 days after planting the leaf growth rate declined to approximately zero. For maize a short period of constant growth rate was also reported by Stephen and William (1996) as was reported for *Lolium perenne* (Schnyder, Seo, Rademacher and Kuehbauch, 1990). A number of graminaceous species show constant growth rate during the extended period of leaf development (Robson, 1972; Wilson, 1975; Gallagher, 1979; Durand, Onillon, Schnyder and Rademacher, 1995).

4.3.2.4 Relative growth rate

Overall leaf elongation of maize was therefore measured to assess leaf and shoot expansion. Growth of such a unidirectional growing organ of monocotyledonous leaf segment can be characterized by relative growth rates (Silk and Erickson, 1979; Gardner *et al.*, 1985). The relative growth rate for all planting dates is illustrated in figure 4.11. The result shows that the relative growth was higher during the first planting date in both cropping systems, reaching to a maximum of 0.3 day^{-1} for first planting and 0.25 day^{-1} for second planting, whereas in the third planting the relative growth was less than about 0.12 day^{-1}. Thus the third planting maximum growth was only 34% of the first planting's highest growth and about 67% of the second planting. This result also clearly demonstrated the variation of growth duration of the crop as temperature declines for the third planting date.

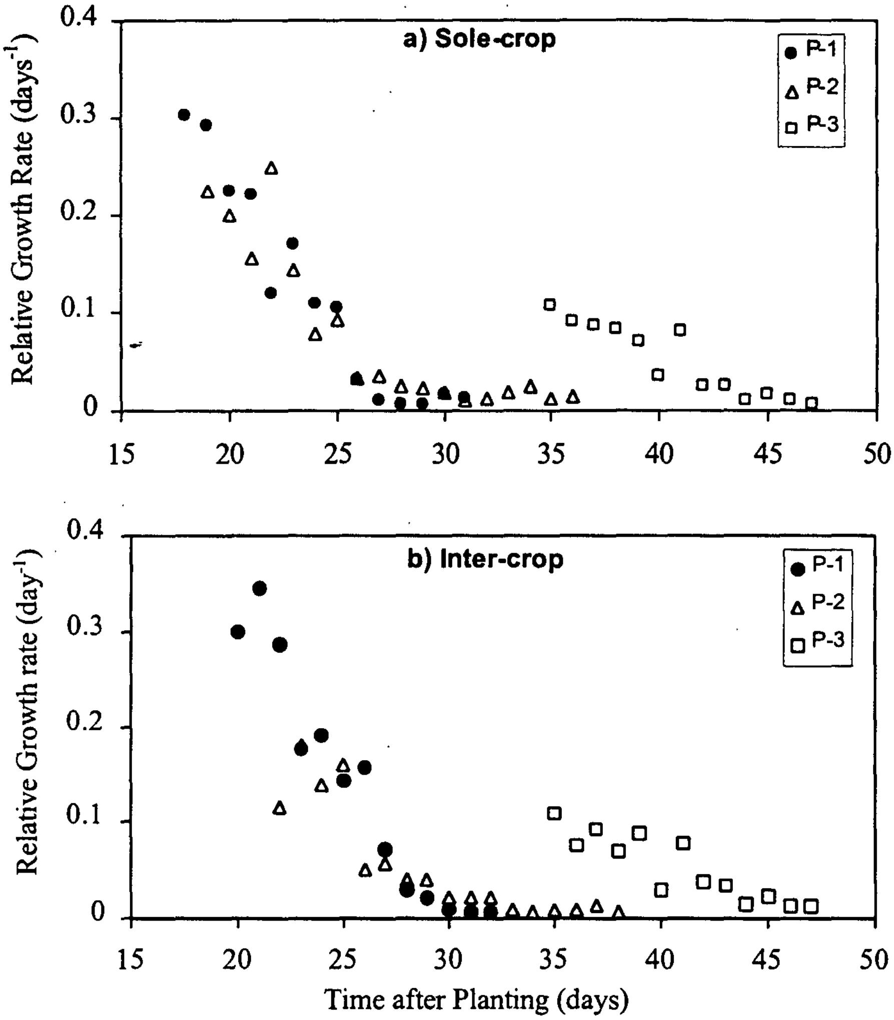


Figure 4.11 Relative growth rate for leaf 6 versus days after planting for three planting dates. The top figure is for sole-crop and the lower for inter-crop.

Therefore, maize leaf growth rate has been shown to be constant only for a short period. The decline in leaf growth rate as the leaves becomes older was related both to decrease in the length of the growing zone increment and the maximum relative growth rate occurring during the active growing period. The Stephen and William (1996) studies show the effect of development on the spatial distribution of the growth rate as maize leaves get older and the rate declines. There was maintenance of relative growth rate towards the base of the growing zone. A similar effect has been reported for maize growing in dry vermiculite (Sharp, Silk and Hsiao, 1988) subjected to drought stress and sorghum subjected to stress (Bernstein, Lauchli and Silk, 1993) and tall fescue leaves (Durand *et al.,* 1995).

4.3.2.5 Leaf growth responses to thermal time in maize

Temperature greatly influences the rate of leaf expansion in chronological time especially for the leaves in the field, so it is difficult to resolve leaf growth data without recourse to thermal time analysis. In order to account for the influence of temperature on leaf growth, it then becomes necessary to use the thermal time calculated from the measured temperatures. This study describes the responses of leaf growth in terms of leaf length under a wide range of temperature through chronological time and with the application of thermal time.

Data analysis advantages

a) Interpretation of thermal time equation for screen temperatures

The effect of temperature on growth rate has been described using the thermal time concept. In this analysis the growing degree-days (GDD), which assumes that phenological growth is constant per degree of temperature between base temperature and an upper threshold temperature are used. Consider that above the threshold and below base temperature, the leaf growth is zero. Stewart *et al.* (1998) reported on the simplicity of the growing degree-days concept. Its improvement on the over a day counter for prediction of development has led to its widespread adoption, particularly for the vegetative period (planting to silking).

The base temperature used for this analysis was 10°C (as estimated by Cross and Zuber, 1972; Brown and Bootsman, 1993; from the collections of McMaster and Wilhelm, 1997; and others). However, some researchers used 8 - 10°C for the vegetative period (Ritchie and Nesmith, 1991). The upper threshold temperature used was 30°C as commonly applied to maize crop. But Ellis *et al.* (1992) and Tollenaar *et al.* (1979) applied the range of 19-34°C for the vegetative stage of the maize crop. In general, Stewart *et al.* (1998) concluded that the phenological response to temperature was sigmoidal from planting to silking but much flatter from silking to maturity, using the function of $GDD_{30,10}$.

b) Descriptive ability of the Richards function model

The data was analyzed using the curve fitting Richards' function of a comprehensive computer model (Curve Expert 1.3 for Windows). The former Richards' function method made use of a mathematical property of Richards (1959) and Causton (1978) and was more summarized for studies of leaf growth. This program processes data to establish the best fit automatically using Curve Expert systems. This program was designed to be simple yet powerful.

Various empirical curves have been used to describe leaf growth; generally some form of sigmoid curve is used. Richards (1959) comprehensively reviewed these and other growth curves. Dennett *et al.* (1978) also mentioned the advantages of this model as the Richards function, unlike the straight-line model, can adequately describe the changes in the shape for leaves growing in a steady, gradually changing, or fluctuating environment. The four parameters of the Richards function in equation 4.1 essentially comprise an absolute growth rate, a duration of growth, a size at some initial time and a shape parameter which has biological significance (Dennett *et al.,* 1978).

$$y = \frac{a}{(1+e^{b-cx})^{1/d}} \tag{4.1}$$

where y is the length of the leaf at accumulated thermal time x and a, b, c and d are fitted parameters. a estimates the maximum length of the leaf, c is essentially a rate constant, b is a function of area when $x = 0$ and d determines the shape of the curve with e the exponential value.

From the analysis the least square regression (r^2) for simple linear regression between values of observed leaf length and calculated thermal time or chronological time was used to estimate the influence of temperature on leaf growth. The four values for parameters with standard errors are also presented for the analysis.

Overall comparison of thermal and chronological time

To assess a more effective method for analysing the effect of temperature on leaf growth, overall comparisons of combined data were fitted by the given curve model.

Table 4.3 shows the values of the parameters with standard error and the estimation of linear regression for leaf 4-9 through chronological and thermal time series. In chronological time series the coefficient of determination (r^2) ranges from 0.39 to 0.62 whereas for thermal time r^2 ranged from 0.61 to 0.88. Therefore thermal time displayed a better fitting correlation with the leaf length than that using chronological time. This higher correlation of leaf length with the thermal indices suggested that a better sigmoid curve for the leaf growth was possible. On the study of leaf area of maize a similar result was reported by Dwyer and Stewart (1986) when it correlated well ($r = 0.98$) with thermal time and produced a better sigmoid curve fit.

Table 4.3 Estimates of the four value parameters with standard error in the Richards' function curve fitting model and comments on correlation for the observed leaf length values in maize crop. It was estimated by combining all the cropping systems and planting dates. The parameters were fitted by using equation 4.1.

Leaf No	Model Parameters (Coefficients)				Standard error (SE)	Correlations	
	a	*b*	*c*	*d*		r	r^2
Chronological time							
4	33.44	0.29	0.25	0.04	4.86	0.789	0.623
5	42.83	0.69	0.25	0.03	8.43	0.724	0.524
6	57.34	-0.71	0.11	0.09	11.62	0.651	0.424
7	56.31	66.75	0.37	45.49	10.83	0.773	0.603
8	62.51	6.25	0.41	0.05	13.09	0.682	0.465
9	63.85	6.77	0.49	0.01	13.17	0.629	0.395
Thermal time							
4	36.24	-0.08	0.03	0.27	2.71	0.939	0.883
5	46.37	6.37	0.05	3.59	5.38	0.898	0.806
6	56.31	66.75	0.37	45.49	7.64	0.867	0.751
7	62.06	45.15	0.22	27.99	10.80	0.784	0.615
8	72.50	1.73	0.02	0.28	10.33	0.817	0.667
9	82.48	-0.99	0.01	0.07	10.47	0.786	0.617

For instance, leaf 4 in figure 4.12 illustrates the basis of relatively high correlation ($r = 0.88$) between leaf length and thermal time after emergence. The growth curve showed a typical sigmoid form. Although the growing degree-day system is attractive due to its simplicity and its higher accuracy in predicting phenological events compared to number of days per se (Kiniry and Keener, 1982), it has also been criticised over the years.

As cited by Dwyer and Stewart (1986) the classical work of Lehenbauer (1914) on the elongation of maize seedlings in relation to temperature showed a rapid decline of the elongation rate when the optimum temperature was exceeded. Watts (1971) fitted the data between 0 and 30°C with an exponential curve by which the rate is increased as the temperature rises above 10°C. This approach does not account for the rapid decline in the rate above optimum temperature. Crops growing under sub-optimal temperatures are known to lengthen their development in real time. This was clearly indicated by Bollero, Bullock and Hollinger (1996) as thermal indices accumulate various combinations of daily temperatures above a threshold temperature during the growing season.

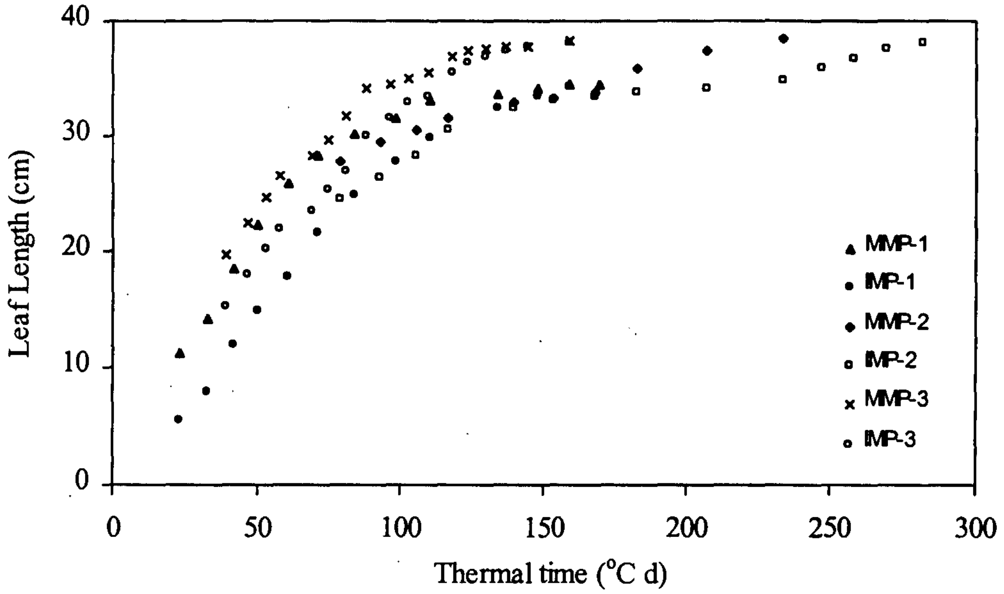


Figure 4.12 Actual leaf length (leaf-4) from time of emergence based on all three planting dates on both sole and inter-crop systems as a function of thermal time. MMP represents sole-crop plantings 1, 2 and 3. IMP indicates corresponding to inter-cropping systems of all three planting dates.

Comparison between planting dates and cropping systems

The correlation coefficient between the leaf length and thermal time after emergence was analyzed separately for all sole and inter-crop maize plants. The estimated correlation (r) result from the two cropping systems was between 0.73 - 0.96 and 0.83 – 0.98 respectively (Table A 1, Appendix I). However, the absence of the statistical analysis of variance of a significant interaction between the effect of temperature and leaf length in both cropping systems and in all planting dates requires an additive equation *(LRE= a+b*TT)*. It is formed by transformed data and requires a linear regression analysis. This follows since the thermal time approach to modeling leaf growth assumes a linear relationship between leaf length and temperature between base and optimum temperature (T_{base} and T_{opt}). The result of the linear equation, which was fitted to all data sets for leaf 4-9, is presented in table A 2 (Appendix I). Though there were some variations between different leaves, statistics showed significant differences (at the $P < 0.05$ level) among all treatments according to the T test procedure. The confidence interval limits were also observed as overlapping each other among the treatments. This indicated that almost all the slopes were in the same range. This is clearly listed in the statistical analysis in Appendix I (Table A 2).

As mentioned earlier in this study, the three planting dates had some variations in temperature as well as in leaf growth. But all the treatments had a strong correlation with their proportionate leaf lengths. The coefficient of determination (r^2) ranged from 0.71 to 0.99; for each leaf at least five out of six treatments of those values were ≥ 0.85. Therefore a significant response of thermal time to leaf growth was detected for both cropping systems in all planting dates (at the $P < 0.05$ level). In this case it is preferable to combine the cropping systems to assess the variation in temperature on leaf growth among the planting dates.

Similar linear equations based on natural logarithmic transformation functions for exponential leaf growth were fitted to the thermal time for the three planting times. Consequently, the statistical analysis variance results are presented in Appendix I (Table A 3). In the three planting dates, it is clear that there were some variations in temperature as well as in leaf growth. The coefficient of determination (r^2) for different leaves ranged between 0.34 - 0.96, but in most cases the correlation was good. This demonstrates that relations between leaf length and thermal time were detected at highly significant differences (at the $P< 0.05$ level) but on leaf number 4 and 9 in the third planting it was approaching insignificant differences at $P=0.046$ (at the $P < 0.05$) level for the effect of temperature on leaf growth. However, the confidence interval limits were included on the same range of interval and are likely to overlap each other.

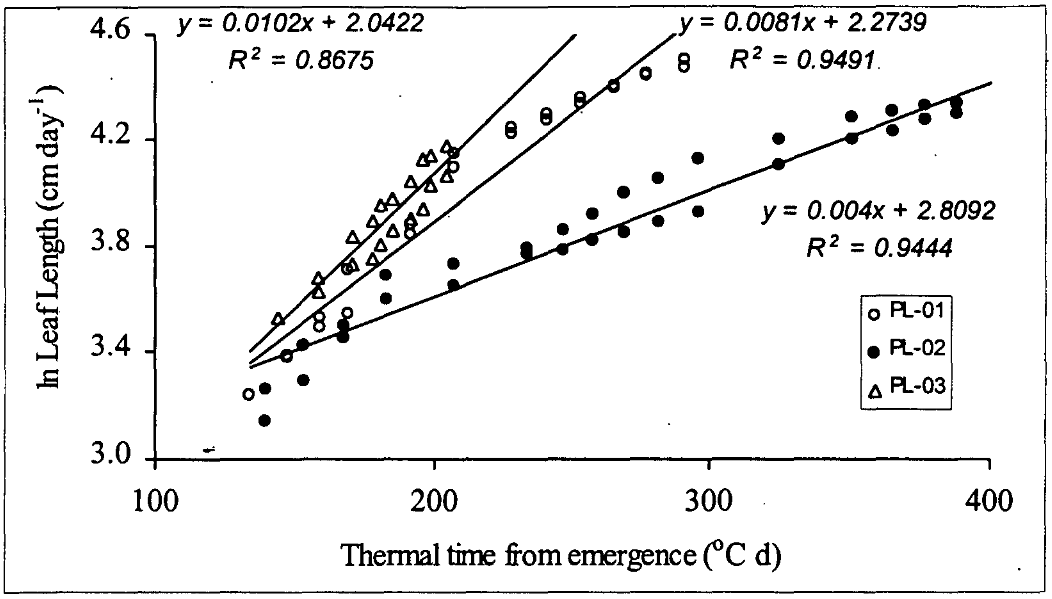


Figure 4.13 Relation between leaf length for (leaf 8) and thermal time from emergence for three planting dates, PL-1, PL-2 and PL-3 in sequence, and a linear regression is shown.

The study also illustrates that the accumulation of thermal time influences the leaf length and the growth rate according to various temperatures. For instance, for leaf 8 in all planting dates the correlation of leaf length with the thermal time was fairly high; the coefficient of determination showed 0.94, 0.94 and 0.86 for the first, second and third planting respectively (Figure 4.13). The highest mean accumulated degree-days between 10-30°C (base and optimum temperature for development) during the early growth stage were in the second planting, which was about 390°C d. The lowest accumulation was in the third planting with 205°C d and the growth slowed because of lower temperature in the third planting period. In contrast, for the second planting it was observed that higher thermal time accumulation accrued and the growth was lower than for the first planting. This was due to temperatures higher than optimal during some period of the growth.

4.3.2.6 Maize leaf number during early vegetative growth

The leaf ligule was visible and the leaf became fully expanded, when leaf counting was occurred. The mean temperature during the early growth was lower in the third planting when compared to the previous two planting dates. The increase in number of visible leaves was nearly linear with time at all planting dates and cropping systems (Figure 4.14).

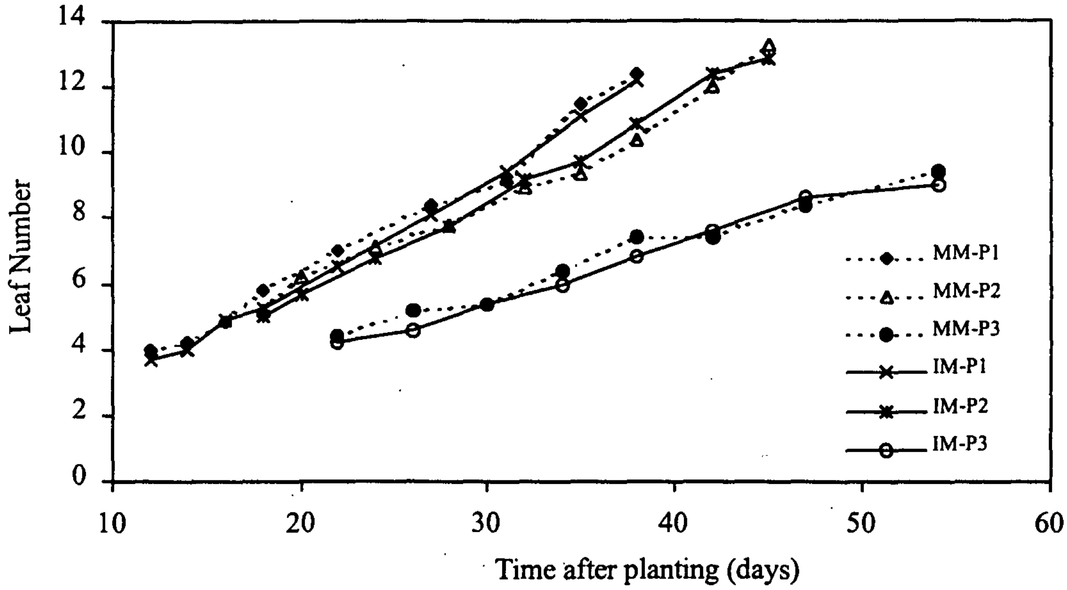


Figure 4.14 Relationship between leaf number of visible leaves and time after planting for three planting dates of maize crop as grown in sole and inter-crop systems during the early vegetative growth period.

The leaf number of maize did not show variations between the sole and inter-cropping systems. In the third planting the leaf number increased more slowly and reached a maximum of 9 leaves at 54 days after planting as the temperature was lower during the growing period, with mean maximum and minimum temperatures of 21 and 11°C. This agrees with observations made for maize (Thiagarajah and Hunt, 1982) when the rate of increase in leaf number was greater at the higher temperature.

In the case of the second planting, initially the leaf number was similar to the first planting date but after leaf 8 it was found to require a longer time to expand, presumably as a consequence of the lag effect of the higher temperatures experienced 24 days after planting. At that time the maximum temperature was in the range of 29-33°C and the crops might have been affected by heat stress. Warrington and Kanemasu (1983b), in a controlled environment room experiment with maize, found that the leaf initiation and leaf appearance rate showed a near linear increase as mean temperatures were increased from 15 to 18°C, with a maximum rate occurring at 30 to 32°C. On the other hand, similar increases in the number of actively growing leaves through the ontogeny of the maize plant were also observed at 15/10 to 35/30°C (Thiagarajah and Hunt 1982). These results are at variance with Jewiss (1966) who found that, for a particular environment and species, the number of externally visible leaves, which are actively growing, is constant.

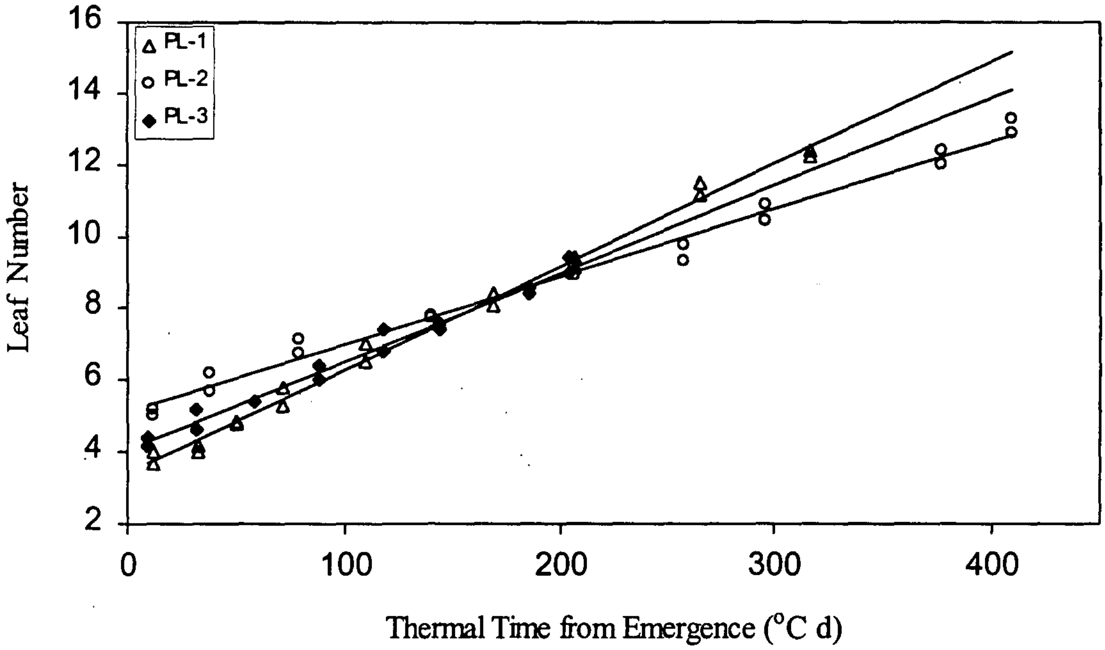


Figure 4.15 Leaf number as a function of thermal time (°Cd, $GDD_{10,\ 30}$) from emergence for first planting (Δ), second planting (o) and third planting (ט).

The relationship obtained from the temperature variations after planting dates with leaf number were checked against thermal time after emergence by fitting them to the linear regression equation *(LRE= a+b*TT)*. Figure 4.15 shows number of leaves versus thermal time ($GDD_{10,\ 30}$) for the three planting dates. In all cases (Table 4.4), the linear slope strongly correlated with temperature as thermal time after emergence for each planting date. A significant response of thermal time to leaf number was detected from the analysis of variance (at the $P < 0.05$ level) according to the F test procedure among the planting dates and the combined effect of the planting dates. A similar type of statistical data analysis was applied by Villalobos and Ritchie (1992) for different hybrid sunflower varieties as a function of thermal time. By combining the planting dates the correlation was also good (r^2= 0.96), since each planting date had different leaf numbers in relation to accumulated temperature within that particular period. Hence the result indicates that the leaf number was high at the optimum temperature. Low temperature during early growth stage was also associated with a lower leaf number. However, some differences appear in the thermal time required to produce a specific leaf number.

Table 4.4 Linear regression equation of leaf number as a function of thermal time from emergence (°C d). The data corresponds to the first, second and third planting dates and the combined effect. n= 18, n= 18, n= 16 and for combined n= 52.

Planting Date	*a*	Confidence Interval*	*b*	Confidence Interval*	*SE*	r^2	*P*
First Planting	3.412	3.208 0.027	0.028	3.616 0.029	0.243	0.993	0.000
Second Planting	5.104	4.831 0.017	0.018	5.378 0.020	0.306	0.987	0.000
Third Planting	1.290	3.843 0.022	0.026	8.920 0.130	0.226	0.983	0.000
Combined	4.708	4.013 0.020	0.022	4.518 0.021	0.55	0.958	0.000

**Calculated at the 0.05 level*

Some similar findings have been reported for differences in the duration of the phenological periods across sowing dates which were adequately described by differences in temperature. Using thermal time, Muchow and Carberry (1989) obtained no effect of time of year on the relationship between leaf appearance and thermal time, nor between fully expanded area of each leaf and leaf number, provided that account was taken of differences in total leaf number across sowing dates. Under a field experiment of maize in Northern Europe (45°24′N; 75°43′E) the leaf tip appearance rate and elongation rate (for leaves 6, 9 and 12) were evaluated over successive periods of 3-4 days and the mean leaf tip appearance rate varied from 0.17 to 0.22 leaf tip per day. The mean leaf elongation rate varied from 10 to 21 mm/day for leaf 6 and from 29 to 58 mm/day for leaf 9 (Giauffret, Bohomme and Derieux, 1995).

4.3.2.7 Plant height in maize

The progression of plant height during the early growth stage over the three planting dates is presented in figure 4.16. The typical sigmoidal shape was very prominent for the first planting, starting at 10 cm at day 12 after planting and reaching a maximum average of 66 cm at 38 days after planting. This constituted an average height increase growth rate of 3.5 cm d^{-1} ± 0.9 cm d^{-1} from 27 to 35 days after planting, i.e. when the plant was growing rapidly.

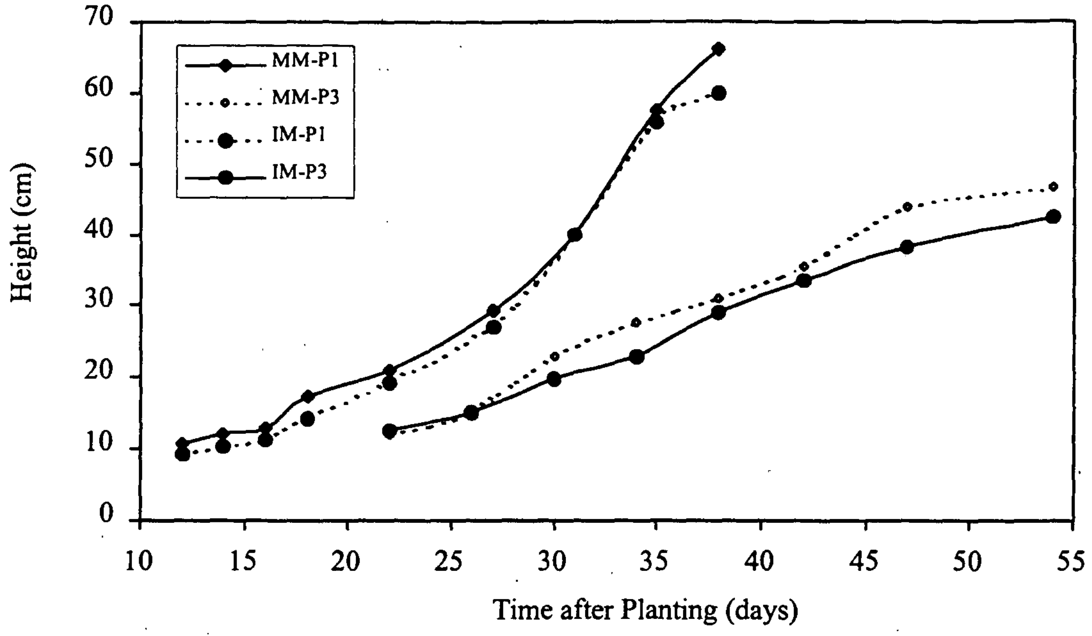


Figure 4.16 Changes in plant height during the early vegetative growth stage of a maize crop after planting dates for first and third planting.

There was no effect of cropping system on height at any of the planting dates. The average growth rate for the third planting from 30 to 47 days after planting was 1.1 cm d^{-1} ± 0.3 cm d^{-1}. The height of maize in the third planting was less and growth slower. To reach an average of 44 cm required 54 days, whereas in the first planting the height reached 66 cm after 38 days. This is probably due to lower temperatures in the third planting date. To assess the effect of temperature on maize plant height a linear regression equation was fitted to data of each planting date as a function of thermal time (Figure 4.17).

Linear regressions were plotted against the thermal time axis to simplify comparison of plant height between planting dates (Table 4.5). The result showed a strong correlation, which stressed the high response of plant height to temperature. There were significant differences (at the $p < 0.05$ level), according to the T test procedure, in slope between planting dates (Table 4.5). The correlation of both plant height and leaf number to temperature indicated that the internode length definitely has a large influence on the height of the crop.

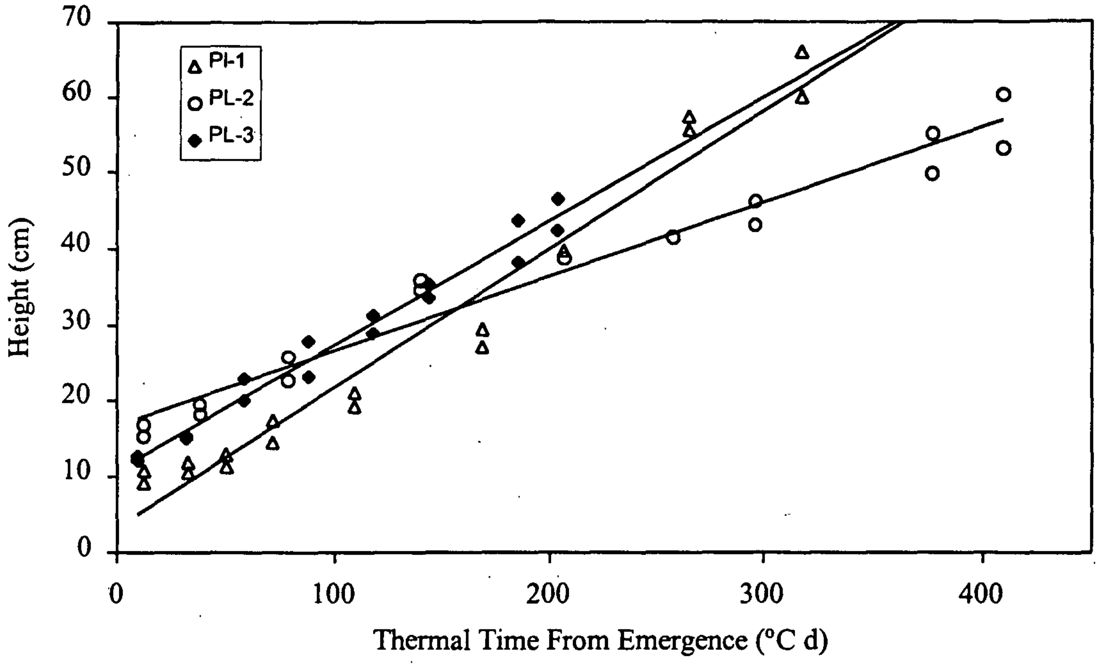


Figure 4.17 Plant height as a function of thermal time (°C d, $GDD_{10,\ 30}$) from emergence, for first planting (△), second planting (o) and third planting (♦). The solid line represents the result of the linear regression slope of the data.

Table 4.5. Linear regression equation of plant height as a function of thermal time from emergence (°C d). The data corresponds to the first, second and third planting dates. n= 18, n=18, n=16 and for combined n= 52.

Planting Date	*a*	Confidence Interval*	*b*	Confidence Interval*	*SE*	r^2	*P*
First Planting	6.558	6.006 0.063	0.066	7.110 0.069	0.659	0.991	0.000
Second Planting	4.926	2.959 0.037	0.045	6.893 0.053	2.020	0.899	0.001
Third Planting	8.095	7.035 0.075	0.084	9.155 0.082	1.057	0.969	0.000
Combined	8.601	6.830 0.036	0.046	0.371 0.055	3.855	0.661	0.023

* *Calculated at the 0.05 level.*

4.3.2.8 Leaf area index and biomass production for maize

In the first planting the increase in leaf area index (LAI) up to 23 days after planting was small in both cropping systems for maize, but a rapid increase occurred between 33 and 49 days after planting (Table 4.6).

Table 4.6 Change in Leaf area index and biomass production (g m^{-2}) in the early growth stage for three planting dates: (a) for sole-crop maize and (b) for inter-crop maize.

First Planting			**Second Planting**			**Third Planting**		
DAP	LAI	Biomass	DAP	LAI	Biomass	DAP	LAI	Biomass
a) Sole-cropping maize								
23	0.06	2.07	32	0.18	11.48	51	-	7.36
33	0.29	21.13	43	0.58	41.06			
49	0.69	76.43						
b) Inter-cropping maize								
23	0.05	1.52	32	0.10	6.48	51	-	5.24
33	0.27	17.90	43	0.48	43.79			
49	0.61	64.65						

DAP days after planting, LAI leaf area index

This agrees with findings of Mukhala (1998), as the LAI of sole-crop maize increased rapidly 36 days after planting and Watiki *et al.* (1993) who found that maize inter-cropped with cowpea increased rapidly between 20 and 43 days after planting. They observed that there was a higher LAI in sole-crop than in inter-crop maize. Similarly, in this experiment the LAI was slightly higher in the sole-crop relative to the inter-crop.

Even though the available data was too little to determine and analyse the effect of temperature in terms of thermal time on LAI, it appeared from superficial observations that there was some difference between the planting dates, as the temperature varied. Similar results for leaf growth in maize (Muchow and Carberry, 1989) suggested that the relationship between total leaf area per plant and thermal time was significantly different with respect to sowing dates under full irrigation. This was associated with differences in total leaf number for different sowing dates and consequently a difference occurred in final leaf area per plant. Since leaf area per plant cannot be predicted solely from thermal time, it is necessary to consider the component processes of leaf appearance as a function of thermal time and individual leaf area as a function of leaf number. More generally, however, temperature during early vegetative growth may influence canopy size through its effect on leaf number (Pearson, 1975).

In the same way as the leaf area, the dry matter distribution in the maize sole-crop showed higher accumulation of biomass, except that during the 43 days after planting the second planting showed the reverse (Table 4.6). The accumulation of dry matter was very low in the third planting due to lower temperatures with an average of 11°C minimum and 21°C maximum temperatures. In contrast, in the second planting the accumulation of dry matter was nearly half of that of the first planting though the average minimum and maximum temperatures were much closer to the previous planting date. But during the growing period the temperatures reached the range of 31 - 35°C. In this case, when the temperatures rose above the optimum so that the crops were probably too stressed to process their regular expansion and development.

4.4 Conclusion

This study provided several simple analysis relationships of leaf growth to describe the influence of temperature on maize sole- and inter-crop for different planting dates. Reference to the weather data in figure 4.1, shows that temperatures were higher during January during the second planting date, with a monthly mean maximum of 30.4°C, while in the third planting the temperature was lower with a mean maximum temperature of approximately 21°C during April.

From the data presented in the study it was apparent that leaf length increase was rapid during the first planting dates but the increment of leaf growth became slow with nearly constant growth rate during the second planting date. This was due to the high temperature effect, with the result that the crops were exposed to heat stress at the later growing period of the early growth stage. This is clearly illustrated by the leaf length and growth rate of leaf 5 in figure 4.10. This result agreed with maize crops whose growth was inhibited at 36°C (Squire and Ong, 1983). There were also some differences among the cropping systems, with higher growing rate in the sole-cropping systems. On the other hand, on the third planting dates the growth was slow with minimum relative growth rate because of lower temperatures during that period. The other growth variables (leaf number, plant height, leaf area and biomass production) also displayed similar responses to temperature. Muchow and Carberry (1989) clearly illustrated the need to consider the components of growth variables as a function of leaf number through individual area.

Throughout the comparison of the planting date, the use of chronological and thermal time of leaf growth for sole- and inter-crop has proved useful in the analysis using the Richards function, when the temperature showed differences between the planting dates. The leaf length over various temperatures as a function of thermal time gave a sigmoid type of growth curve. The result of the analysis showed that the higher accumulation of thermal time (°C day) occurred during the second planting but the growth was lower than the first planting dates, due to temperatures exceeding the optimal, causing heat stress on the crops. On the other hand, leaf growth for different growing processes was linearly related to temperature, for temperatures higher than 10°C and lower than 30°C during the growth period. This work agrees with the best equations for predicting growth on the basis of thermal unit utilizing a base temperature of 10°C and optimum of 30°C (Cross and Zuber, 1972).

CHAPTER 5

FIELD MEASUREMENTS OF LEAF GROWTH FOR SOLE- AND INTER-CROP BEANS IN RELATION TO TEMPERATURE

5.1. Introduction

It must be borne in mind that monocotyledonous and dicotyledonous leaf growth are different so that one should not necessarily expect comparable results from maize and beans. Hsiao and Jing (1985) explained that the spatial variations and developmental history of the broad leaves are challenging to analyze, even if the leaf changes shape and physiological properties in a perfectly predictable way. The growth of beans, unlike monocot plants (maize), is limited to the formation of new shoots developing from quiescent buds of basal nodes. Many previous studies, models and analyses provide estimates of leaf growth by considering the production and distribution of dry matter (Dennett, 1975). The rate of increase in leaf mass can be found by calculating the mass of the leaves capable of further growth and using a temperature dependent relative growth rate (De Wit, Brouwer and Penning De Vries, 1970).

Details of the experimental sites, cropping system, measurements and meteorological conditions during the experimental period have already been provided in the previous chapters. The results obtained in this study on dry bean (*Phaseolus vulgaris*) as a sole-crop and together with maize as an inter-crop with different planting dates are used to assess the temperature variations for leaf growth during the early growth stage.

In the same way as in the previous chapter the influence of temperature on bean leaf growth was analysed using different methods with planting date and cropping system variations. To estimate the effect of temperature in terms of thermal time on leaf growth, the growth curve fitting method (Richards' function model) was also applied to individual leaves.

Therefore the main objective of this study was to develop a temperature function and relate it with the leaf growth during the early growth stage of sole-beans and beans inter-cropped with maize.

5.2. Experimental Procedures

Measurements were made of leaf length at daily intervals, since smaller interval measurements of the rate of leaf growth vary considerably during a daily cycle (Digby and Frin, 1985). Leaf length was taken as the straight-line distance along the midrib of the leaf from the leaf tip to the junction of the blade and the petiole. A ruler was used for the measurement. Daily measurements were continued on the middle trifoliate leaf until at least three consequetive measurements were equal or displayed no appreciable (i.e. negligible) growth.

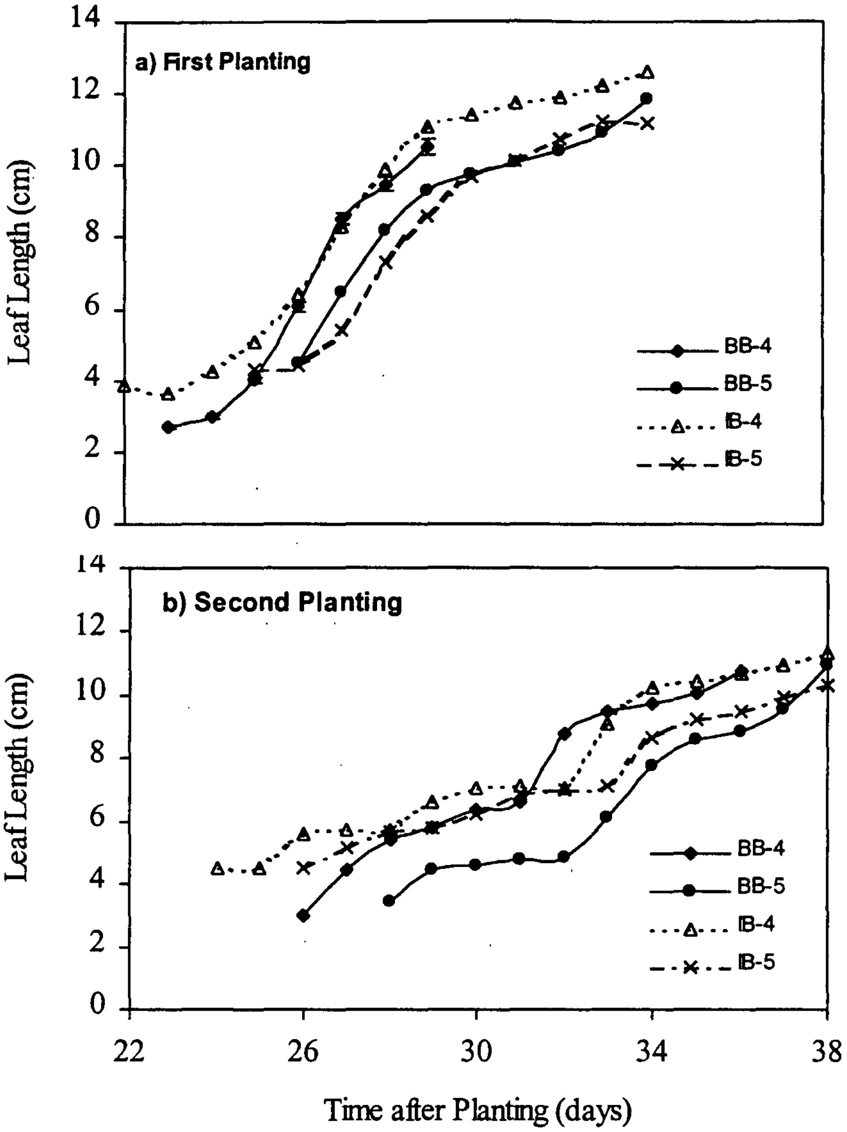
Other measurements made were leaf number, plant height, leaf area and biomass production for both sole- and inter-cropped beans during the early growth stage of all three planting date experiments. The calculations of leaf growth rate and relative growth rate were performed from the daily leaf length measurements. Some attempts were also made to apply the Richards function model as a function of thermal time after time of emergence.

5.3 Results and Discussion

5.3.1 Beans leaf growth for sole and inter-cropping systems

5.3.1.1 Beans leaf length

During the first planting the lengths of leaf 4 and 5 increased in the form of a sigmoid curve without large differences between the cropping systems (Figure 5.1a). Initially the growth was slow then after a few days the growth increased linearly and finally remained stable. In the second planting the shape of the growth curves was different from those of the former planting. Due to some variations in temperature it appears to have two sigmoidal cycles with a 'plateau' between them during the extremely high temperature periods (Figure 5.1b).



**The range of standard deviation (std) for leaf 4 and 5 in first and second planting.

Cropping systems	a) First Planting		b) Second Planting	
	Leaf-4	Leaf-5	Leaf-4	Leaf-5
Sole-crop	±0.92-±1.84	±0.81-±1.62	±0.84-±162	±0.75-±1.50
Inter-crop	±1.33-±191	±0.98-±2.01	±0.65-±1.32	±0.65-±1.20

Figure 5.1 Bean leaf length (leaf 4 & 5) of sole and inter-crop for first planting (above) and second planting (lower) as measured from the end of midrib straight to the leaf tip. All the points are means of 15 sample plants in each cropping system and sowing dates. The standard deviation (Std) is summarized in the above table**.

From 26 - 32 days after planting (on second planting) the maximum temperature was in the range of 28.2 - 33.3°C and the growth was impeded but when the temperature again decreased to about 23 - 24°C the leaf growth continued.

Therefore the length of the leaves for the second planting from about 26 days after planting seemed to be retarded due to heat stress periods.

The final length in both planting displayed some similarities but used a different time period to attain that size. In planting one, to reach 10.5 - 12.6 cm took about 34 days but in the second planting 38 days after planting the leaf length reached a maximum of 10.3-11.3 cm. Dale and Milthorpe (1983) explained that the temperature can exert a strong influence on the rate and duration of leaf growth, as well as the rate of leaf appearance and also the size of mature leaves. On the contrary Gallagher (1985) was uncertain about the nature of the response of leaf expansion rate to temperature but cited some other workers results on the concept of thermal-rate advocated by a linear response of expansion rate to temperature.

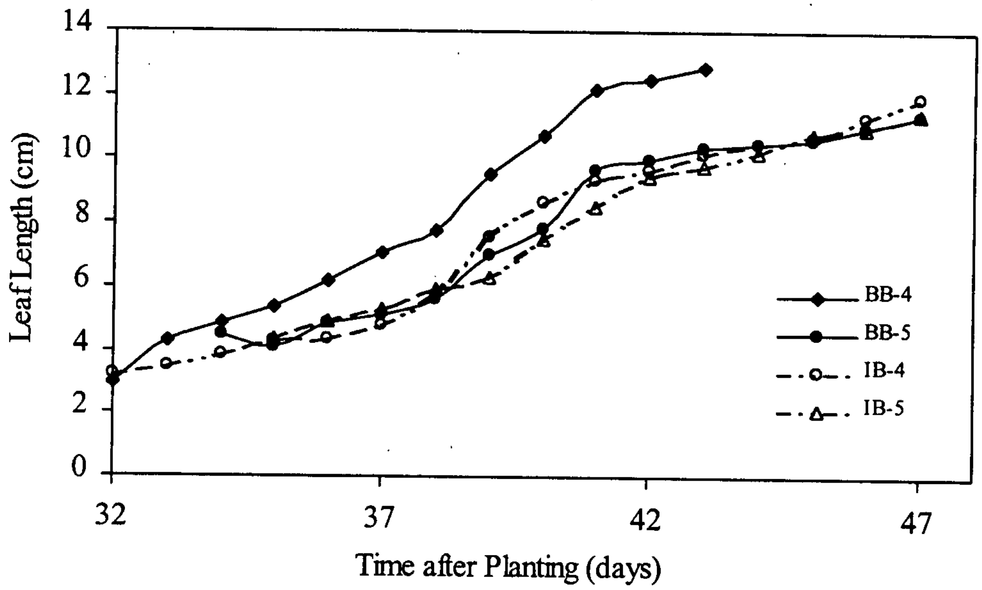


Figure 5.2 Bean leaf length (leaf 4 & 5) of sole and inter-crop for third planting as measured in a straight line from the end of the midrib to the leaf tip. All the points are mean of 15 plants in each cropping.

In the third plantings, the daily mean temperature during 32 - 48 days after planting was in the range of 13.0 -17.5°C, and there was delay in emergence as well as for the start of leaf development (Figure 5.2). The leaf growth of leaf 4 and 5 for both cropping systems showed slow increment with slightly higher growth for sole-crop beans leaf 4. In a field experiment with *Vicia faba,* Dennett (1975) found that the mean growth rate increased from 20-30°C. Compensatory changes in duration gave similar final areas at 25 to 30°C, but at 20°C leaves were smaller in size. Therefore the effect of high/low temperatures on the vegetative and early reproductive growth stages of *Phaseolus* may depend on the specific species type and other related environmental factors, such as water stress or low soil fertility.

5.3.1.2 Leaf growth rate

The methodology for determining the growth rate of dicotyledonous leaves takes on a further degree of complexity when the time and duration of events are considered (Digby and Frin, 1985). Even if the leaf changes shape and physiological properties in a perfectly predictable way, expansion is a two-dimensional process (Hsiao and Jing, 1985). But in this study an attempt is made in order to understand the effect of temperature on leaf growth rate by calculating rate from the leaf length measurements. In the analysis two methods were used to compare the three planting dates in both cropping systems. These are in terms of mean growth rate and by using the slope of the linear regression of each fast growing leaf.

Analysis of average leaf growth rate

To calculate the average values, as representing the growth rate for each individual leaf, some attempts have been made to synchronize together the time sequence of all possible leaf numbers. Figure 5.3 illustrates the mean leaf growth rate in sole- and inter-crop systems. In the first planting of sole-crop beans the growth rate was between 0.5 - 1.0 cm day^{-1}. On the second planting only the very first leaf was as low as 0.25 cm day^{-1} and at higher leaf numbers the rate was larger. But the general trend in all three planting dates and cropping systems showed very similar growth rates. For the sole-crop, from leaf 2-6 for all three planting dates the growth rate was about 0.6cm day^{-1} and similarly from leaf 7-10, it was about 0.8 cm day^{-1} (Figure 5.3a). While in inter-crop for leaf 2-6 and leaf 7-10 the leaf growth rate was more widely spread in the range 0.6 – 0.9 cm day^{-1} and 0.8 – 1.1 cm day^{-1} respectively (Figure 5.3b).

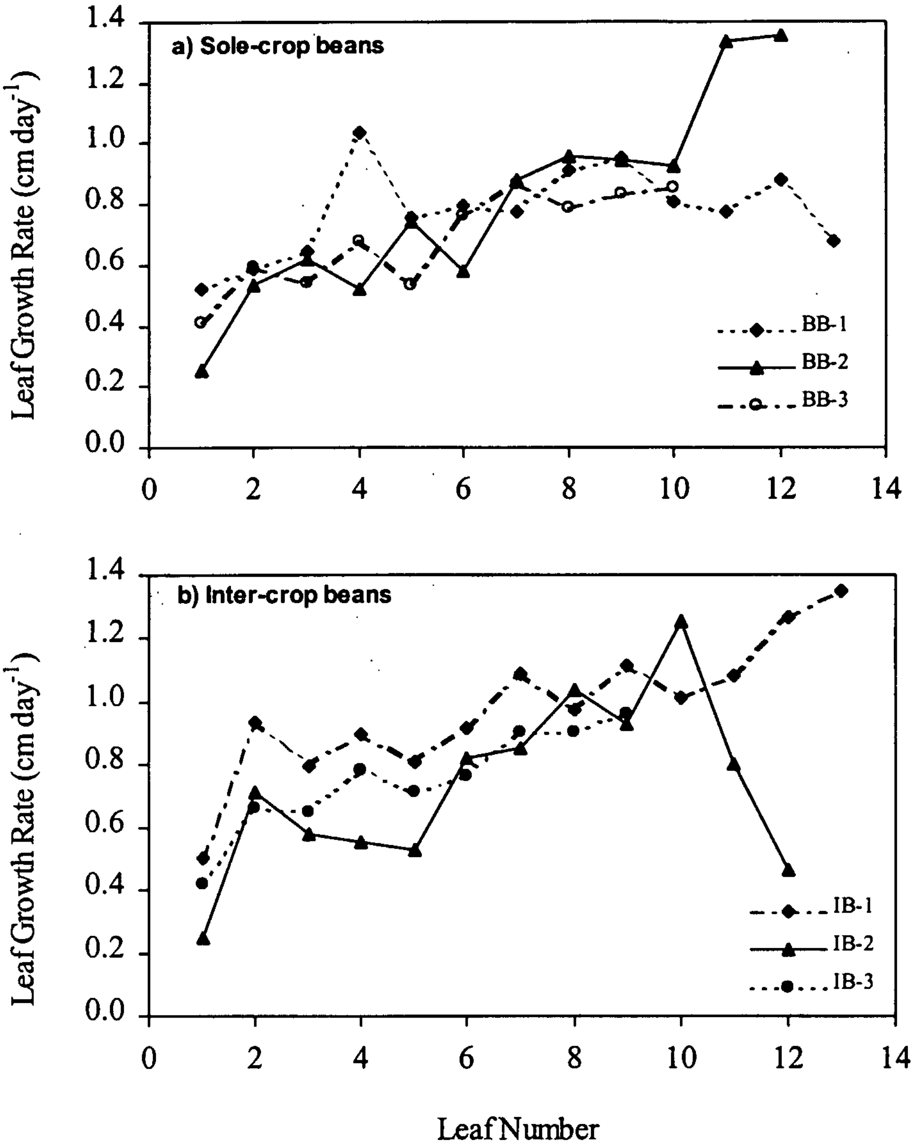


Figure 5.3 Mean leaf growth rate per day (cm day^{-1}) for three planting dates for individual leaves versus leaf number. (a) Sole-crop in the upper figure and (b) for inter-crop the lower figure. Each point is the mean of daily observations of 15 sample plants.

Therefore, the inter-crop leaf growth rate showed slightly higher values and over a wider range relative to sole-crop beans. But the result of leaf 11-13 showed an opposite trend as the rate of the second planting declined sharply from the highest value 1.25 to 0.5 cm day-1 for leaf 12. While in the first planting the rate had increased from 1.0 - 1.35 cm day^{-1}. The higher leaf growth rate exhibited by inter-crop beans were probably due to some shading effects as well as due to well being protected from the wind. Lawlor and Leach (1985) have related such occurrences to water stress of varying magnitude and duration which occur commonly during leaf development by slowing the rate and shortening the duration of leaf growth and hastening senescence of leaves as a water saving mechanism.

Analysis using linear regression slope

In the analysis using linear regression slope to determine leaf growth rate, first planting showed higher rates than third planting but they showed the same trend with almost stable rate from leaf 5-8 and then it started to decline (Figure 5.4a).

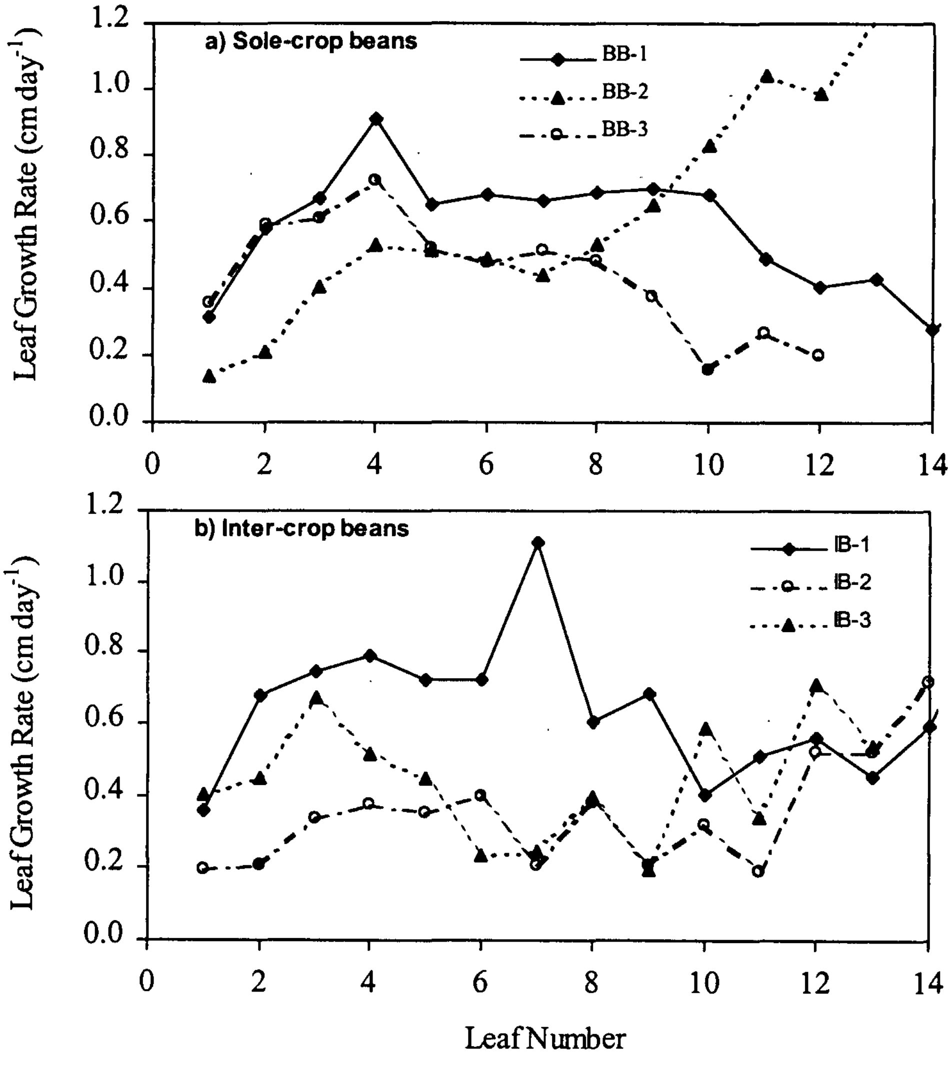


Figure 5.4 Leaf growth rate using the analysis regression slope leaf length in sole and inter-crop systems in three planting dates. (a) sole-crop beans and (b) inter-crop beans.

In all planting dates for sole-crop the leaf growth rate increased steadily from 1-4 but the rate was higher in first and second planting as compared to third planting date. After leaf 4 onwards the second planting showed a similar rate to third planting and after leaf 8 the rate increased linearly as opposed to first planting date. In this case in second planting the rate was stretched from 0.5 - 1.2 cm day^{-1}, whereas in first planting the leaf growth rate decreased from 0.6 - 0.2 cm day^{-1}. These occurrences were due to some temperature changes towards the end of measurement periods or the heat stress in the middle. When at end of first planting the temperature raised the rate appeared to be decrease. While in second planting though the crops were stressed at the middle of measurements, the temperature showed to decrease during end of measurements and the rate started to increase after reaching leaf 8.

In the case of inter-crop beans (Figure 5.4b) the first planting gave the highest values when compared to the other planting dates. But initially until leaf 3 growth rates of all planting dates were increased. After leaf 4 onwards the growth rate of the first and third planting remained constant until leaf 7 but in second planting the leaf growth rate appeared to be declining sharply with leaf number. At leaf 7 the leaf growth rate in the first planting date showed the highest value of about 1.1 cm day^{-1} and decreased to the end. Likewise for second and third planting the leaf growth rate after leaf 7 fluctuates inbetween 0.1 - 0.3 cm day^{-1} and again after leaf 10 stage onwards increased with little fluctuation in between 0.5 and 0.7 cm day^{-1}. No measurements were made of leaf width (laminar width) along the leaf length, as these would have enabled area expansion rate to be calculated. However, some similar results have been reported for field beans by Dennett, Elston and Milford (1979) where the variations of leaf size with position for leaves up to leaf 10 were due to differences in leaf area growth rate. Other results also showed that in field beans the final area increases with position until a point about midway up the stem and may then decline. The pattern may depend upon variety and sowing density and sowing dates (Rajaratnam, 1969).

These two calculation methods used for the analysis of leaf growth rate (Figures 5.3 & 5.4) had some differences during the growth period for all planting dates. However, the analysis that used the approach average growth rate might have great variations due to averaging a wide range of growth rate during various periods. Since the daily growth measurements for each leaf were highly influenced by the temperature changes and other environmental factors, even though some attempt has been made to synchronize the data. So that it might be difficult to consider it as a perfectly representative rate for each particular individual leaf, but on the other hand, it might give some indication of the general trend of the leaf growth rate. In the case of the analysis using linear regression slope, the value (rate) is from the linear portion of each curve of the leaf length. This could be more representative for leaf growth rate as long as the fast growing portions of the leaf grow linearly with time.

5.3.2 Leaf growth responses to thermal time in beans

The work presented here investigated the thermal time for dry beans in sole- and inter-cropping systems in the form of leaf length and used different planting dates to compare temperature variations. Legumes belonging to the tropical tribe, *Phaseoleaes*, generally have mean growth temperatures, which are above the mean day temperature of temperate climates (Sprent, 1982). For this reason it is likely that cool temperatures can be a major factor limiting the growth of *Phaseolus vulgaris* (Austin and Maclean, 1972). On the contrary dry beans is a crop adapted to a moderate climate (Wallace, 1985). By taking into account the variability of temperature during the early growing stages, which can be realized by different environmental variations in cropping systems and for different sowing dates.

It was reviewed that the generalization of many tropical crops are adapted to environments with high temperatures at the early growing season. Therefore, in this analysis, to compute thermal time for dry beans, 10°C was used as base temperature and 30°C as highest (extreme) temperature values, as is the common usage for tropical crops.

Richards function model application for beans

The application and the descriptive ability of the model have already been mentioned in the maize crop section (4.3.2.5). The form of the function and the fitting procedure are as described in Dennett *et al.* (1978) for *Vicia faba* leaf area development. In this analysis the same method was applied by using leaf length of the trifoliate leaf on the main stem of a bean crop from emergence through the early growth stages. Based on this type of analysis, this study had three aims: first, which method (chronological/thermal time) will best describe the effect of temperature variation on leaf growth; second, to allow comparison between sole and inter-crop; and third, whether the response of temperature influenced the leaf growth on specific planting dates. To estimate the correlation between the calculated chronological/thermal time and leaf length, individual leaf growth (leaf 2-9) was used for comparison purposes. The growth of each leaf in the experiment was described with the Richards function equation.

Overall comparison of thermal and chronological time

Temperature effects on leaf growth rate or length were more difficult to detect because there were systematic variations between plants in response to temperatures. According to Robson (1972) the difference in mean growth rate between growing seasons could be explained by differences in radiation and temperature, but other factors may also be responsible. Results of fitting of the Richards function to the data with chronological time and thermal time after emergence are listed in Table A. 4 (Appendix II) and it also illustrates the correlation magnitude shown in figure 5.5.

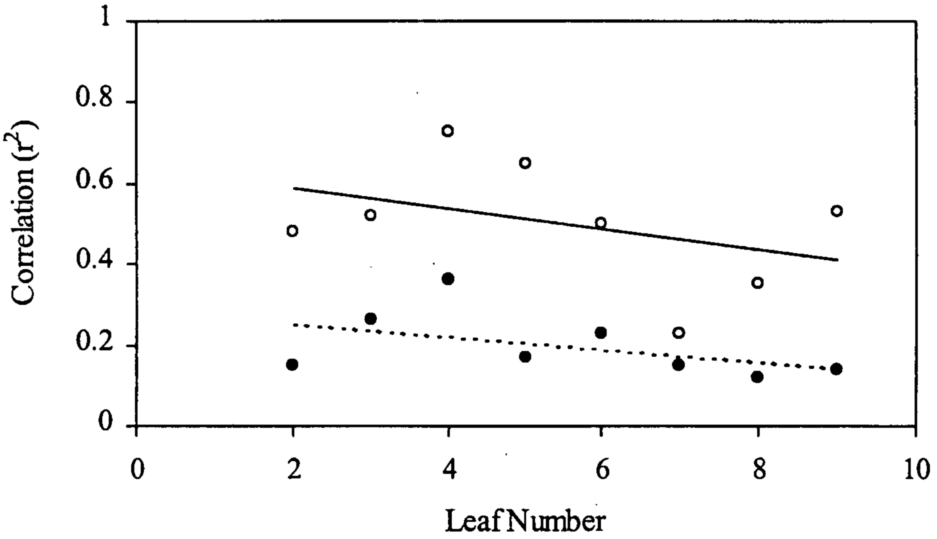


Figure 5.5 The estimated correlation coefficient versus leaf number for chronological (λ) and thermal time series (o) after time of emergence for leaf 2-9 during vegetative stage for the Richards equation.

The r^2 values of the fits were not high compared to maize data set, and showed the opposite result to maize crop. The r^2 values for leaf length of beans obtained by the analysis were in the range of 0.23 - 0.72 and 0.11 - 0.36 for chronological time and thermal time respectively. Therefore in all cropping systems common to both planting dates the estimates of correlation with thermal time had weak correlation, as the r^2 showed low values (Figure 5.5). But it is important to investigate the effect of other environmental factors together with the temperature. However in field studies of the growth of the field beans have demonstrated a statistical correlation between screen temperature in the few days immediately after a leaf unfolded and the duration of the growth and maximum relative rate of expansion of that leaf (Dennett, 1975).

Comparison of relationship to thermal time between planting dates

The temperatures of the three planting dates varied with higher values in January planting and lower in March planting. Therefore, the results from the calculated thermal time and individual leaf length (leaf 2-8) for each planting dates showed strong correlations. The general values of the parameters with the standard errors resulted from Richards' function curve fitting model between planting dates are presented in table A 5 (Appendix II). In the second planting the correlation was stronger, almost all the leaves were correlated with above 0.96 whereas in the first and third planting some of the leaves were correlated to about 0.60 - 0.80.

For statistical convenience all the data were transformed to the form of a natural-logarithmic function with some expectation to have exponential type of growth at the initial stage. The estimation of the linear regression equation for leaf length (*ln leaf length*) in relation to thermal time with coefficient of determination and error probability between the effects for the interaction is presented in table A. 6 (Appendix II). In all leaves to both planting dates the result showed a significant differences (at the $P < 0.05$ level) according to T test. The linear coefficient of determination ranged between 0.63 and 0.95 and most of the treatments showed r^2 above 0.80 correlations. Therefore in general, the relation of temperature based on thermal time and bean leaf length showed high correlation and the confidence interval within the planting dates clearly overlapped each other.

The changes in temperature during the leaf growth seemed to affect the duration of the growth time. In figure 5.6 for leaf 5 the highest degree-days accumulated was during the first and second planting to about 320 and 390 °Cd with slow leaf growth and the lowest were in the third planting estimated to about 205 °Cd. In contrast the highest leaf size in the first planting was required around 150 °Cd while the growth rate declined when the leaf became older. Whereas in third planting despite lower degree-days the leaf growth seems to be faster.

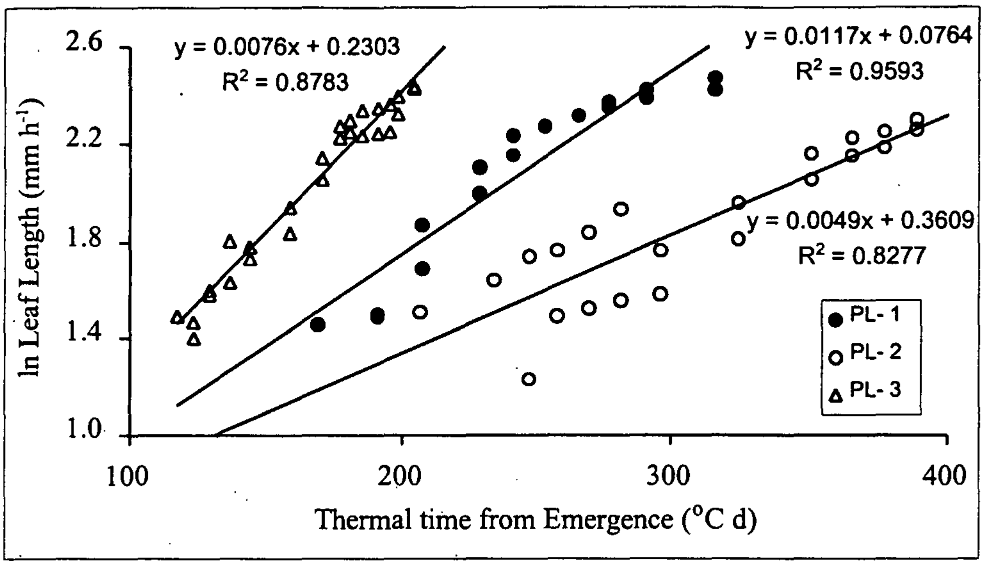


Figure 5.6 Relation between leaf length for leaf 5 and thermal time for days after plant emergence in three planting dates by combining both crop systems. PL- 1, PL- 2 and PL- 3 represent the three planting dates in sequence.

The sensitivity of high temperature for second planting clearly illustrated from the leaf growing duration to attain relatively similar leaf size. In particular during second planting due to high temperatures the plants were shown the exposure to heat stress. The final size of a specific leaf length reached to the maximum of 11.2 cm while in second planting was reached only to about 9.9 cm.

On the other hand the measured data in figure 5.6 it was likely to fit the slope of linear regression with high correlation coefficient (r=0.88, 0.83, 0.96) in the three consecutive planting dates. But to assess the possibility of using one regression line and interception point for all planting dates a 'Bartletts test' was applied. The result showed F-calculated less than F-tabulated, which means insignificant relations or statistically it is impossible to use one regression model. And all the regression lines did not intercept at one point. Therefore, the usage of thermal time in bean leaf length study was not the main ruling or driving force in comparing the planting dates through using 10°C T_{base} and 30°C high limit (T_{max}) temperature.

As evidence from the experiment the final size in the first two trials influenced by the higher temperature experienced during the growth period. The result of McWilliams (1980) in common bean agree with this condition as the high temperature is one of the major environmental factors that limit crop performance in beans, especially when temperature extremes coincide with critical stage of plant development. The common bean is a heat sensitive plant species in which excessive abscission or reproductive organs occur during hot weather (Austin and Maclean, 1972). The rate of growth in bean leaf expansion increased with temperature from 20-30°C but at 35°C decreased to that of the lowest temperature (Wilson and Ludlow, 1968). So it is important to select T_{max} less than 30°C for calculating thermal time for bean crop.

Low temperatures are also a major factor limiting the growth of beans. Thomas and Norris (1977) used leaf growth in selection of cold tolerance bean species. They showed that the growth of leaves as measured by the increase in the length of the lamina to attain the final leaf length at three different temperatures, 15/10, 20/15 and 25/5°C. In this result the development of the leaves (time to reach final leaf length and rate of elongation) was retarded at 15/10°C compared with the warmer temperatures during the vegetative growth phase. In general, to calculate the thermal time for growing bean variety it is important to select the right cardinal temperatures according to the type of variety used. From the experiment it was possible to suggest using lower T_{base} and T_{max} than it has already applied for the calculation (10°C and 30°C) for the dry bean variety Pan 148.

5.3.3 Beans leaf number during early growth stage

During all planting dates the leaf number was counted every 3-4 days during the early vegetative stage. The leaf number increased linearly with time, but on both planting dates the magnitude (rate) of increment was different (Figure 5.7). In first planting the leaf number increased at a faster rate and reached a higher leaf number of 47 and 43 leaves after 38 days after planting on sole- and inter-crop respectively. This result showed that an average leaf number increment rate of 2.8 in sole-beans and 2.5 in inter-crop beans per day from 27 to 38 days after planting.

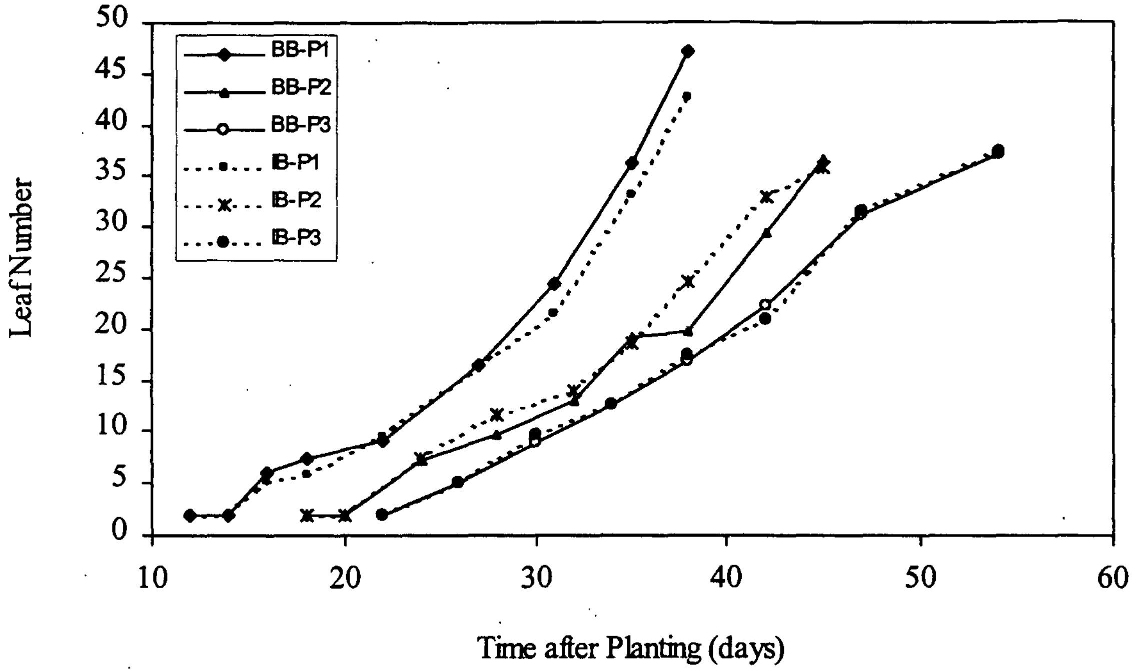


Figure 5.7 Relationship between bean leaf number of visible leaves and time after planting for three planting dates of beans crop as grown in sole and inter-crop systems during the early vegetative growth period. (The symbols BB and IB represent for sole- and inter-crop beans respectively 1,2 and 3 planting dates).

In the third planting the increment in leaf number was very slow and it only reached a maximum of 38 leaves 54 days after planting. The increment rate was about 1.5 leaves per day from 34 to 47 days after planting. Similarly the leaf number increment in the second planting was slow but markedly faster than that of the third planting date. The rate of increment was 1.7 per day from 35 to 45 days after planting. In general variation of temperatures in planting dates seems to have the largest effect on the leaf number and the duration of growth. Leaves are produced more rapidly as the temperature approaches 20 or 30°C (Fukai and Loomis, 1976; Dennett *et al.*, 1979). The duration of leaf growth, however, often increases with decrease in temperature below 20-25°C (Auld *et al.,* 1978; Dennett *et al.*, 1979). The expansion of leaf surface also depends on a number of factors including rate of leaf production (leaf number) and senescence. Rawson and Turner (1982) clearly showed that the leaf area is dependent on the leaf number, on the duration of expansion and the expansion rate of individual leaves.

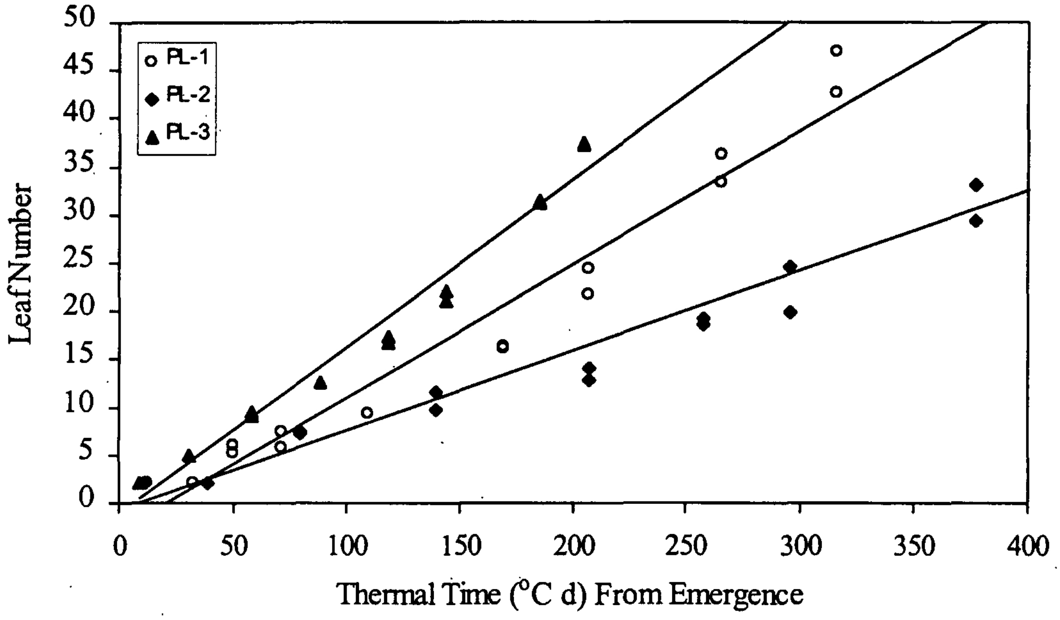


Figure 5.8 Leaf number as a function of thermal time (°C d) from emergence for three planting dates, PL-1 (o), PL-2 (υ) and PL-3 (σ). The result was obtained by combining the data of all the cropping systems.

To assess the effect of temperature on leaf production during the early growth stage on each planting date the data was expressed as the slope of the linear regression of leaf number against thermal time ($GDD_{10,30}$). These slopes were used to construct temperature response curves on the three different planting dates for various temperatures (Figure 5.8).

Results are presented in table 5.1. There was strong correlation with respect to the effect of temperature on leaf number increment. Statistically there were a significant difference between leaf number and thermal time (at the $P < 0.05$ level) according to the T test procedure. The results of leaf number with thermal time seemed to contradict with the leaf length measurements in beans, but physiologically leaf number has a wide possibility to increase quantitatively with extending growing period. A similar phenomenon has been observed in different hybrid varieties of sunflower (Villalobos and Ritchie, 1992) where the leaf number increased from 7 to 20 leaves with increment of temperatures during the early development.

Table 5.1 Linear regression equation of leaf number of beans as a function of thermal time from emergence (°C d). The data corresponds to the first, second and third planting dates. (n=18 for each treatment).

Planting Date	*a*	Confidence Interval*	*b*	Confidence Interval*	*SE*	r^2	*P*
First Planting	-2.97	-5.518 0.124	0.138	-0.427 0.153	3.04	0.961	0.000
Second Planting	-0.802	-2.802 0.075	0.083	1.197 0.091	2.240	0.967	0.000
Third Planting	-1.180	-3.086 0.158	0.173	0.726 0.189	1.901	0.977	0.000
Combined	1.887	-1.039 0.080	0.096	4.814 0.112	6.301	0.756	0.000

** Calculated at the 0.05 level.*

5.3.4 Plant height in beans during early growth stage

Bean plant height increase during the early growth stage was greater during the first planting dates than the third planting date (Figure 5.9). During the first planting, over the first 22 days after planting sole-crop beans were slightly taller than inter-crop but eventually continued their growth to similar heights. Regarding the third planting the sole crop beans were slightly taller than inter-crop throughout the growing stage. The trend in both planting dates was similar but varied in elongating duration.

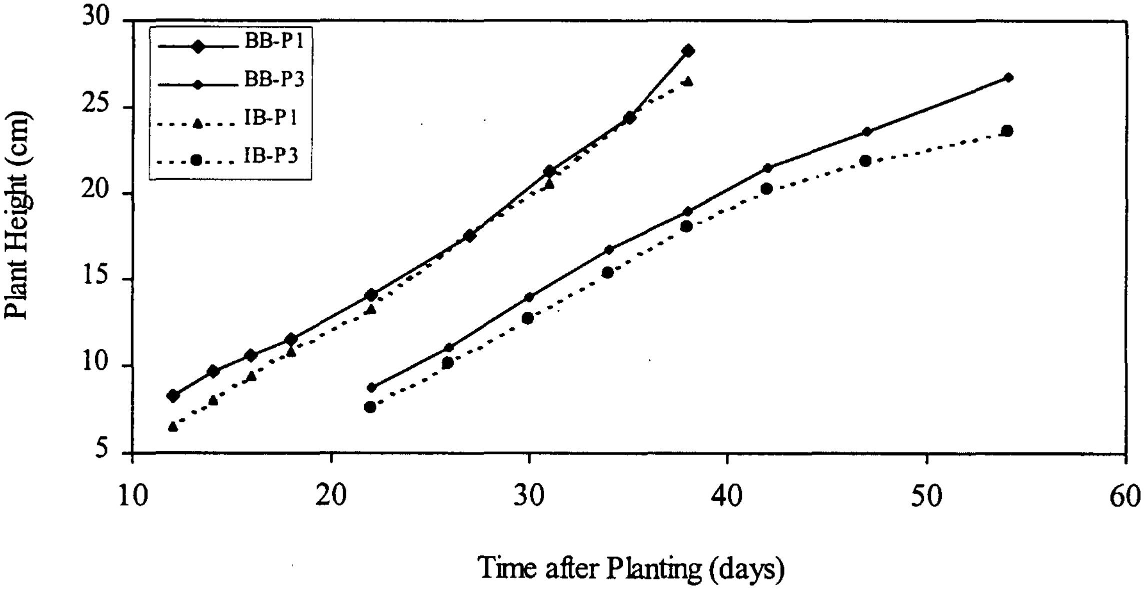


Figure 5.9 Change in plant height of beans for the first and planting dates against days after planting. The dotted line represents the inter-crop and the solid line represents the sole-crop.

The average height growth rate of beans at first planting date from 22 to 35 days after planting was 0.84 ± 0.11cm d^{-1}, whereas in the third planting date the average rate of height growth elongation was about 0.57 ± 0.14 cm d^{-1} from 30-47 days after planting. Elliot and Miller (1974) showed that the stem of *Phaseolus sp*. elongates according to the degree of shading, as is common for most plants. Therefore, by measuring plant height during active vegetative development one can assess the degree of shading imposed by the associated inter-crop. But in this experiment the measurements were done only at early growth stage, that is before the plants were affected by shading from the maize crop.

5.3.5 Beans leaf area index and biomass production

Leaf area index data for first planting at the early growth stage is listed in table 5.2. From the plotted lines, it was clear that an increase in LAI up to 49 days after planting was higher in sole-crop and the difference was greater at during the last date of measurement than at 23 and 33 days after planting.

Table 5.2 Change in Leaf area index and biomass production (g m^{-2}) in the early growth stage for three planting dates; (a) for sole-crop beans and (b) for inter-crop beans.

First Planting			**Second Planting**			**Third Planting**		
DAP	LAI	Biomass	DAP	LAI	Biomass	DAP	LAI	Biomass
a) Sole-cropping beans								
23 33 49	0.08 0.41 0.71	3.35 24.43 59.28	32 43	0.11 0.21	7.19 14.06	51	-	49.64
b) Inter-cropping beans								
23 33 49	0.08 0.29 0.48	3.07 15.50 42.59	32 43	0.12 0.38	8.33 31.27	51	-	35.29

DAP days after planting, LAI leaf area index

Monteith and Elston (1985) found that LAI can be treated as the product of the number of leaves per unit ground area and their vegetative size. During the early stage of growth in an arable crop, both these quantities increase with time so that leaf area increases rapidly. At least in a favourable environment, the density of sowing usually ensures that sufficient foliage is generated within a few weeks to intercept more than 90% of the incident radiation. At this stage the LAI has a maximum value and tends to decline thereafter for a number of reasons. However, temperature has a substantial effect on the area of leaves, as well as upon their rate of initiation and appearance.

For example, Dennett, *et al.* (1979) found that at daily radiation of less than about 19.5 MJ m^{-2}, the final area to which *Vicia* leaves grew increased with temperature. At higher irradiance, however, increasing temperature tended to reduce final leaf area. In the study of maize/bean inter-crop of growth and light interception it was also found that there was a decrease in leaf area index, average growth rate and mean net assimilation of beans growing in the inter-crop as compared to sole-crop (Gardiner and Craker, 1981).

During the early vegetative growth stage of beans the above-ground biomass accumulation was observed to be higher during the first planting date, and followed by the third planting date, 51 days after planting (Table 5.2). In comparing the dry matter production of sole and inter-crop beans, it was observed that the sole-crop beans showed higher accumulation than inter-cropping, except on the second planting, the result was reverse on both 32 and 43 days after planting. The relationship between biomass per square meter and planting dates did not exhibit maximum accumulation on the higher temperature planting dates (second planting date) due to heat stress effects. On the other hand biomass production appeared to be higher in the third planting date (at relatively lower temperatures) but the accumulation of the biomass was too slow.

5.4 Conclusion

Temperature has strong effects on crop growth and development with respect to the bean crop. This effect often exerts a primary influence on selection of cultivars and planting dates at a given site, even though farmers and researchers may not recognize this influence. The result was obtained from the experiment carried out on beans in sole and inter-cropped systems and on a series of planting dates, which covered only the early growth stage. During first planting, the leaf length showed a typical sigmoidal curve without large differences in the cropping systems, while in the second planting the growth was slower in comparison with that of the former planting (Figure 5.2). But in the third planting, following the delay in emergence, the leaf growth was faster compared to the high temperature planting dates. The final dates. The final leaf length of the bean crop decreased from leaf 4 onward. In most cases the leaf growth of sole-crop was higher than inter-crop. Therefore the general trend in all planting dates pointed to a high growth rate with increasing leaf number but a decrease in the final leaf length with increasing leaf number.

There are standard values of cardinal temperatures for particular cultivars. This study has helped to extend the estimation of threshold temperature. The application of thermal time and descriptive ability of the Richards function fitting model appeared to be an effective method of analysis. The result showed that poor relations of thermal time and leaf length by taking 10 - 30°C as a cardinal temperature. Therefore it is suggested to use less than 30°C as the threshold temperature to calculate thermal time. The temperatures of three planting dates had shown some variations with higher thermal time accumulation during second planting date and lower with the third planting date albeit with relatively faster growth rate. The relationships between different growth variables and thermal time after emergence showed a possibly linear correlation.

The key consideration in the effective use of temperature for bean growth is that it exhibits less tolerance to high temperature. In other words the bean crop is more sensitive to high temperatures than the associated maize crop.

CHAPTER 6

LEAF EXTENSION RATE IN MAIZE IN RELATION TO LEAF TEMPERATURE

6.1 Introduction

In most experimental systems it is difficult to uncouple the response of leaf extension rate to temperature and other factors, such as solar radiation and water vapour saturation deficit. However, Ong (1983a & b) described that in the relationship between leaf extension and temperature it is important to monitor extension over a short period because of fluctuating weather conditions. Several previous studies attempted to relate leaf extension to other crop growth variables (Peacock, 1975; Gallagher, 1979; Squire and Ong, 1983; Walker, 1988) and modified the concept to incorporate it into different physiological processes. For a detailed analysis and to account for the short-term temperature variations on leaf extension an hourly rate measurement during the active growing period is important.

Therefore the main objective of this study was to use a field measurement method for measuring leaf extension on an hourly basis with reasonable precision and to be able to recognize errors in the field. The other objective was to investigate the diurnal temperature variations in warm (high temperature) and cool planting dates on both cropping systems through hourly leaf temperature measurements.

6.2 Experimental Procedure

In this experiment a semi-mechanical auxanometer (growth transducers) suitable for measuring hourly rates of leaf extension was used to measure the leaf extension rate (LER) of maize crops in the field for sole- and inter-cropping systems. Similar auxanometers measuring LER for grasses and cereals have been described by many workers (Gallagher and Biscoe, 1979; Acevedo *et al.*, 1971; Ong, 1983b; Busso and Richards, 1992; Inman-Bamber, 1995; Salah and Tardieu, 1995). The measurements were taken over three days during February (18th-20th) when the temperature was expected to be high and late on the third planting (April 27th-29th) when the temperature was lower. The measured LER was related directly to leaf temperatures, which was measured by attaching the copper-constantan thermocouples to the similar exposed leaf during the measurement time.

All necessary equipment calibration and frequent adjustments with close monitoring was done to minimize the error of measurements, since the transducers and thermocouples are sensitive enough to obtain reliable data measurements. Auxanometer outputs and the leaf temperature variables were monitored by appropriate sensors connected to a data logger.

6.3 Results and Discussion

6.3.1 Measurements of leaf temperature

To monitor leaf temperature of both cropping systems, thermocouples were moved up in the middle canopy level on the underneath side of the leaves in different selected plant samples on each plot.

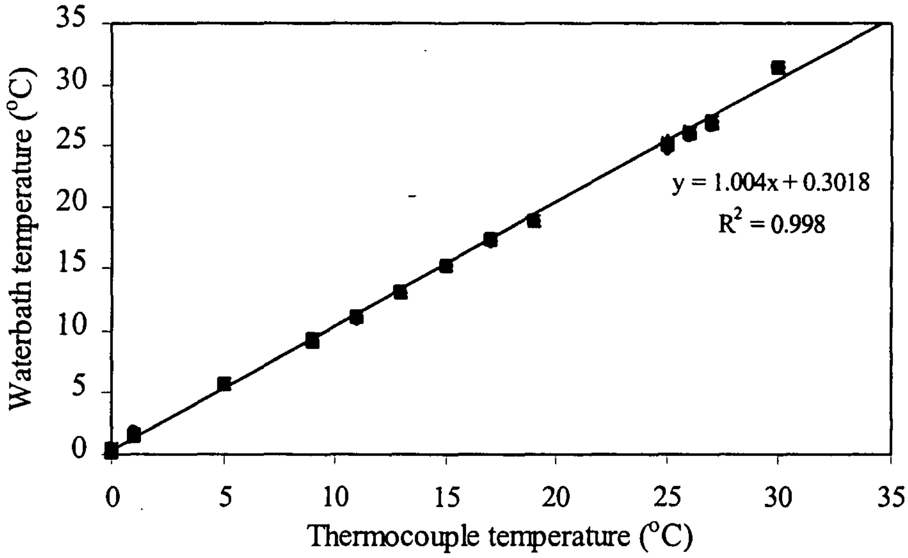
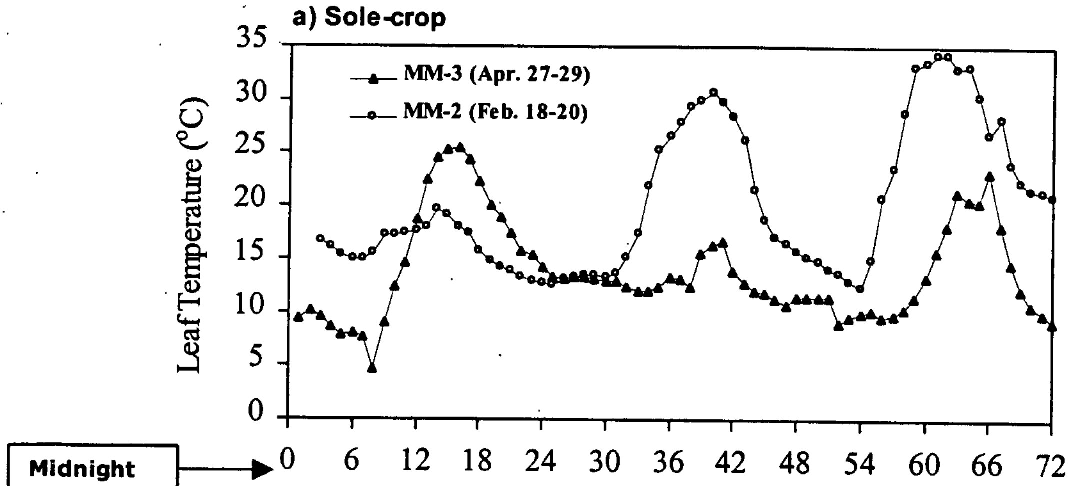


Figure 6.1 Calibration curve obtained for ten different thermocouples in the waterbath. The linear relationship of the thermocouples and waterbath temperature confirmed a strong correlation (R^2= 0.998).

The copper-constantan thermocouples were calibrated at different temperatures for each thermocouple in the range of 0 to 35°C. Figure 6.1 presents the calibration curve of the bath temperature and 10 thermocouples in the waterbath. The resultant regression illustrates the accuracy of the instruments (r^2= 0.998).

a) Sole-crop



b) Inter-crop

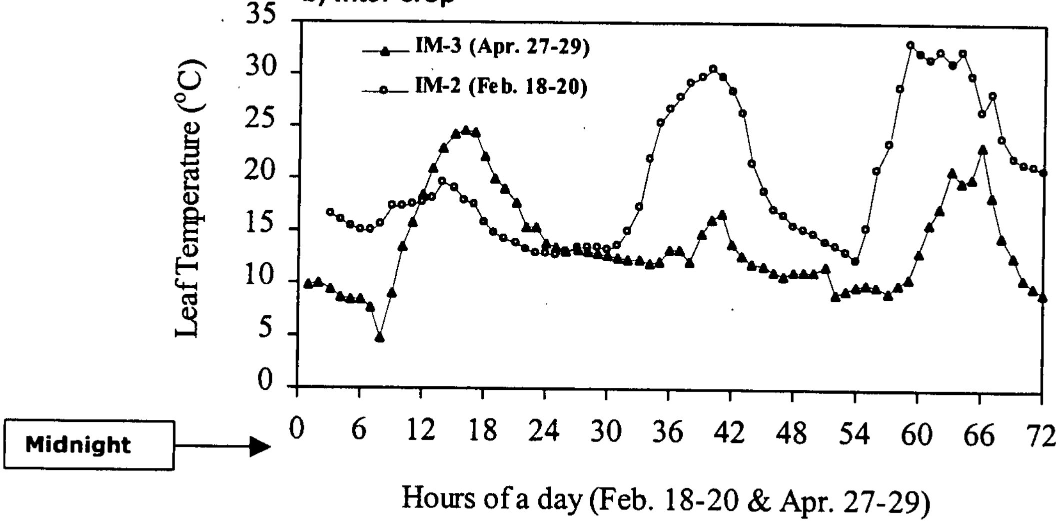


Figure 6.2 Hourly leaf temperature measurements for three days (Feb. 18-20 & Apr. 27-29). MM-2, IM-2 represents second planting and MM-3, IM-3 indicates third planting. The upper figure shows sole-crop and the lower figure inter-crop maize.

Diurnal variations in leaf temperature of the cropping system as measured on Feb. 18-20 and Apr. 27-29, 2001 are presented in figure 6.2. During the second planting date (Feb 18-20) the leaf temperature was higher than third planting time (Apr. 27-29) except during Feb 18 after midday the leaf temperature was lower due to rainfall (Figure 6.2).

The average difference of leaf temperatures in the former planting date was 7.7°C higher than later planting. However, the night leaf temperatures were much closer on both planting dates. On Feb. 20 after midday (12-16 hours) the sole crop maize leaf temperatures became higher by 0.8 - 2.7 °C. During this period the field was wet due to 51 mm of rain over the three previous days so that the temperature on Feb. 18 was low. Tardieu, Granier and Muller (1999) showed that leaf extension rate varied with leaf temperature, photo flux density, evaporative demand and soil water status. However, leaf expansion rate is considerably reduced by mild water deficit, which may not affect photosynthesis.

The relationships between leaf temperature and air temperature were not studied in the experiment. The thermocouples were simply attached to the abaxial side of the leaf, without using a radiation shield as the thermocouple was shaded by the leaf. During the measurement time the crop canopy did not cover the soil surface completely, as the experiment was conducted only in the early growth stage. As cited by Idso, Reginato, Jackson and Pinter (1981) a report of Linacre (1964) showed that foliage temperature of well-watered, thin leaved plants exposed to bright sunlight would be greater than air temperature below a critical value of 33°C and less than air temperature above that value. Shortly thereafter, basing these remarks on certain theoretical energy balance considerations, Gates (1968) stated that the specific equivalence point of 33°C could not be universal but must depend on other factors.

6.3.2. Auxanometer calibrations and errors in the field measurements

After the final installation performed at the field level, each auxanometer (12) was calibrated by measuring the displacement of the armature. The output signals from the auxanometer changes from the highest 2500mV (millvolts) corresponding to full stroke displacement of armature giving 20 mm V^{-1}. As rate of leaf extension measured in the field in the order of 2 mm h^{-1}, the change in output is only 100mV or so compared with the possible maximum signal of 4000 mV. The precision required to measure these small changes in a large output signal is easily obtained using an accurate datalogger. The signals were recording at the end of each hour, using a computer-controlled datalogger.

The calibration factor, (C_f) was calculated from the initial and end reading output signal differences of constant length (100mm) for each auxanometer in mm mV^{-1} (Table 6.1). The hourly rates of leaf extension (LER) were calculated for each auxanometer as follows:

$$LER = C_f (V_{initial} - V_{end}) / \Delta t \qquad (6.1)$$

Where $V_{initial}$ and V_{end} are the output at the measured beginning and end of each period of time (t) and multiplied with C_f the calibration factor (mm mV^{-1}) for auxanometer 'n', then divided by the time interval, Δt. The calibration factor was in the range 0.241- 0.137 mm mV^{-1} with standard deviation of ± 0.029.

Table 6.1 The calibration factor (C_f) of each auxanometer in mm mV^{-1} calculated from the 100mm displacement in measuring the initial and end output signal differences with standard deviation 0.029.

Auxano. No	Intial Reading (mV)	End Reading (mV)	Difference (mV)	Calculated calibration factor, Cf (mm mV^{-1})
1	1711.1	2439.0	729.9	0.137
2	820.6	1521.4	700.8	0.143
3	1369.2	2091.7	722.5	0.138
4	1224.1	1960.7	736.5	0.136
5	1361.4	1775.6	414.2	0.241
6	1791.4	2498.3	706.9	0.141
7	367.4	1058.6	691.2	0.145
8	1239.7	1916.0	676.3	0.148
9	1194.2	1918.8	722.6	0.138
10	1348.3	2043.8	695.5	0.144
11	1707.6	2377.6	670.0	0.149
12	1456.0	2169.6	713.5	0.140
Mean	-	-	681.5	0.150
Std.	-	-	86.59	0.029

LER could have been increased to some extent when tension on leaf was at or near maximum. This should not detract from the value of the transducers as a means of determining the short time interval of leaf extension rate, but a correction would be necessary when using the data in an absolute sense. The instrument should exert a minimum tension on the leaf to avoid deformation and excessive stress on the cell extension zone (Gallagher *et al.*, 1976). Agreement between auxanometer readings was not always good and it was necessary to reject some LER values greater than 8 mm h^{-1} and less than 0.09mm h^{-1}. Inman-Bamber (1995) in a sugar cane experiment used to reject plant extension rate values of greater than 10.0 and less than -1.0 mm h^{-1}.

Readings also had to be rejected when leaves become detached from the connecting leaf clip for some reason or when consecutive hourly reading of single transducers fluctuated more than 3 mm h^{-1} and were clearly out of synchrony with readings from other auxanometers. In addition faulty connections, much rain, changing new leaf attachment, strong wind, bird interference, torn or broken leaves and auxanometer adjustment gave an unavoidable gap of 2-3 h during the measurement period.

6.3.3 Leaf extension rate at high temperatures (second planting date)

From February 18-20, continuous measurements were taken in both sole- and inter-cropping systems for the upper fully expanding leaf (Figure 6.3). This indicated that the LER of sole-crop maize (MM) was slightly higher than that of inter-crop maize (IM). The variation between the cropping systems on the first two days (Feb. 18 and 19) was less than 2 mm h^{-1} and not noticeably different.

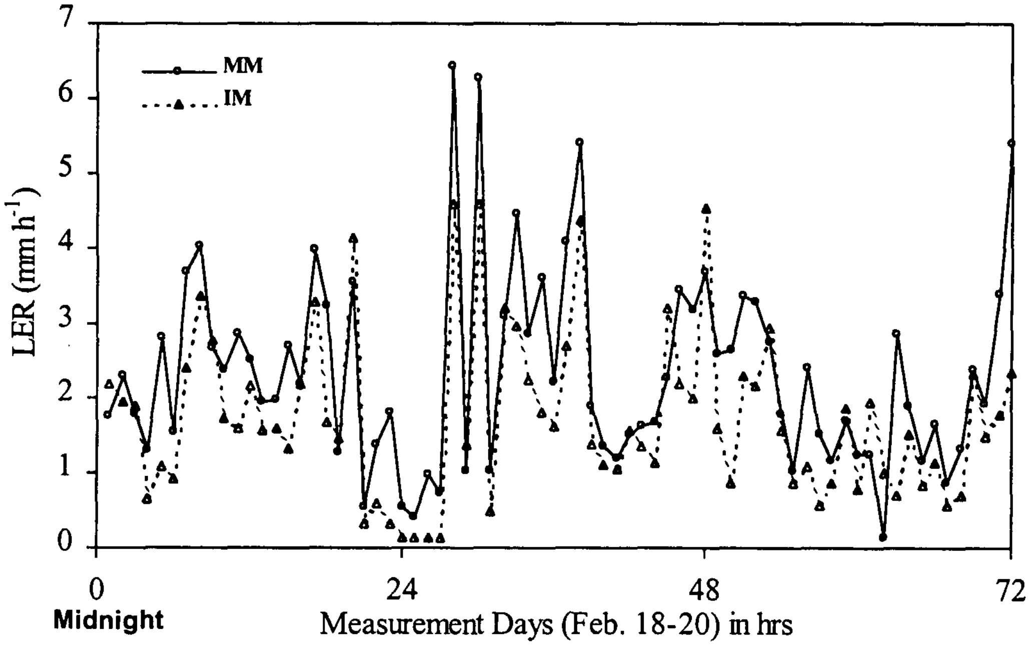


Figure 6.3 Average leaf extension rate measurements (mm h^{-1}) during warm (high) temperature on the second planting date (Feb. 18 - 20) using 6 auxanometers in each sole and inter-crop maize plants.

But the difference increased during the next day (Feb. 20) reached a peak of 2.16 and 3.07 mm h^{-1} at 63 and 72 hours (Figure 6.3). In both cropping systems there was a zigzag pattern of extension rate throughout the measurement time. The diurnal cycle in LER will be discussed later but no clear explanation could be found for such fluctuations occurring during the measurement time.

An attempt is made to relate the hourly response of maize LER at the field level to diurnal temperature change,, independently of other environmental conditions. There is a possibility of influences of other factors such as wind, water stress effect, or radiation. In a previous study on barley, Gallagher and Biscoe (1979) obtained a linear relation between LER and temperature by measuring LER on a bright day and when the soil water deficit was less than 50 mm.

From the field measurements of hourly LER and leaf temperature there were many fluctuations. However, in this study to assess the linear relationship between the LER and leaf temperature an average over a period of three hours during daytime (6:00-18:00) was used for the purpose of the analysis. The leaf temperature measured in both cropping systems did not show differences due to the reason that the average was used for the analysis. Figure 6.4 shows the LER and leaf temperature trends for 18th- 20th February. On Feb 18 and 19 the highest LER were measured at midday when the temperature reached 19°C and 29°C respectively. The extension rate for sole-/inter-crop during that period measured 3.02/2.61 and 3.48/ 2.8 mm h^{-1} on 18th and 19th respectively (Figure 6.4a, b).

While on Feb. 20 the LER values were lower to about 1.39 and 0.83mm h^{-1} respectively as the leaf temperature increased to nearly 33°C. But at 15:00 on Feb. 20 when the temperature dropped to 29.8°C the LER of the inter-crop also increased to 1.53mm h^{-1} and the sole crop LER remained the unchanged (Figure 6.4c). On the same day at 18 hours after the very hot temperature around midday time, caused a lag effect of high temperatures. Due to this residual effect of high temperatures during midday the growth showed slower recovery.

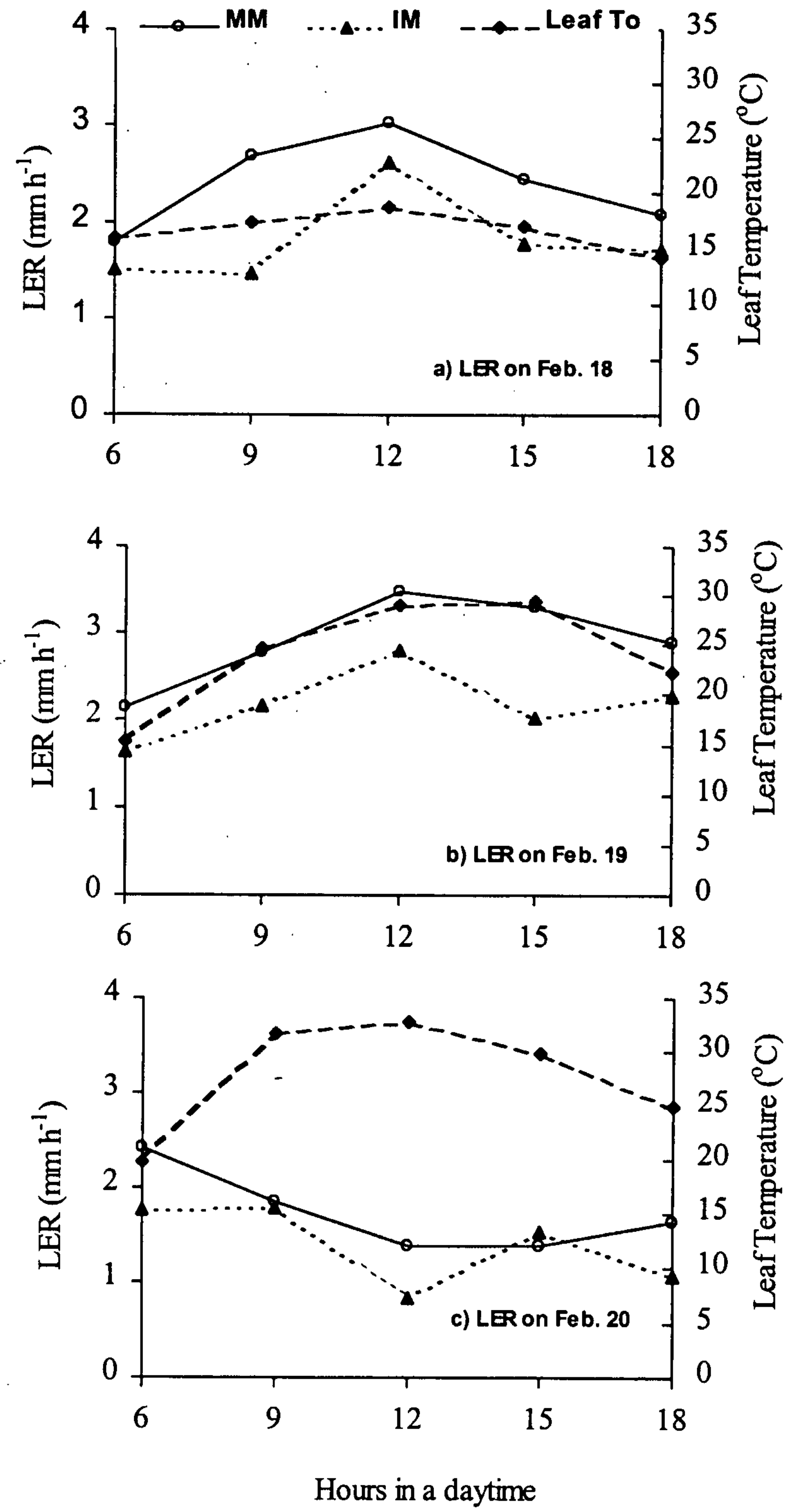


Figure 6.4 Temporal changes in three-hours average LER with diurnal leaf temperature as measured by auxanometers in both sole and inter-crop maize plants. (a) for Feb. 18, 2001, (b) for Feb. 19, 2001 and (c) for Feb. 20, 2001.

In contrast on the first two days the LER was likely to decrease after midday but on date Feb. 20 the LER was lower than 2mm h^{-1} during 9:00- 15:00 hours, when the temperature exceeded 29.5°C. Watts (1974) described a similar result of the leaf extension rate of young maize plants with large diurnal fluctuation of temperature from about 5-35°C where the extension rate varied from 0.40 mm h^{-1} to 3.6 mm h^{-1}. The leaf temperatures during these three days showed a typical record of a warm day with a range of 15-20°C during night and sharply increased from the early morning to a maximum of 33°C in the late afternoon. In general during this warm period the LER decreased when the leaf temperature exceeded around 29.5°C. A similar result concerning leaf area was suggested by Ong and Monteith (1985) where the increase in leaf area was slightly slower at 31°C than 28°C, probably because of a greater demand for transpiration.

6.3.4 LER measurement during cool temperature (third planting date)

The measurement was carried out over the period of three days (Apr. 27-29), when the leaf temperature was expected to be lower than during the previous measurements. The plants grew during the third planting with a spell of cold weather and the leaf temperature ranged between 5-25°C. The observations in figure 6.5 illustrated the field measurements of LER in both cropping systems during the cool period. On date Apr. 27 the LER measurements were relatively higher as compared to the next two days. The peak growth was about 3.79mm h^{-1} at 11 hours. On Apr. 28 the LER seemed to be lower than an Apr 27 but around midday (35 hours) a peak point reached about 3.56mm h^{-1}. While on the third day (Apr. 29) the LER was lowest with only one peak point (2.69mm h^{-1}) at the same hour as the previous measurements.

However, the LER was lower than the previous (high temperature) measurements. In Feb. (high temperature period) most measurements of LER showed higher values in the range 1.5 - 4 mm h^{-1} with some peak rates in the range 4.5 - 6.5. But during the cool period (Apr. measurements) most LER value showed less than 1.5 mm h^{-1} with very few peak values in between 1.8 –3.8 mm h^{-1}. Likewise the actual measurement of LER showed smaller fluctuation as compared to previous measurements in the second planting.

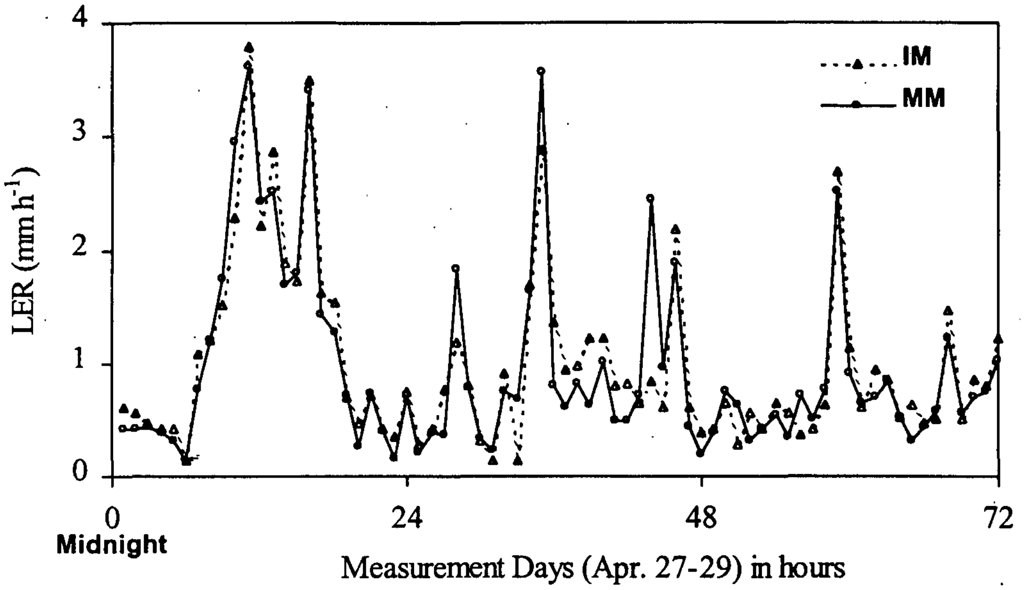


Figure 6.5 Average leaf extension rate measurements (mm h^{-1}) during cool temperature on the third planting date (Apr. 27-29th) using 6 auxanometers on each sole and inter-crop maize plants.

Later in the third planting, autumn approaches and the temperature declines sharply. The leaf temperature of less than 10°C on Apr 27th and most nighttime temperatures during 28th and 29th the temperature were recorded near to 10°C. During daytime the range of leaf temperatures were 18-25°C relative to high temperature period (Figure 6.6). So it was possible to study the LER with lower temperatures. Figure 6.6a,b,c shows a typical example of the relation between the LER and leaf temperature versus time during daytime.

On date Apr. 27 during late morning hours until midday the LER increased sharply to the peak of 3.69mm h^{-1} with increase of temperatures to about 24°C and again decreased slowly after 15 hours throughout the evening time (Figure 6.6a). In figure 6.6b (Apr. 28th) it was found that LER decreased close to zero during 9:00 hour and accelerated temporally at midday with 16°C and then decreased sharply until late evening. On the third day due to accumulated effect of low temperatures the growth remains low, even though the temperature rose to about 20°C around midday. (Figure 6.6c).

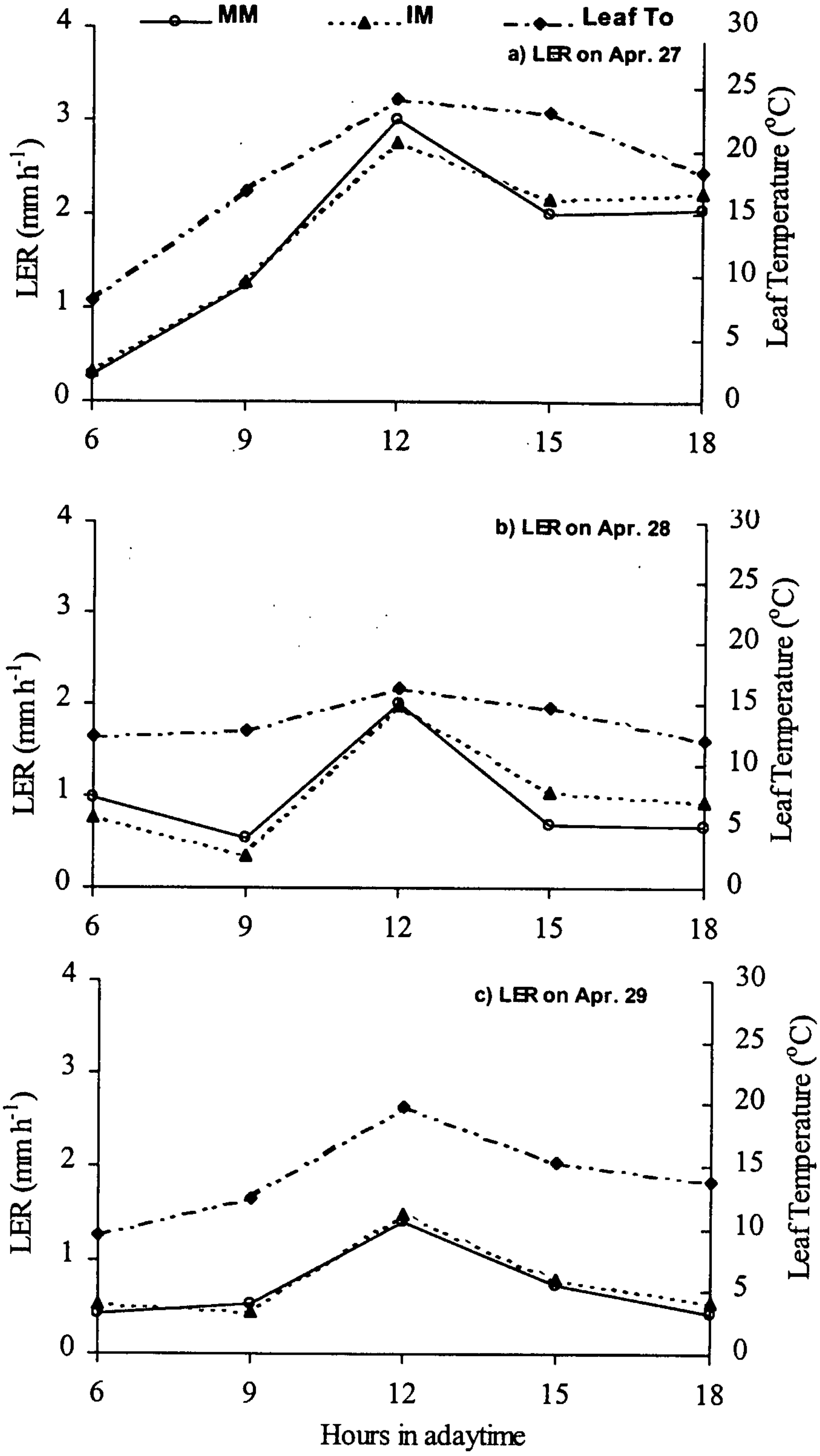


Figure 6.6 Temporal changes in average three-hours LER with diurnal leaf temperature as measured by auxanometers in both sole and inter-crop maize plants. (a) for Apr. 27, 2001 and (b) for Apr. 28, 2001 and (c) for Apr. 29, 2001.

6.3.5 Effect of a range of temperatures to LER

From the wide range of leaf temperatures in both cool and warm planting dates (in the range 5-25°C and 13 – 33°C) the maize leaf extension was shown to continue its rate but that during the low leaf temperatures (< 10°C) the rate was lower than 0.5 mm h^{-1} and very slow. On the other hand the average of three hours LER showed a decrease in rate when it exceeded 29°C during Feb. 20. The cropping system showed some differences in leaf extension rate in particular in the second planting date and in most cases the sole cropping was slightly higher than inter-cropping. While on the third planting, the LER differences were relatively minimal in between the cropping systems. However, in both planting dates the LER showed similar trends with many fluctuations with some of the diurnal temperatures.

The average leaf extension rate for each cropping system increased with temperature reaching a maximum at around 29°C and decreasing above that temperature. The highest LER rates (3mm h^{-1}) were observed at about 24°C with a gap until 29°C, then they began to decrease again. Therefore by assuming the LER was declining when the leaf temperature exceeds 29°C the linear regression equation fitted to the average of three hours data for each treatment to three-hour average leaf temperatures. The results are shown in table 6.2 with significantly differences (at the $P<0.05$ level) according to T test. The coefficient of determination (r^2) for linear relationship between LER and temperature in each treatments were highly correlated in the range of 0.76 - 0.78 with the exception of inter-cropping of the second planting, which is correlated lower at $r^2=0.58$. The values of LER during Feb. 20th at 18:00 hour in both sole- and inter-crop were not included in the analysis, due to the crops highly being influenced by the high temperatures at midday time, the crops could not recover after the stress periods. Thus they gave lower LER at about 24°C for both cropping systems.

Table 6.2 Linear regression equation of three-hour average LER and leaf temperature for all treatments over a wide range of temperatures. Where MM - 2 and MM - 3 represent for sole cropping in the second and third planting and IM - 2 and IM - 3 also represent for inter-cropping. (n= 15).

Cropping system	*a*	Confidence Interval*	*b*	Confidence Interval*	*SE*	r^2	*P*
MM - 2	1.124	1.834 0.414	0.071	0.109 0.043	0.232	0.780	0.001
IM - 2	-0.526	0.109 -0.639	0.075	1.692 -0.639	0.323	0.578	0.017
MM - 3	-1.210	-2.010 -0.411	0.153	0.102 0.203	0.357	0.769	0.000
IM - 3	-1.121	-1.873 -0.370	0.150	0.103 0.197	0.374	0.784	0.000

**Calculated at the 0.05 level*

For further combined analysis among treatments it was assumed that statistically differences between the treatments and the range of confidence intervals included the parameters. But for linearly increasing of LER with increasing temperature to the optimum and also decreasing LER linearly when exceeding optimum temperature to reach maximum temperature (where growth is expected to be zero). The temperatures were calculated by forming an intersection point. The overall data showed linear increasing up to a temperature of 29.5°C but there were some gaps in between the 24°C and 29.5°C with only three values around 29°C – 29.5°C. These values (29.02, 29.02 and 29.44°C) are used as common values for increasing and decreasing linear fitting lines.

Figure 6.7 illustrates the data distribution when the temperature was below or equal to 29.5°C and above or equal to 29.5°C and their fitted linearly regressions. Therefore from the given equations it was found that leaf growth was zero at 6.2°C and the highest LER of 3.2 mm h^{-1} measured at the optimum temperature of 27.8°C and at about 35.3°C the leaf growth is expected to stop completely. The average values of each cropping system and measurement periods were clearly shown in figure 6.7. Most of the data were between 13-24°C with a few measurement data of more than 29.5°C with lower LER. The intersection point of the two fitted lines was calculated as 27.8°C at highest LER.

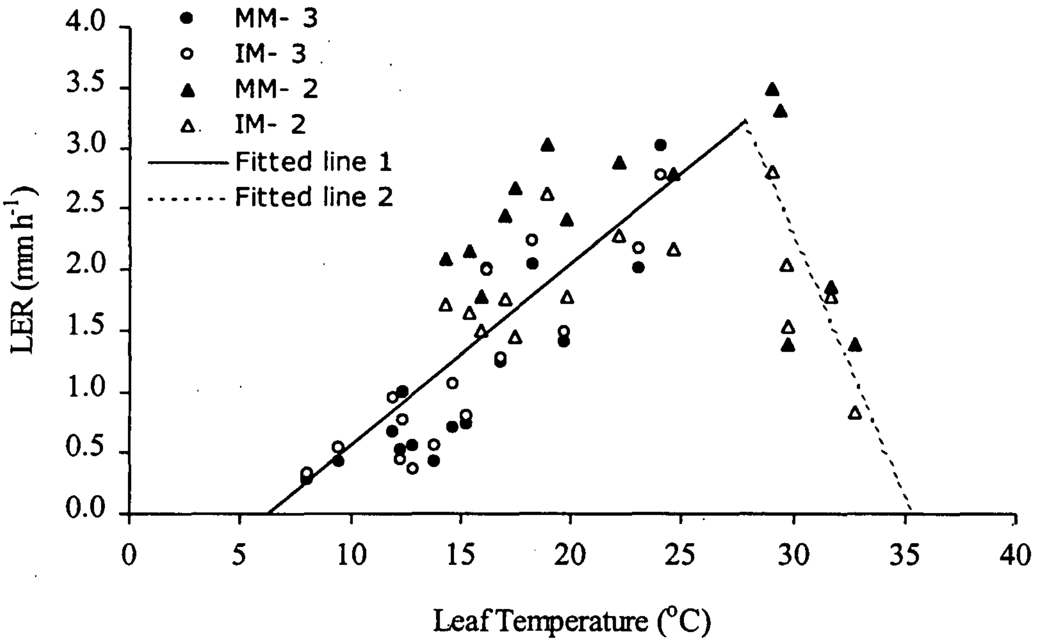


Figure 6.7 The relation between three hours average LER and leaf temperature during daytime (6:00 –18:00) for both cropping systems and seasons.

The produced equation from the two fitted lines (fitted line 1 and 2).
The fitting line 1, where To ≤ 27.8°C ***$Y= 0.1488x - 0.9268$, $r^2=0.717$***
The fitting line 2, where To ≥ 27.8°C ***$Y= -0.4274x + 15.092$, $r^2= 0.522$***

Both the equations had significant relations (at the $P < 0.05$ level) according to T-test; to increase the LER up to 27.8°C while in decreasing sharply beyond that specific temperature (27.8°C) the statistical differences were nearly insignificant (Table 6.3). But the optimum temperature by interacting the two fitted lines would be 27.8°C.

Table 6.3 Linear regression relationship between average of three hour LER and leaf temperatures greater and less than 29°C.

Temp. Variation	*a*	Confidence Interval*	*b*	Confidence Interval*	*SE*	r^2	*P*
LER at ≤27.8°C	-0.927	-1.434 -0.420	0.148	0.120 1.176	0.49	0.717	0.000
LER at ≥27.8°C	15.092	2.102 23.113	-0.427	-0.690 -0.007	0.597	0.522	0.046

**Calculated at the 0.05 level*

Therefore, from the result it was important to determine rates of leaf extension in the response to the diurnal fluctuation of temperature. In a field measurements by

Blacklow (1972) daily maximum temperature throughout the season ranged from about 20-35°C, whereas minimum night temperature were sometimes less than 5°C with optimum temperature for growth maize at 31°C. But the result of this experiment showed that LER increase rapidly with increase air temperature from 6.2°C and reached the highest LER. at 27.8°C.

The LER also declined sharply to less than 1.8 mm h^{-1} at about 31.6 –32.7°C and the equation pass through zero LER at 35.3°C (Figure 6.7). This result for maize showed similar trend with different temperatures as Ong and Monteith (1985) for millet extension rate increased linearly with temperature from a base 10 -12°C to a sharply defined optimum at 33-34°C and declined to zero at about 45-47°C. Some evidence from maize (Watts, 1974) and sorghum (Peacock and Heinrich, 1984) suggests that the rate of leaf extension declines rapidly between 35 and 40°C. Ong and Monteith (1985) suggestions that high temperature in relation to LER were associated with rapid transpiration, so that maximum rate of extension is seldom mentioned except for brief periods in the morning.

6.4 Conclusion

This study revealed that temperature exerts a major effect on leaf extension rate at of maize sole- and inter-crop grown under different temperature conditions in the field. But the LER is also sensitive to other weather variables. Ong (1983a) mentioned that temperature, radiation, moisture and vapor pressure deficit are the major environmental factors governing the rate of leaf extension rate.

However, this study has defined temperature as amongst the most important single factors for determining the leaf extension. Therefore it has described the linearity of the rate and leaf temperature relations up to optimum of 27.8°C at which the maximum rate of leaf extension (3.2mm h^{-1}) can be measured for maize leaves. The result has similarity with highest LER measurements at temperature of a 25-30°C (Cross and Zuber, 1972) and up to optimum of 30°C for other cereals (Gallagher and Biscoe, 1979; Keating and Evenson, 1979). The maximum temperature of 35.3°C on which growth ceases was also found from the formulated simultaneous equation. Watts (1972b) also reported sharp decline at 35°C of LER as temperature is major the limiting factor for leaf extension.

The constructed equation allows for summarization and hence possible uses for the models of temperature response to LER and development would be valuable in several applications. Therefore, knowledge of optimum and maximum temperatures for leaf growth is of vital importance to successful predicting growth and potential for biomass accumulation for crop production and silage purposes.

CHAPTER 7

GENERAL CONCLUSION

This work has endeavored to describe the strategy for physiological leaf growth on maize/bean intercrop in relation to temperature in the semi-arid tropics of South Africa. Although there are many unsolved questions concerning temperature effects on leaf growth in a maize/bean inter-crop, several points have been reported in this study:-

- Field measurements of daily leaf growth for early growth period of monocotyledonous and dicotyledonous crops under sole- and inter-cropping systems.
- The linearity of leaf growth with respect to chronological time series.
- The sigmoidal relationship between leaf length and thermal time using Richards function.
- The heat stress as a cause of reduced leaf growth during high temperature periods.
- The best representative way of leaf growth rate analysis using different approaches.
- The usage of cardinal temperatures for leaf growth and the knowledge of base, optimum and maximum temperatures.
- Assessment of short period measurements of LER in relation to leaf temperature.

Therefore this study has mainly been initiated to clarify microclimate modifications in a maize/bean inter-crop system, namely "field measurements of leaf growth and temperature". It is apparent that temperature is one of the main factors influencing the leaf growth rate, since then many physiologists have become aware of the need to measure appropriate microclimatic variables in relation to plant growth (Marshall, 1984). However, there is still room for improvement in the assessment of the effect of temperature on leaf growth.

In Chapter 4 the leaf growth showed a linear relationship with chronological time across the planting dates and cropping systems. But during the second planting (January planting) the crops were stressed due to exposure to high temperatures. While in the third planting (March planting) the growth showed a minimum relative growth rate when the temperature declined sharply during the later measurement periods. In field studies it is difficult to compare exact leaves (leaf number) across different planting dates as one would in a controlled temperature growth chamber study. So from the relative comparisons between the same leaf number (from different planting dates) sometimes that affects the other leaves at a higher leaf numbers.

The leaf growth also generally increased with increasing leaf number. The relation of leaf growth to temperature as a function of thermal time using the cardinal temperature of 10°C - 30°C gave a satisfactory result in maize crop. In Chapter 5, during the first planting the bean leaf growth showed a typical sigmoidal shape but when the temperature increased in the second planting the leaf growth appeared to have two sigmoidal cycles, due to extremely high temperature the first sigmoid growth curve reached a plateau value. Following the reduction of the temperature again to a value below the extreme, the growth resumed and formed a second sigmoidal curve. This clearly indicated the sensitivity of beans to heat stress. Though the different types of analysis have shown some differences in growth rate, it has given an indication for the general trend of the leaf growth rate.

By using base temperature of 10°C and maximum or extreme temperature of 30°C the relations of thermal time and leaf growth showed weak correlations. It appears that temperature is not the major driving force when comparing planting dates for beans. Therefore comparison of leaf growth and thermal time relations with those obtained in the study was difficult because different workers use different values of base and maximum temperature. Thermal time has also been calculated from sowing, germination or emergence. This indicated that in this semi-arid tropical environment, values of base and in particular extreme temperature for beans are not as important as those for maize leaf growth. In comparing the leaf growth of maize and beans on various temperature conditions, the maize plant had more linear relations with time series and gave a sigmoid curve against thermal time. The heat stress effect during the second planting was observed in both crops but it was more severe in the bean crop, since beans are more adapted to a moderate climate.

It must also be recognized that in the field microclimatic variables, soil, and air temperature, radiation and humidity are coupled to a varying degree. This is especially true when the objective of the research is to determine the influence on growth of a single environmental factor isolated from the complex situation present in the field. Hence in the study temperature is considered as a dominant factors in determining the leaf extension rate. The growth transducers (auxanometers) measuring LER during warm and cool season gave satisfactory results in the field. Even though they require further detailed research to minimize the field errors and to obtain more precise data for coupling temperature variations with LER in short periods of time, these types of measurements may prove the usefulness of the equipment for research and for monitoring growth, at least in a short period of time, to couple with environmental factors.

The equation relating LER to temperature will be useful in model development. The daytime pattern of LER provided a clear means of characterizing the heat stress and effect of low temperatures on the maize plants but this pattern needs to be correlated with a more widely collected data set also including other weather variables.

In conclusion the information that has been reported in this study may be valuable and helpful for the following reasons:-

- Primarily growth curve analysis might be a useful technique for developing phenological models and the shape of the temperature response profile uses for experimental information more efficiently and to make it applicable to any experimental design. Since the current state of the art apart from the sole-crop could be used for early growth phase in inter-cropping models, and only the later phases need to be studied in detail for the inter-cropping models.

- To agricultural scientists and officers with regarding farm advice for traditional cropping system on the combination of the associated crops to ensure efficient utilization of resources during the growing period.

- Due to greater weather variability between and within seasons, the inter-cropping system may imply lower risk to the farmer by selecting the appropriate planting date. In addition to at least escape the heat stress periods during the growing season.

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APPENDICES

APPENDIX I

For Maize Leaf Growth

Table A. 1. Estimates of the four value parameters with standard error resulted from the Richards' function curve fitting model and their regressions for the observed maize leaf length values in sole and inter-crop systems in all planting dates.

Leaf No	Model Parameters (Coefficients)				Standard error (SE)	Correlations	
	a	*b*	*c*	*d*		r	r^2
Sole-crop							
4	36.21	-0.31	0.04	0.25	1.90	0.962	0.925
5	46.00	9.86	0.09	5.80	4.60	0.929	0.863
6	57.00	23.18	0.15	16.06	70.07	0895	0.800
7	-37.89	112.76	80.04	1.14	1.14	0.727	0.529
8	69.08	0.37	0.02	0.06	0.06	0.778	0.605
9	74.81	1.35	0.02	0.03	0.30	0.759	0.577
Inter-crop							
4	36.21	0.44	0.03	0.34	2.21	0.987	0.938
5	48.10	3.58	0.03	1.34	2.37	0.981	0.964
6	56.04	88.46	0.47	43.65	5.18	0.942	0.887
7	66.14	7.58	0.04	2.51	079	0.897	0.805
8	76.65	-0.28	0.02	0.06	9.24	0.869	0.755
9	89.35	-0.33	0.01	0.13	10.26	0.832	0.692

Table A. 2. Estimates of the constant for equations of leaf length in relation to thermal time from emergence with coefficient of determination and the error probability for the interaction in all planting dates and cropping systems of maize crop.

a) sole-cropping

Leaf No (Treatment)	*a (SE)*	*Confi. interval*	*b (SE)*	*Confi. interval*	R^2 (*df*)	Interaction
4 MM-P1	2.66 (0.12)	2.39 2.93	0.006 (0.001)	0.003 0.008	0.718 (12)	S, 0.000 $P < 0.05$
MM-P2	3.11 (0.001)	3.15 3.24	0.002 (0.000)	0.001 0.002	0.97 (9)	S, 0.000 $P < 0.05$
MM-P3	2.95 (0.05)	2.82 3.08	0.005 (0.000)	0.003 0.006	0.84 (16)	S, 0.000 $P < 0.05$
5 MM-P1	2.307 (0.121)	2.044 2.569	0.009 (0.001)	0.007 0.011	0.877 (13)	S, 0.000 $P < 0.05$
MM-P2	3.188 (0.078)	3.019 3.358	0.003 (0.000)	0.002 0.003	0.762 (13)	S, 0.000 $P < 0.05$
MM-P3	2.727 (0.082)	2.553 2.900	0.008 (0.000)	0.007 0.009	0.883 (18)	S, 0.000 $P < 0.05$
6 MM-P1	2.673 (0.119)	2.411 2.934	0.009 (0.001)	0.007 0.012	0.865 (13)	S, 0.000 $P < 0.05$
MM-P2	3.119 (0.084)	2.941 3.297	0.003 (0.000)	0.002 0.004	0.819 (16)	S, 0.000 $P < 0.05$
MM-P3	2.515 (0.064)	2.380 2.649	0.009 (0.009)	0.008 0.009	0.954 (20)	S, 0.000 $P < 0.05$
7 MM-P1	2.794 (0.132)	2.503 3.085	0.008 (0.001)	0.006 0.010	0.875 (12)	S, 0.000 $P < 0.05$
MM-P2	2.892 (0.082)	2.720 3.063	0.004 (0.000)	0.003 0.004	0.887 (19)	S, 0.000 $P < 0.05$
MM-P3	2.386 (0.040)	2.298 2.473	0.009 (0.000)	0.009 0.009	0.992 (13)	S, 0.000 $P < 0.05$
8 MM-P1	2.259 (0.132)	1.965 2.553	0.008 (0.001)	0.007 0.009	0.949 (11)	S, 0.000 $P < 0.05$
MM-P2	2.890 (0.050)	2.783 2.998	0.004 (0.000)	0.004 0.003	0.966 (16)	S, 0.000 $P < 0.05$
MM-P3	1.932 (0.049)	1.819 2.046	0.011 (0.000)	0.010 0.012	0.995 (11)	S, 0.000 $P < 0.05$
9 MM-P1	2.301 (0.104)	2.054 2.548	0.008 (0.000)	0.007 0.009	0.978 (8)	S, 0.000 $P < 0.05$
MM-P2	2.818 (0.075)	2.656 2.979	0.004 (0.000)	0.003 0.004	0.951(14)	S, 0.000 $P < 0.05$
MM-P3	1.724 (0.208)	1.189 2.258	0.011 (0.001)	0.008 0.014	0.957(6)	S, 0.000 $P < 0.05$

Table A 2. *cont.*

b) inter-cropping

Leaf No (Treatments)	*a (SE)*	*Conf. Interval*	*b (SE)*	*Conf. interval*	*R2 (df)*	Interaction
4 IM-P1	1.942	1.556	0.012	0.008	0.809 (11)	S, 0.000
	(0.173)	2.329	(0.002)	0.016		$P < 0.05$
IM-P2	3.161	3.074	0.002	0.001	0.860 (13)	S, 0.000
	(0.039)	3.248	(0.000)	0.002		$P < 0.05$
IM-P3	2.627	2.485	0.008	0.006	0.898 (16)	S, 0.000
	(0.067)	2.769	(.001)	0.009		$P < 0.05$
5 IM-P1	1.710	1.529	0.047	0.042	0.973 (12)	S, 0.000
	(0.082)	1.891	(0.002)	0.052		$P < 0.05$
IM-P2	3.029	2.878	0.003	0.002	0861 (15)	S, 0.000
	(0.071)	3.181	(0.000)	0.004		$P < 0.05$
IM-P3	2.268	2.117	0.009	0.008	0.959 (14)	S, 0.000
	(0.069)	2.418	(0.001)	0.012		$P < 0.05$
6 IM-P1	1.754	1.452	0.011	0.009	0.954 (10)	S, 0.000
	(0.133)	2.055	(0.001)	0.013		$P < 0.05$
IM-P2	2.956	2.754	0.003	0.002	0.798 (20)	S, 0.000
	(0.097)	3.159	(0.000)	0.004		$P < 0.05$
IM-P3	2.389	2.248	0.009	0.008	0.972 (15)	S, 0.000
	(0.066)	2.529	(0.000)	0.009		$P < 0.05$
7 IM-P1	1.971	1.672	0.009	0.008	0.947 (12)	S, 0.000
	(0.136)	2.271	(0.001)	0.010		$P < 0.05$
IM-P2	2.883	2.694	0.004	0.003	0.894 (17)	S, 0.000
	(0.089)	3.072	(0.000)	0.004		$P < 0.05$
IM-P3	2.033	1.878	0.010	0.009	0.986 (11)	S, 0.000
	(0.069)	2.187	(0.000)	0.011		$P < 0.05$
8 IM-P1	2.289	1.979	0.008	0.007	0.951 (10)	S, 0.000
	(0.137)	2.598	(0.001)	0.009		$P < 0.05$
IM-P2	2.728	2.563	0.004	0.004	0.946 (16)	S, 0.000
	(0.077)	2.893	(0.000)	0.005		$P < 0.05$
IM-P3	2.046	1.777	0.009	0.008	0.973 (8)	S, 0.000
	(0.114)	2.315	(0.001)	0.011		$P < 0.05$
9 IM-P1	1.918	1.626	0.009	0.008	0.978 (8)	S, 0.000
	(0.124)	2.210	(0.001)	0.010		$P < 0.05$
IM-P2	2.725	2.615	0.004	0.004	0.983 (13)	S, 0.000
	(0.050)	2.835	(0.000)	0.005		$P < 0.05$
IM-P3	2.505	2.092	0.007	0.004	0.971 (4)	S, 0.000
	(0.129)	2.918	(0.001)	0.009		$P < 0.05$

Table A. 3. Estimates of the constant equations for leaf length in relation to thermal time from emergence with coefficient of determination and the error probability for the interaction for three planting dates for leaf 4-9 on maize crop. Since a significant response of thermal time to leaf growth was detected for both cropping systems in all planting dates (at the P < 0.05 level). It has combined the cropping systems to assess the variation in temperature on leaf growth among the planting dates. From the analysis it is clear that there was some variations in temperature as well as in leaf growth.

Leaf No (Treatments)	*A (SE)*	*Conf. Inter.*	*B (SE)*	*Conf. Inter.*	R^2 *(df)*	Interaction
4 PL-1	2.10 (0.10)	1.88 2.33	0.008 (0.004)	0.009 0.007	0.958 (17)	S, 0.000 P < 0.05
PL-2	2.77 (0.04)	2.68 2.87	0.004 (0.000)	0.004 0.004	0.964 (28)	S, 0.000 P < 0.05
PL-3	2.43 (0.63)	1.02 3.84	0.007 (0.003)	0.000 0.014	0.341 (11)	S, 0.000 P < 0.05
5 PL-1	2.15 (0.11)	1.92 2.39	0.009 (0.001)	0.007 0.010	0.823 (26)	S, 0.000 P < 0.05
PL-2	3.11 (0.05)	2.99 3.21	0.003 (0.001)	0.003 0.002	0.812 (29)	S, 0.000 P < 0.05
PL-3	2.67 (0.10)	2.46 2.88	0.006 (0.001)	0.006 0.009	0.706 (33)	S, 0.000 P < 0.05
6 PL-1	2.68 (0.17)	2.332 3.04	0.007 (0.001)	0.004 0.009	0.577 (24)	S, 0.000 P < 0.05
PL-2	3.05 (0.069)	0.069 0.002	0.003 (0.000)	0.002 0.004	0.762 (37)	S, 0.000 P < 0.05
PL-3	2.50 (0.05)	2.39 2.61	0.008 (0.000)	0.007 0.009	0.945 (36)	S, 0.000 P < 0.05
7 PL-1	2.86 (0.17)	2.50 3.23	0.005 (0.000)	0.004 0.008	0.593 (25)	S, 0.000 P < 0.05
PL-2	2.88 (0.05)	2.768 3.506	0.003 (0.000)	0.003 0.004	0.896 (37)	S, 0.000 P < 0.05
PL-3	2.29 (0.08)	2.12 2.46	0.009 (0.000)	0.008 0.010	0.93 (25)	S, 0.000 P < 0.05
8 PL-1	2.27 (0.09)	2.084 2.46	0.008 (0.000)	0.007 0.009	0.940 (22)	S, 0.000 P < 0.05
PL-2	2.80 (0.04)	2.768 2.909	0.004 (0.000)	0.004 0.004	0.945 (33)	S, 0.000 P < 0.05
PL-3	2.042 (0.17)	1.669 2.415	0.010 (0.000)	0.008 0.012	0.866 (18)	S, 0.000 P < 0.05
9 PL-1	2.109 (0.104)	1.888 2.331	0.008 (0.000)	0.009 0.007	0.958 (17)	S, 0.000 P < 0.05
PL-2	2.776 (0.04)	2.68 2.87	0.004 (0.001)	0.004 0.004	0.964 (28)	S, 0.000 P < 0.05
PL-3	2.43 (0.63)	1.02 3.84	0.007 (0.003)	0.001 0.015	0.340 (11)	S, 0.000 P < 0.05

APPENDIX II

For Beans Leaf Growth

Table A. 4. Estimates of the four value parameters with standard error in the Richards' function curve fitting model and their regressions for the observed leaf length values in beans crop (leaf 2-9). It was estimated by combing all the cropping systems and planting dates for bean crop.

Leaf No	Model Parameters (Coefficients)				Standard error (*SE*)	Correlations	
	A	*b*	*c*	*d*		r	r^2
Chronological time							
2	8.778	19.193	1.480	14.535	1.810	0.6925	0.4796
3	8.954	30.941	1.766	15.609	1.947	0.7210	0.5196
4	11.431	13.613	0.624	5.320	1.608	0.8530	0.7276
5	10.653	14.328	0.615	6.238	1.84	0.8038	0.6461
6	9.508	4.791	0.274	1.299	1.502	0.7072	0.5001
7	6.942	6.457	0.595	0.108	1.452	0.4829	0.2332
8	7.922	3.485	0.186	1.499	1.341	0.5922	0.3507
9	6.635	21.391	1.049	5.560	0.889	0.7265	0.5278
Thermal time							
2	-6.280	648.224	7.805	2.137	2.315	0.3850	0.1482
3	-8.889	244.048	9.691	1.480	2.417	0.5085	0.2586
4	9.573	0.807	0.021	0.203	2.456	0.6040	0.3638
5	-19.246	14.104	10.143	1.332	2.27	0.415	0.1722
6	25.174	5.083	0.005	2.968	1.860	0.4829	0.2332
7	6.870	3.632	0.057	0.006	1.521	03977	0.1582
8	20.590	12.124	0.009	7.908	1.341	03401	0.1157
9	20.637	10.400	0.007	6.576	1.209	0.3818	0.1458

Table A. 5. Values of the four parameters with standard error resulted from the Richards function curve fitting model and their regressions for the observed leaf length values in comparing among three planting dates by combining the cropping systems.

Leaf No	Model Parameters (Coefficients)				Standard error (*SE*)	Correlations	
	a	*b*	*c*	*d*		r	r^2
First planting							
2	10.572	0.529	0.020	0.369	0.404	0.988	0.976
3	9.990	50.295	2.320	244.505	1.803	0.832	0.692
4	12.462	11.320	0.492	3.088	0.531	0.990	0.980
5	11.519	12.326	0.049	3.494	0.412	0.988	0.977
6	11.874	1.698	0.0207	0.079	0.478	0.981	0962
7	10.046	23.457	0.081	8.110	0.517	0.969	0.940
8	23.866	8.858	0.018	2.916	0.418	0.956	0.915
9	7.012	83.634	0.294	22.874	0.857	0.882	0.778
Second planting							
2	7.065	23.204	0.113	28.269	0.750	0.822	0.676
3	11.506	11.505	0.034	7.317	0.589	0.957	0.916
4	11.286	16.303	0.045	7.737	0635	0.970	0.941
5	40.160	10.466	0.015	3.110	0.773	0.945	0.893
6	36.266	7.497	0.011	2.188	0.758	0.946	0.895
7	19.898	10.50	0.015	4.617	0.710	0.850	0.723
8	10.380	4.009	0.014	0.607	0.369	09810	0.962
9	13.955	15.704	0.011	13.896	0.906	0.459	0.211
Third planting							
2	18.566	-0.468	0.0152	0.252	0.937	0.935	0.875
3	13.569	13.278	0.087	5.564	1.329	0.921	0.849
4	11.262	39.376	0.222	13.932	1.028	0.953	0.908
5	11.706	15.193	0.078	5.676	0.511	0.980	0.961
6	50.898	7.941	0.021	2.107	0.761	0.912	0.831
7	71.979	6.583	0.020	1.136	0.711	0.892	0.796
8	75.369	7.892	0.024	1.131	0.499	0.926	0.857
9	7.178	9.082	0.0626	0.303	0.590	0.788	0.620

Table A.6. Estimates of the constant equations for leaf length in relation to thermal time from emergence with coefficient of determination and the error probability for the interaction in three planting dates.

Leaf No	*A* *(SE)*	*Conf. Interval*	*B* *(SE)*	*Conf. interval*	R^2 *(df)*	Interaction
2 PL-1	0.674	0.480	0.010	0.008	0.879 (21)	S, 0.000
	(0.092)	0.860	(0.000)	0.012		$P < 0.05$
PL-3	1.298	1.13	0.002	0.001	0.635 (23)	S, 0.000
	(0.080)	1.46	(0.000)	0.003		$P < 0.05$
PL-3	1.32	1.15	0.011	0.008	0.814 (24)	S, 0.000
	(0.080)	1.49	(0.000)	0.013		$P < 0.05$
3 PL-1	0.346	-0.23	0.008	0.005	0.646 (16)	S, 0.000
	(0.272)	0.92	(0.001)	0.012		$P < 0.05$
PL-2	0.895	0.730	0.004	0.003	0.874 (24)	S, 0.000
	(0.07)	1.061	(0.000)	0.005		$P < 0.05$
PL-3	0.459	0.109	0.013	0.010	0.775 (25)	S, 0.000
	(0.16)	0.809	(0.001)	0.016		$P < 0.05$
4 PL-1	-0.007	-0.405	0.009	0.007	0.861 (19)	S, 0.000
	(0.189)	0.390	(0.001)	0.011		$P < 0.05$
PL-2	0.548	0.307	0.004	0.004	0.866 (25)	S, 0.000
	(0.116)	0.790	(0.000)	0.006		$P < 0.05$
PL-3	-0.112	-0.401	0.014	0.012	0.895 (27)	S, 0.000
	(0.14)	0.176	(0.000)	0.015		$P < 0.05$
5 PL-1	0.230	-0.132	0.007	0.006	0.878 (18)	S, 0.000
	(0.17)	0.59	(0.000)	0.009		$P < 0.05$
PL-2	0.360	0.044	0.004	0.003	0.827 (23)	S, 0.000
	(0.15)	0.677	(0.000)	0.005		$P < 0.05$
PL-3	0.076	-0.564	0.008	0.006	0.844 (16)	S, 0.000
	(0.081)	0.440	(0.000)	0.010		$P < 0.05$
6 PL-1	-0.06	-0.091	0.011	0.018	0.95 (26)	S, 0.000
	(0.23)	0.244	(0.000)	0.013		$P < 0.05$
PL-2	0.133	-0.215	0.005	0.004	0.844 (21)	S, 0.000
	(0.167)	0.482	(0.001)	0.006		$P < 0.05$
PL-3	0.224	-0.145	0.009	0.007	0.803 (23)	S, 0.000
	(0.17)	0.007	(0.001)	0.012		$P < 0.05$
7 PL-1	-0.050	-0.460	0.007	0.006	0.889 (15)	S, 0.000
	(0.19)	0.358	(0.001)	0.009		$P < 0.05$
PL-2	0.67	0.274	0.003	0.002	0.687 (17)	S, 0.000
	(0.18)	1.073	(0.000)	0.004		$P < 0.05$
PL-3	-1.31	-2.11	0.016	0.123	0.819 (16)	S, 0.000
	(0.37)	-0.504	(0.002)	0.012		$P < 0.05$
8 PL-1	0.174	-0.123	0.006	0.005	0.915 (14)	S, 0.000
	(0.137)	0.471	(0.000)	0.007		$P < 0.05$
PL-2	-0.899	-1.33	0.008	0.006	0.935 (13)	S, 0.000
	(0.19)	-0.468	(0.000)	0.009		$P < 0.05$
PL-3	-1.464	-2.273	0.018	0.012	0.852 (14)	S, 0.000
	(0.10)	-0.656	(0.000)	0.021		$P < 0.05$