ANALYSIS OF GROWTH AND YIELD OF EXTRA-SHORT-DURATION PIGEONPEA (*Cajanus Cajan* [L.] Millsp.) IN RELATION TO SOIL MOISTURE AVAILABILITY

By

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CERTIFICATE

This is to certify that the thesis entitled "**ANALYSIS OF GROWTH AND YIELD OF EXTRA-SHORT-DURATION PIGEONPEA (*Cajanus Cajan* [L.] Millsp.) IN RELATION TO SOIL MOISTURE AVAILABILITY** " submitted to Ministry of Education and Training, Government of Vietnam in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Agronomy** is a faithful record of the research work carried out by Mr. Nguyen Hai Nam, under my supervision and that no part of this thesis has been submitted for any other degree or diploma.

The assistance and help received during the course of these investigations have been properly acknowledged by him.

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CONTENTS

CHAPTER I

INTRODUCTION

Pigeonpea (*Cajanus Cajan* [L.] Millsp.) ranks sixth in area and production in comparison to other grain legumes worldwide and is one of the most important grain legume crops of the tropics and sub-tropics (Nene & Sheila 1990). The crop is reputed to be well adapted to marginal conditions and can produce an economic yield in soils characterized by moisture deficits (Pathak 1970; Whiteman *et al.* 1985; Troedson *et al.* 1990). Traditional pigeonpea varieties are normally grown under rainfed conditions after the beginning of a rainy season, mostly as an intercrop, and most of their reproductive growth relies on stored soil moisture in the following postrainy season. Although these varieties have a deep and extensive root system (Rachie & Roberts 1974; Sheldrake & Narayanan 1979) which enables them to avoid drought, they have been shown to suffer from terminal drought stress due to progressive depletion of residual soil moisture in the postrainy season (ICRISAT 1984; Muchow 1985a; Singh & Subba Reddy 1988).

The full potential of a crop is seldom reached because of the limitations on physiological processes imposed by environmental stresses, of which drought is the most important factor that limits productivity and crop yield on a worldwide basis (Turner & Kramer 1980). Although drought is common in the semi-arid regions, there are many humid or sub-humid areas as well where either a deficit or an excess of water is a frequent limitation to crop productivity (Krizek 1981; Raper & Kramer 1983; Turner & Kramer 1980).

Early maturing food legume crops, such as cowpea and mung bean, are primarily chosen for growing under rainfed conditions in semi-arid regions because of their ability to fit into environments where the effective length of cropping season is short, and certainly shorter than the duration of traditional pigeonpea varieties. They also provide considerable scope for being fitted into new cropping systems and for cultivation in non-traditional areas. This, however, invariably requires both appropriately adapted plant types in conjunction with different agronomic management practices for overcoming the impact of drought and waterlogging.

In recent years, extra-short-duration (ESD) pigeonpea genotypes that can mature in as few as 90-110 days have been developed. They are suitable for intensive cultivation as sole crops and have been tested for adaptation to rainfed semi-arid environments (Chauhan *et al.* 1993). In some situations, they are capable of producing even higher yield than the medium-duration genotypes which can be attributed to their better ability to match the length of growing season and escape from terminal drought stress (Chauhan 1990). Although ESD pigeonpea genotypes have good yield potential, its realization seems very sensitive to soil moisture status. Large seasonal and locational difference in grain yields of ESD pigeonpea genotypes have been observed (Chauhan *et al.* 1993; Nam *et al.* 1993) indicating a lack of stability in yield. These differences can largely be attributed to variation in soil moisture availability. Depending on the likely pattern of rainfall during the rainy season and consequent availability of soil moisture, ESD pigeonpea can face intermittent drought or waterlogging due to poor distribution of rainfall. With delayed sowing, it can also face excess of soil moisture during vegetative growth (Chauhan *et al.* 1993; Nam *et al.* 1993). Although irrigation is an effective option to alleviate drought effects in pigeonpea (Bhan & Khan 1979; Makhan Lal & Gupta 1984), this is not a practical or economic approach for most pigeonpea growing areas. Further, if irrigation is followed by moderate or heavy rains this might result in waterlogging. Thus, selection of genotypes which are better able to resist both water deficit and its excess is likely to be a better option to increase yield and stability of production of pigeonpea, particularly that of shorter duration, grown in semi-arid regions.

Resistance to drought and waterlogging is conditioned by a number of components and may differ for different crops and in response to different types, intensity and duration of drought or flooding (Bradford & Yang 1981; Kawase 1981; McWilliam 1990). Therefore, it is necessary to develop understanding of the nature of physiological adaptation of pigeonpea genotypes under variable soil moisture availability conditions.

Literature on physiological traits of some other important food legume crops such as groundnut, soybean, cowpea, etc., that are affected by water stress is well documented (Bunting & Kassam 1988; Devries *et al.* 1989; Nageswara Rao 1992; Mathews *et al.* 1988; Wright *et al.* 1991; Stegman *et al.* 1990; Turk & Hall 1980; Lawn 1982a; Muchow 1985a, b). Despite the considerable importance of waterlogging to grain legume crops, very little work has been done to understand the response as well as mechanisms of waterlogging resistance of these crops. In addition, ESD pigeonpea is virtually a new plant type and the information on the effects of both water stress and waterlogging is not available. The need for identifying desirable traits of ESD pigeonpea that play a major role in resistance to these adverse conditions is crucial for the development of breeding strategies in genetic improvement or to determine appropriate agronomic practices for ESD pigeonpea.

The major objectives of this investigation were, therefore:

1) To assess crop growth and development and to quantify grain yield losses of ESD pigeonpea genotypes in relation to timing and duration of drought stress.

2) To identify physiological traits associated with higher yield of ESD pigeonpea genotypes under drought stress.

3) To assess the effects of timing of excess soil moisture on plant growth and grain yield of ESD pigeonpea.

4) To identify the effects of different soil moisture levels prior sowing time and during crop growth on growth and grain yield of ESD pigeonpea.

5) To determine specific factors affecting stability of grain yield of ESD pigeonpea under variable soil moisture conditions.

CHAPTER II

REVIEW OF LITERATURE

2.1. FOOD LEGUME PRODUCTION UNDER VARIABLE SOIL WATER ENVIRONMENTS

In the tropics and sub-tropics, food legume crops are grown in a wide range of environments such as arid, semi-arid, sub-humid and humid. Depending on the climate, soil type and management systems, different crops are chosen for different cropping systems. For example, in semi-arid environments where rainfall is low and growing season is short pigeonpea and groundnut are sown in the rainy season either as a sole crop or intercrop while chickpea, lentil or pea are grown in the postrainy season. Other grain legumes, such as soybean and mung bean are commonly grown in the dry season on residual soil moisture or under rainfed conditions in the humid and sub-humid areas (Reddy and Willey 1982; Papendick *et al.* 1988; Willey *et al.* 1986; Ali 1990; Wood & Myer 1986; Squire *et al.* 1986). Yield levels of all food legume crops in such conditions are generally low because they are grown in marginal areas, on residual soil moisture, under rainfed conditions and with very low production input (Carangal *et al.* 1986).

There are large differences between genetic yield potential and realized yield both among and within species of food legume crops (McWilliam & Dillon 1987). Water stress caused by the variation in the timing and intensity of rainfall during the growing season is one of the factors responsible for this gap. In addition, topographic and edaphic factors through their influence on run-off, infiltration, storage and subsequent availability also have a large effect on crop growth and yield (Lawn & Williams 1986).

2.1.1 Drought Stress

In semi-arid environments, drought stress is a major factor responsible for yield loss (Simpson

1981). Drought not only affects growth and yields of crops in arid or semi-arid environments, where crops frequently experience dry spells within the rainy season itself, but also in other areas where evaporative demand greatly exceeds rainfall during the growing season, depending on the rainfall pattern and soil types. The detrimental effects of water deficit which restrict crop growth and yield are largely dependent on intensity of drought and the timing of stress related to crop ontogeny, duration and crop species. The sensitivity of yield to drought during specific stages of growth is relevant to the development of improved management practices and cultivars. It has been established that there are periods during which crops are especially susceptible to drought. For example, cowpea is an indeterminate crop and harmful effects of drought during specific stages of growth depend upon subsequent environmental conditions (Turk *et al.* 1980). Droughts during the vegetative stage generally have no influence on seed yield when subsequent environmental conditions are conducive for recovery but severe drought at flowering can cause nearly complete abscission of flowers and young pods (Turk *et al.* 1980; Hall & Grantz 1981).

Planchou *et al.* (1986) found that the timing of drought stress during the growing phase of soybean determines the type and extent of damage. Late drought stress caused poor seed filling and a reduced seed weight but early drought stress reduced yield due to increased seed abortion. Drought stress effects in groundnut depend primarily on the stress pattern because genotype variation is usually of secondary significance (Williams *et al.* 1986). The magnitude of the water deficit is also important in addition to its timing and duration because it may occur either continuously over the total growing period of the crop or it may occur during any one or more growth period such as establishment, vegetative, flowering and yield formation or seed development.

2.1.1.1 Effect of drought stress at the vegetative stage

The effects of water deficit during the vegetative growth of food legumes normally are less severe than at the reproductive stage and have been well documented by various earlier studies (Sionit

& Kramer 1977; Constable & Hearn 1978; Korte *et al.* 1983; Turk *et al.* 1980;; Shouse *et al.* 1981). In soybean, stress at the vegetative stage reduced grain yield by 15-19% (Bartels & Caesar 1987; Eck *et al.* 1987). Seed yields of cowpea were not reduced by the pre-flowering stress because after stress was relieved plants resumed growth and established adequate numbers of nodes and leaf area to support adequate flowers and pod set (Turk *et al.* 1980; Akyeampong 1985). Highly indeterminate cowpea cultivars may have greater ability to recover from drought during the vegetative stage and may therefore have greater yield stability in semi-arid environments (Hall 1981). The relative insensitivity to drought in groundnut reflects the extreme plasticity of the growth and development of this crop since most processes resumed rates similar to the pre-stress levels once stress was released (Stirling *et al.* 1989a).

In contrast, drought stress at the vegetative stage was found to be more detrimental in navy bean (Gunton & Evenson 1980) and mung bean (Sadasivam *et al.* 1988). Field trials with three mung bean cultivars subjected to water stress during three growth stages showed that the greatest adverse effects on yield components and seed yields were exerted by stress imposed during the vegetative stage, followed by the flowering and the pod development stages (Sadasivam *et al.* 1988). Yield of mung bean is generally determined by its capacity to grow vigorously and accumulation of as much dry matter as possible before anthesis (Kuo *et al.* 1978). Moisture stress during vegetative phase was most sensitive for mung bean. Some indetermine genotypes of groundnut (Williams *et al.* 1986), cowpea, mung bean or black gram (Lawn 1982a) can produce new branches, leaf area and new flushes of flowers and pods when stress is relieved and were found to be less sensitive to vegetative drought because they could compensate for some of the reductions that occurred earlier. Long- and medium-duration pigeonpea are less sensitive to vegetative drought. Mild drought at this stage may help develop a deeper and more vigorous root system (Ariyanayagam & Griffith 1987). However, drought at the vegetative stage was harmful to SD pigeonpea (ICRISAT 1989).

2.1.1.2 Effect of drought stress at the reproductive stage

Almost all the food legume crops are generally sensitive to water deficit during the reproductive stage. Soybean is more sensitive during flowering and pod set and most sensitive during the seed filling stage (Pahalwan & Tripathi 1984; Eck *et al.* 1987; Kpoghomon *et al.* 1990). Seed yields were reduced by 20-30% and 25-45% under stress at flowering and seed-filling stages, respectively (Brown *et al.* 1985). Stress during the full pod to full seed development periods was the most detrimental to yield than that imposed earlier (Stegman *et al.* 1990). This is the result of little compensation for stress-induced pod abortion and reduced seed weight (Eck *et al.* 1987). Drought stress at the beginning of seed growth resulted in the largest decrease in seed yield as compared to any other crop growth stage (Muchow & Sinclair 1986).

In groundnut, stress during the flowering stage can reduce number of flowers and delay flowering time (Boote *et al.* 1982). However, reduction in the number of flowers did not directly influence the pod yield (Nageswara Rao *et al.* 1988). Groundnut can compensate for reduced number of flowers by producing a new flush of flowers when stress has been relieved (Nageswara Rao *et al.* 1988; Harris *et al.* 1988). Pod yield was most reduced by drought stress during pegging and pod set primarily by reducing pod number rather than kernel weight per pod (Boote *et al.* 1976; Pallas *et al.* 1979; Roy *et al.* 1988). Stress at this stage reduced groundnut yield by 15-30% (Stansell & Pallas 1985; Nageswara Rao *et al.* 1985a; Chapman 1989; Wright *et al.* 1991). Drought at the pod-filling stage reduced pod number and kernel weight and thus was more harmful to yield. Pathak *et al.* (1988) recorded a yield reduction of 62.7% compared to the control when stress was imposed at the pod-filling stage. Late season drought has been shown to reduce pod yield more severely in long-duration varieties than in early ones, mostly through reduction of pod number and seed size (Pallas *et al.* 1979; Wright *et al.* 1991).

Cowpea is a drought tolerant crop and can yield satisfactorily under a greater diversity of climatic, soil and cultural conditions than most other grain legume crops. Seed yield did not reduce during drought stress at vegetative or flowering stages (Wien *et al.* 1979). However, the flowering and pod-filling were considered as the most sensitive stages and a reduction in yield of 35-69% was recorded depending on the timing and the length of drought (Turk *et al.* 1980; Shouse *et al.* 1981).

There have been conflicting reports on the existence of water sensitive stages in faba bean (*Vicia faba*). Some studies have shown that flowering and pod development are sensitive stages (Singh *et al.* 1987) while other results indicated that drought stress during any developmental phase of faba bean was equally effective in reducing yield (Korgman *et al.* 1980; Husain *et al.* 1990; Pilbeam *et al.* 1992).

Navy bean (*Phaseolus vulgaris*) or dry bean is also sensitive to drought at all stages. A reduction of grain yield of 28-37% and 24-40% (Gunton & Evenson 1980) of 37-39% and 42-50% (Gallegos & Shibata 1989) was recorded under stress at the pre-flowering and flowering stages, respectively.

2.1.2 Physiology of yield formation

For increasing crop productivity in low rainfall areas, it is important to select and breed genotypes requiring less water for growth without losing their yield potential. This strategy may involve breeding better adapted and higher yielding genotypes which can effectively use residual soil water, through identifying reliable traits of drought tolerance to complement a conventional breeding program. The physiological basis of crop performance under drought conditions (Shorter *et al.* 1991; Williams & Saxena 1991) as well as many physiological traits in crop plants (Seetharama *et al.* 1983; Turner 1986a; b) have been proposed for improving the performance and yield of crops under drought. However, Passioura (1986) suggested that for any traits to be useful in a crop improvement program it must benefit one of the main functional components in the following biological model for grain yield:

$$\underset{(Y)}{\text{Grain yield}} = \underset{(E_t)}{\text{Total Transpired}} \times \underset{(WUE)}{\text{Water Use Efficiency}} \times \underset{(HI)}{\text{Harvest Index}}$$

This model has been recently used to analyze and identify desirable drought resistance attributes in different groundnut varieties (Mathews *et al.* 1988; Harris *et al.* 1988; Wright *et al.* 1991).

2.1.2.1 **Crop evapo-transpiration**

Total water transpiration (E_t) consists of two components, namely transpiration from the canopy (T) and evaporation from the soil surface (E_s). Biomass accumulation of the crop is linearly related to cumulative transpiration of water and is also directly proportional to the amount of water transpired (Fisher & Turner 1978; Tanner & Sinclair 1983). This indicates that in order to obtain maximum productivity, E_s should be minimized relative to E_t and crops should extract as much water as possible.

During the growing season of rainfed crops, loss of moisture through E_s can be substantial but this is difficult to quantify. Estimations of E_s losses from food legume crops are especially scarce. By contrast, far more attention has been paid to cereal crops (Ludlow & Muchow 1988; Cooper *et al.* 1988). Singh & Russell (1979) estimated that 21% and 23% of total seasonal evaporation was lost as direct evaporation from a sorghum crop growing on Alfisol during the rainy season and post-rainy season, respectively. The E_s accounted for 33% of E_t in a wheat crop (French & Schults 1984). Such a range of losses due to E_s is also likely to apply to rainfed food legumes (Cooper *et al.* 1988). Total water transpiration (E_t) is influenced by many factors which have been reviewed by Taylor *et al.* (1983). Soil water deficit has the greatest effect on E_t by restricting water uptake in the root zone, thereby affecting leaf area development, closing stomata to restrict water loss and ultimately reducing carbon assimilation.

There is very little published information for food legume crops on the critical level of available soil moisture below which E_t declines. However, the effect of drought to reduce E_t through reducing LAI, and thus total dry matter and grain yield, of food legume crops has been reported in different studies with groundnut (Dancette & Forest 1986; Wright *et al.* 1991), chickpea (Singh & Sri Rama 1989), soybean (Stegman *et al.* 1990), mung bean (Phogat *et al.* 1984; Pannu & Singh 1988) and cowpea (Phogat *et al.* 1984). Leaf expansion in soybean was sensitive to shortage of available soil water and leaf area duration and LAI of the groundnut crop was also progressively reduced as soil water deficit developed (Bunce 1978; Pandey *et al.* 1984). Seasonal variation showed a six-fold reduction in daily mean transpiration during the period when groundnut underwent drought stress (Sivakumar & Sarma 1986). Drought resistant groundnut cultivars had higher transpiration rates than susceptible ones under stress conditions although leaf diffusive resistance was similar in both types of cultivars.

Excessive LAI can be detrimental when transpiration exceeds the capability of soil to adequately supply water under drought stress at later stages of the growing season (Reicosky & Heatherby 1990). In this circumstance the risk of a rapidly falling water status is great, with its concomitant rapid senescence of leaves (Passiora 1983). The transpiration rate at high LAI can be controlled by closing stomata, however, droughted crops tend to vary their transpiration rate by varying LA rather than stomatal conductance (Legg *et al.* 1979; Leach 1980) because photosynthesis is reduced with stomatal closure (Joshi *et al.* 1988).

2.1.2.2 **Water use efficiency and transpiration efficiency**

Water use efficiency (WUE) is generally defined as dry matter production per unit of E_t, while transpiration efficiency (TE) is dry matter produced per unit of water transpired (T).

$$\mathrm{WUE} = \frac{\mathrm{DM}}{} \qquad (1)$$

$$TE = \frac{DM}{T} \qquad (2)$$

From equations (1) and (2), WUE can be expressed following Cooper (1988) as:

$$WUE = \frac{TE}{1 + E_s/T} \qquad (3)$$

Because roots are difficult to harvest, WUE is usually defined as above-ground biomass per unit of water used. In practice, WUE is calculated as economic yield per unit of water used. For agronomic purposes, it is often useful in a water limited environment to compare the WUE of crops on the basis of grain yield or economic yield per unit of growing season rainfall (Turner 1986b).

Water use efficiency can be increased by crop management strategies which aim to increase the TE of the crop or to reduce E_s/T or both. However, for the rainfed food legume crops an increase in WUE largely results from changes in the ratio E_s/T (Ritchie 1983), such as adjusting canopy structure or plant population which modify evaporation loss relative to transpiration (Tanner & Sinclair 1983). Generally, any management practices which increase early canopy development and radiation interception will reduce soil evaporation and increase transpiration with little or no increase in total evapo-transpiration (Cooper *et al.* 1988). Because it is difficult to increase the maximum photosynthetic capacity of a crop (Gifford *et al.* 1984), the prospects for improving grain yield through improving efficiency of water use are seemingly low (Ludlow & Muchow 1988).

Transpiration efficiency varies little between plants of the same metabolic class (i.e., C_3 or C_4) that grow in the same environment and it was earlier considered that there was little scope for improvement (Tanner & Sinclair 1983). However, recent evidence in some food legume crops showed large variation in TE among cultivars within a species. The variations in TE were up to

27% and 60% in a range of groundnut cultivars (Mathews *et al.* 1988; Hubick *et al.* 1986). Differences in WUE between different cultivars also exist among several food legume crop species (Muchow 1985a). Direct measurements of TE using whole plant carbon and water balance have shown that moderate drought stress can cause an increase in TE up to 100% while extreme drought can substantially decrease TE (McCree & Richardson 1987). In contrast, WUE appeared less sensitive to drought at the whole-crop level (Fisher & Turner 1978; Hanks 1983).

Improving drought tolerance mechanisms at the leaf level can improve WUE in some legume crops. These mechanisms include leaf movements, leaf surface reflectance, leaf pubescence and temporary stomatal closure during periods of peak evaporative demand (Ludlow & Muchow 1988; Ashraf & Karim 1991). Using isogenic lines in soybean, it was shown that lines with pubescent leaves had significantly lower transpiration rates than either normal or glabrous isolines (Ehleringer 1980).

2.1.2.3 **Harvest index**

Harvest index (HI) is defined as the ratio of economic yield (grain yield) to total dry matter at harvest. Compared to cereals, grain legumes generally have a low HI, and this is particularly so with legumes such as long-duration pigeonpea (Lawn & Troedson 1990). Harvest index is influenced by relative duration of the vegetative and reproductive phases, the relative proportion of pre- and post-anthesis biomass and the extent of remobilization of storage assimilate to grain. It is generally enhanced when the duration of reproductive growth is long and when most of the assimilate produced after flowering is partitioned into seed. Since water stress after anthesis reduces the duration of the reproductive period as a proportion of total crop duration, in grain legumes it causes a reduction in HI (Dantuma & Grashoff 1984). Generally, the effect of drought stress is to reduce HI, nevertheless HI can be enhanced by stress depending on the pattern, intensity and timing of stress relative to crop ontogeny, and the consequent differential effects on vegetative and reproductive growth (Lawn 1982a; Chapman & Muchow 1985; Ludlow & Muchow

1988). For example, HI of four grain legumes (cowpea, soybean, black gram and green gram) was not decreased by drought until the total biomass accumulation was decreased to less than one-third of the control treatment (Lawn 1982a). The HI of cowpea was constant over a wide variation in total biomass production resulting from drought stress (Turk & Hall 1980). In groundnut, moderate water deficits from planting to the start of peg initiation had no effect on total biomass, but increased pod yield by 12-19%, primarily via an effect on pod harvest index (Nageswara Rao *et al.* 1985b). However, pod harvest index was progressively reduced by longer droughts and by drought later in the life cycle (Pallas *et al.* 1979; Nagesewara Rao *et al.* 1985a). The differences in duration of pod-filling and partitioning of assimilate to pod were the main reasons behind cultivar variation in HI (Wright *et al.* 1991). In food legume crops, shortening crop duration, eliminating phenological plasticity, reducing the degree of indeterminateness and increasing the synchrony of flowering and pod set, all of which are variously conducive to higher HI, are likely to increase the vulnerability of the crop to yield loss from intermittent stress during the reproductive growth (Lawn & William 1987; Ludlow & Muchow 1988).

2.1.3 Mechanisms of drought resistance

Turner (1986b) defined drought resistance as the ability of a crop to grow satisfactorily in areas subjected to water deficit. He also suggested three major physiological mechanisms of drought resistance in crop plants including: drought escape, dehydration postponement and dehydration tolerance. By using Levitt's (1980) terminology, resistance to water stress or drought can be achieved by escape, dehydration avoidance or dehydration tolerance. Drought escape usually involves early maturity to escape onset of severe water deficits, whereas resistance involves either avoidance or postponement of dehydration by maintaining water uptake or reducing water loss or desiccation tolerance, which usually involves osmotic adjustment (Begg & Turner 1976; Levitt *et al.* 1980; Kramer 1980; Turner 1986b).

2.2.3.1 Drought escape

Drought escape implies that plants should have a very short life cycle with rapid establishment, growth and maturity. It is generally associated with large developmental plasticity through ability to rapidly change phenological development, especially at the time of flowering and seed development. The variability and plasticity of phenological development diminishes the risk of damage by water stress during critical stages.

In regions where the growing season is short and terminal drought stress is frequent, the use of shorter duration cultivars that enable the crop to escape severe soil water deficit is an advantage contributing to yield stability. Hall and Patel (1985) have described one example in the selection of extreme earliness in cowpea cultivars. Earliness resulted in no yield loss with adequate rainfall, but it provided an effective drought escape mechanism resulting in yields markedly superior to local checks in a terminal drought situation. The well-know 60 days cowpea varieties of Nigeria are also an example of grain legumes which can flower in a determined time irrespective of daylength and so maximize the chances of producing their grain yield by maturing before any substantial stress has developed (Bunting & Kassam 1988). In cereals, the 60-70 days Indian pearl millet varieties are an example of a plant type that can cope satisfactorily in most years in the dryer parts of the semi-arid tropics. The negative correlation between grain yield and number of days to maturity reported in chickpea (Saxena 1987; Saxena *et al.* 1993) and common bean (White & Singh 1990) shows the advantage of earliness for drought escape. Although earliness may reduce potential yield of the crop by reducing TDM, an increase in plant density or HI can, at least to some extent, offset the reduction in total crop growth which occurs with shorter duration (Chauhan *et al.* 1987).

Short-duration varieties are beneficial when early season rainfall or soil moisture is reasonably predictable, but when the soil moisture is less predictable phenological plasticity may be more beneficial than earliness (Mahalakshmi & Bindinger 1985). Many legumes have phenological plasticity and the ontogenic flexibility exhibited by cowpea and black gram to delay the onset of reproductive growth in response to water shortage is one important character making them adapted to water stress conditions (Lawn 1982a; Muchow 1985a). Turk & Hall (1980) observed differences between harvest dates as large as 21 days for cowpea genotypes that were sown at the same time in limiting and non-limiting water supply conditions.

2.2.3.2 **Drought resistance**

2.2.3.2.1 Role of dehydration avoidance

Drought avoidance is the extent to which plant water status is maintained in the presence of environmental drought (Hall 1981). Dehydration avoidance can be achieved by maintaining turgor through increasing water uptake, by reducing water loss, or by osmotic adjustment (Turner 1986b).

Maintenance of water uptake requires the development of roots into deeper soil layers, which enables the crop to explore a greater soil volume for water. The superior ability of groundnut to maintain favorable leaf water status during periods of soil water deficit was related to greater proliferation of roots in the deeper rooting zone (Bunting & Kassam 1988; Devries *et al.* 1989). Similarly, the higher root density in groundnut at lower soil depths conferred superior drought tolerance compared to soybean and mung bean (Pandey *et al.* 1984). The utilization of profile water stored at depth to 120 cm which was reported by Stansell & Pallas (1985) was apparent and explains to some extent the drought resistance of groundnut. In an experiment comparing root growth of four common bean cultivars in relation to drought, the root systems of two drought resistance cultivars (BAT 85 and BAT 477) reached a depth of 1.3 m under the stress condition while the two other drought sensitive cultivars (BAT 1224 and A 70) did not extend their roots beyond 0.8 m (Sponchiado *et al.* 1989). In contrast, no differences in rooting depth under irrigation were observed.

It is likely that osmoregulation occurs in root tips, which allows roots to penetrate soil layers of a different water status (Davies *et al.* 1986). The growth of roots into deeper soil layers under drought stress is a function of both genotype and environment (Gulmon & Turner 1978; Begg & Turner 1976; Malik *et al.* 1979; Sharp & Davies 1985).

The reduction of water loss is most dependent on reduction of leaf area (LA) due to either a reduction in LA development and/or leaf senescence. Sensitivity of LA expansion rate to water deficit is a mechanism for reducing water loss (Kowal & Kassam 1978; Turk & Hall 1980; Muchow 1985a). When drought stress develops, the crop tends to adjust its transpiring surface to balance the water loss against water uptake and to avoid a steep reduction in shoot water potential (Bradford & Hsiao 1982). Leaf area development appears to be more sensitive to water deficit than either leaf senescence or leaf photosynthesis (Turner 1986a). For example, leaf expansion rate of soybean was significantly reduced when leaf water potential (LWP) decreased below -1.0 to -1.2 MPa whereas leaf senescence and shedding occurred only when minimum LWP fell below -2.0 MPa (Constable & Hearn 1978).

Stomatal closure provides another mechanism for reducing water loss. Stomata of crop plants are sensitive to vapor pressure deficit which is an important mechanism for maximizing TE (Farquhar 1978). By reducing stomatal conductance during periods of maximum daily evaporative demand without a significant reduction in total daily photosynthesis, WUE of the crop will be increased (Schulze & Hall 1982; Davies 1986). For example, partial stomatal closure of cowpea which was subjected to drought resulted in improved WUE (Hall & Schulze 1980). Reduced stomatal aperture can increase TE when the plant is subjected to moderate levels of water stress. The rate of photosynthesis is reduced proportionately less than the transpiration (Bradford *et al.* 1983; Morrison 1985).

Finally, other mechanisms which reduce water loss without affecting LA are shedding of radiation through leaf rolling, leaf movements and radiation reflection. Such changes can effectively reduce the radiation load on leaves and allow the plant to dissipate less energy as latent heat and maintain photosynthesis at a lower transpiration rate (Shackle & Hall 1979; Berg & Heuchelin 1990). For example, leaves of cowpea are oriented perpendicular to incoming solar radiation when water supply is adequate so that photosynthetic rate is at maximum and water loss is high. When water stress occurs, leaves orient parallel to the incoming radiation to reduce heat load to a minimum thereby lowering transpiration (Shackle & Hall 1979). The mechanism of alleviating water stress by leaflet angle variation was also studied in groundnut by Babu *et al.* (1983), where radiation avoidance by leaf closure at different degrees under water stress was demonstrated. Current evidence suggested that leaf rolling is regulated by leaf turgor (Henson 1982; Hsiao *et al.* 1984) and it postpones dehydration and development of leaf water deficit (O'Toole *et al.* 1984). However, the degree of leaf movement, the threshold soil moisture level and plant water status that regulates this movement varies among and within crop species, which could be partly responsible for their relative performance under water stress (Lawn 1982a; Muchow 1985a; Squire 1990).

2.2.3.2.2 Role of dehydration tolerance

Tolerance of dehydration is considered to arise at the molecular level and depends on membrane structure and enzyme activities. It depends on the ability of membranes to withstand degradation and the ability of membranes and cytoplasm to withstand denaturation of the proteins (Gaff 1980). Plant growth regulators may play a role in dehydration tolerance (Levitt *et al.* 1980) but osmotic adjustment which increased the dehydration tolerance in rice leaves may also be important (Hsiao *et al.* 1984). The accumulation of sugars can improve dehydration tolerance by osmotic protection of the membranes or by a high cellular elasticity to reduce injury from mechanical damage at low turgor (Kim & Lee 1984).

Osmotic adjustment is considered to influence a range of physiological processes in plants. It maintains cell turgor, stomatal opening and photosynthesis at low LWP (Turner *et al.*

1978; Ackerson *et al.* 1980; Wright *et al.* 1983; Ludlow *et al.* 1985). Moreover, it enables plants to defer leaf rolling or leaf death to low LWP and maintains root growth which allows greater exploration of soil by roots at low soil water potential (Sharp & Davies 1979; Hsiao *et al.* 1984). Yields were higher in those cultivars or genotypes that osmotically adjusted under water stress conditions compared to those that do not (Morgan 1983; Wright *et al.* 1983). The degree of osmotic adjustment varies with species and genotypes and with the rate and degree of stress (Turner & Jones 1980; Shackel & Hall 1983; Morgan & Condon 1986; Flower & Ludlow 1987; Andersen & Aremu 1991).

Grain legume crops generally have lower osmoregulation than cereal crops (Turk & Hall 1980; Turner *et al.* 1978; Morgan 1984). High osmotic adjustment occurs in expanding leaves of groundnut which allows them to maintain higher turgor levels during periods of severe stress and this adjustment is rapidly lost when stress is released (Stirling *et al.* 1989b). In chickpea, genetic variability for osmotic adjustment between genotypes is important in improving dehydration avoidance and it took place when the stress increased progressively and the differences in osmotic potential were 0.3-0.5 MPa between stressed and non-stressed plants, depending on different cultivars (Lecoeur *et al.* 1992). In soybean, osmotic adjustment plays a more important role in maintaining turgor pressure, reaching values of up to 0.5 MPa at a water potential of -1.0 MPa (Morgan 1992). Common bean (*Phaseolus vulgaris*) cultivars also showed differences in osmotic adjustment when drought stress occurs (Villarreal & Saavedra 1983). However, LWPs were similar in two species of *Phaseolus* tested in a greenhouse experiment and no osmotic adjustment under water stress was observed (Markhart 1985). The capacity of peas (*Pisum sativum*) to adjust osmotically in response to drought seems to be highest (Andersen & Aremu 1991) in comparison with cowpea (Shackel & Hall 1983; Muchow 1985b) or soybean (Cortes & Sinclair 1986). Thus, osmotic adjustment appears to be an important drought resistance mechanism for maintaining productive processes under water limited conditions and it can be used as a selection criterion in breeding for drought tolerance (Ludlow & Muchow 1988;

Al-Dakheel 1991).

2.1.2 Waterlogging

Waterlogging of the soil rapidly and dramatically alters both the physical and biological environment of plant roots which affect their growth and development. Grain legumes are particularly sensitive to waterlogging and their growth and yield response varies with crop species, and duration and timing of waterlogging. Susceptible species include pea (Jackson 1979; Belford *et al.* 1980); bean (Williamson 1968; Forsythe *et al.* 1979); pigeonpea (Rachie & Roberts 1974; Chauhan 1987; Troedson *et al.* 1990) and some cultivars of cowpea and mung bean (Rachie & Roberts 1974; Minchin *et al.* 1978; Lawn & Byth 1979; Stanley *et al.* 1980). Soybean is relatively tolerant to waterlogging (Hunter *et al.* 1980; Troedson *et al.* 1989). Soil saturation caused yield loss of mung bean to the extent of 73% compared with optimally-watered plants (Hamit *et al.* 1989). The yield loss was primarily through reduced canopy development, inhibition of photosynthetic rates and lower dry matter production. It is generally considered that the longer the waterlogging period the more adversely are crops affected. For example, the growth of cowpea is adversely affected by short-term flooding leading to major reduction in root and shoot dry weight and seed yield (Minchin & Summerfield 1976). Leaves turned yellow and crop growth reduced when the duration of waterlogging was short, but when waterlogging is prolonged it can induce death of roots and nodules and thus a greater yield reduction.

Excessive soil moisture stress inhibits various normal physiological and biological processes and often results in morphological alteration (Kozlowski 1984; Jackson & Hall 1987). The most common feature by which excessive soil moisture can limit yield of the food legume crops is by a reduction in nitrogen fixation caused by reduced oxygen supply to the nodules (Smith 1987). Poor nodulation of chickpea grown under conditions of excessive soil moisture has been reported by Argikar (1970).

Waterlogging has also been considered to be a major problem limiting the growth of pigeonpea in deep Vertisol soil of India and has been recognized as one of the major constraints affecting stability of production in most regions where pigeonpea is grown (Reddy & Virmani 1981). By planting the pigeonpea crop on ridges, yield can be increased by 30% over planting in a flat soil surface, probably because of a reduced waterlogging effect (Chowdhury & Bhatia 1971). Growth and grain yield of short-duration pigeonpea were reduced when grown during the rainy season on both Alfisol and Vertisol because it faced temporary waterlogging due to heavy rainfall events resulting in anaerobic conditions in the soil under a saturated condition (Okada *et al.* 1991).

Susceptibility of short-duration pigeonpea to waterlogging is a major concern as it has very little time for compensatory growth. The grain yield on Vertisol which faced waterlogging was generally half of what could be obtained on well-drained Alfisol (Chauhan *et al.* 1992). Extra-short-duration pigeonpea genotypes are also highly sensitive to waterlogging. Dry matter accumulation and seed yield of late-sown ESD pigeonpea genotypes in Alfisol was reduced when their early growth stages coincided with saturated soil condition (Nam *et al.* 1993).

2.2 ADAPTATION OF PIGEONPEA TO DROUGHT

Pigeonpea is often described as a crop well adapted to dry conditions and can be grown in wide range of cropping systems in low rainfall, rainfed areas of the tropics and sub-tropics (Whiteman et al. 1985; Singh and Das 1987). Some evidence shows that it can withstand drought better than other crop, which reflects its adaptation to these areas.

2.2.1. Development of Deep Root Systems

Traditional, longer duration pigeonpea has a deep and extensive root system with large lateral roots (Rachie & Roberts 1974; Sheldrake & Narayanan 1979; Chauhan 1992) which helps the plant in extracting soil moisture from deeper soil layers. Pigeonpea roots can proliferate as deep as 1.9 m and have a root length of more than 1800 m beneath every m^2 of soil surface (Chauhan 1992). Though most of the water was extracted from the 0-52 cm soil layer, the roots of medium-duration pigeonpea could extract water from a soil depth as deep as 187 cm in a deep Vertisol (Singh & Russell 1981). This feature is very important to the pigeonpea crop, especially for long- or medium-duration varieties because they have to reach maturity in a drought stress condition and depend almost entirely on water stored deep in the soil profile during the postrainy season.

In a greenhouse trial, Onim (1983) showed that tap root length of pigeonpea seedlings measured from germination for 31 days showed faster growth in populations selected for drought resistance than in other genotypes. The difference in root depth at 31 days was up to 18 cm and deep rooting was positively correlated with seed yield per plant. The root systems of SD pigeonpea genotype ICPL 87 were also able to penetrate through the hardpan layer of iron nodules of an Alfisol, which generally formed at 40-60 cm depth and can extend up to 165 cm depth, while soybean and maize were generally confined to within 30-45 cm of the soil surface (Arihara *et al.* 1991a).

2.2.2. Reduction in Water Loss

Changes in leaf angle and rolling are common responses to water stress in pigeonpea in order to reduce the water loss. Such movements through leaf angle changes in pigeonpea plants are more pronounced during early afternoon than during the early morning or late afternoon (Lopez 1986). The ability of pigeonpea leaves to reduce radiation absorption by shedding leaves or altering leaf orientation under drought stress is a very common adaptation trait (Muchow 1985b).

Under stress conditions, the pigeonpea crop closes its stomata at 1/3 of full sunlight in young leaves and at 1/4 of full sunlight in older leaves so that leaves transpired at lower rates compared to other grain legume crops (Rawson & Constable 1981). As water deficit develops, both LWP and stomatal conductance declined gradually permitting plants to continue photosynthesis.

2.2.3. Tolerance of Tissue Water Deficit

Pigeonpea exhibits high levels of osmotic adjustment and low critical relative water content of leaves under water deficit development (Flower & Ludlow 1986; Sinclair & Ludlow 1986). The range of osmotic adjustment values of 0.7-1.3 MPa among 22 tested pigeonpea accessions demonstrates that pigeonpea has relatively high capacity for osmotic adjustment compared to other grain legume crops (Flower & Ludlow 1987). Pigeonpea leaves can survive at a water potential of -6.0 MPa while they lose their turgor at a level of -2.5 MPa. Osmotic adjustment permits leaves to survive at a lower water potential by reducing the rate of decline in leaf water content (Flower & Luddlow 1987). Because low critical water status influences survival, it has no direct effect on yield components but it contributes to dehydration tolerance, leaf survival under intermittent drought stress and hence to yield stability. However, genotypic variation in the osmotic adjustment level of a wide range of pigeonpea accessions was relatively small (Flower & Ludlow 1987).

2.2.4. Phenological Plasticity

Pigeonpea has wide range for maturity duration extending from 90 to 300 days (Saxena & Sharma 1990). Thus, there is a great opportunity to use pigeonpea genotypes differing in their duration to match the period of available of water supply for an environment so as to escape drought (Lawn & Williams 1987). The perennial nature and phenological plasticity which enable pigeonpea to adjust its duration, particularly at the reproductive phase by producing another flush of flowers and pods after stress is relieved, is a useful drought escape response. The wide range variation for flowering time and the existence of indeterminate growth habit would increase the adaptation of pigeonpea to different drought stress situations (Lawn 1981; 1988).

2.2.5 Stability of Production.

The traditional mixed or intercropping systems of pigeonpea with sorghum, pearl millet or groundnut in semi-arid environments give another perspective to its adaptation to drought at the level of the cropping system. In these cropping systems, pigeonpea is one of the important crop components which is more stable than the other components over seasons and years. For example, in the sorghum/pigeonpea, pearl millet/pigeonpea or groundnut/pigeonpea intercropping systems, it is pigeonpea that is more stable over environments and seasons than are the cereals or groundnut (Rao & Willey 1980). The stability of sorghum/pigeonpea intercropping systems from 81 experiments showed that the coefficient of variation for grain yield of sole pigeonpea (cv = 44%) was more stable than that for sole sorghum (cv = 49%). The intercrop was even more stable than both (cv = 39%). Regressions of yield against an environmental index indicated that sole pigeonpea was expected to fail once in 5 years, sole sorghum once in 8 years but intercropping only once in 36 years (Rao & Willey 1980).

CHAPTER

EFFECT OF TIMING OF DROUGHT STRESS ON EXTRA-SHORT-DURATION PIGEONPEA GENOTYPES

3.1 INTRODUCTION

Grain yields of short-duration (SD) and medium-duration (MD) pigeonpea grown during the rainy season in India are significantly reduced by moisture stress, particularly on lighter soil such as Alfisols. Terminal drought can reduce grain yield of MD genotypes by 20-50% on different soils (ICRISAT 1987) while intermittent periods of drought can affect growth and yield of SD genotypes (ICRISAT 1988; 1989).

Extra-short-duration (ESD) pigeonpea genotypes, which mature within 90-110 days, have the potential of being grown in rainfed semi-arid environments where they can exploit limited quantities of soil moisture during the crop growth cycle. Their grain yield compared favorably with that of SD genotypes grown under rainfed conditions in Alfisol (Chauhan *et al.* 1993). This is probably because the growing period better matched the length of growing season, as determined by available soil moisture, so that they escaped severe drought. However, large differences in the grain yield of ESD genotypes on different soil types and across seasons were seemingly related to fluctuations in amount and distribution of rainfall (Chauhan *et al.* 1993). Depending on prolonged dry spells during the rainy season, ESD pigeonpea can face drought of varying insensitivity at any growth stage and their grain yield will be reduced.

Food legume crops are particularly sensitive to water deficit during the flowering and when pod numbers are being determined in cowpea (Babalola 1980; Ziska *et al.* 1985), in dry bean (Gallegos & Shibata 1989; Gallegos & Adams 1991), in groundnut (Nageswara Rao *et al.* 1988; Wright *et al.* 1991), in soybean (Brown *et al.* 1985) and in various tropical legume crops (Muchow 1985a). The effects of timing of drought on physiological traits of some other important food legume crops such as groundnut, soybean and cowpea are well documented (Devries *et al.* 1989; Mathews *et al.* 1988; Wright *et al.* 1991; Stegman *et al.* 1990; Muchow 1985a; b), but very few data are available for SD and ESD pigeonpea. Because ESD pigeonpea represents virtually a new plant type, little is known about the effects of water stress during crop growth associated with its physiological characteristics and grain yield.

At ICRISAT Center, investigations on the effects of drought stress at different growth stage of SD pigeonpea had revealed that the flowering stage was most susceptible to drought. Drought at the pre-flowering and pod-filling stages appeared to reduce grain yield less than drought at the flowering stage (ICRISAT 1989). Yields of indeterminate genotypes were relatively more stable under stress compared to those of the determinate genotypes. Non-synchronous flowering and high leaf retention in some SD genotypes under stress were found to be related to higher grain yield.

The major attraction in using ESD pigeonpea in drought prone environments is their ability to escape terminal drought stress. It is, however, necessary to know if they possess any other traits that may assist them in overcoming water deficits during the crop growth cycle, especially at the reproductive stage. The need for identifying desirable traits in ESD pigeonpea that may play a major role in the resistance mechanism is crucial to understand the nature of their yield stability under water stress conditions. Such knowledge may open the way for the development of breeding strategies to enhance drought resistance of ESD pigeonpea. This would require a greater understanding of the effect timing and duration of drought stress at different crop growth stages affecting plant traits essential to yield and drought resistance.

The main aims of this study were to identify the most drought susceptible stage of ESD pigeonpea, to investigate the effect of different timing of drought stress on physiological traits, yield and yield components, and to evaluate plant traits associated with better performance under any particular type of drought stress so as to better focus on improving drought resistance.

3.2. MATERIALS AND METHODS

3.2.1. Site of the experiment

Two experiments were conducted at ICRISAT Center, Patancheru (18° N, 78° E), Andhra Pradesh, India during the rainy seasons of 1991 and 1992. These experiments were carried out on medium-deep Alfisols (Udic Rhodustalf) with 60-100 mm plant available water holding capacity (AWHC). Relevant chemical characteristics of the soil are given in Table 3.2.1.

Table 3.2.1: Soil chemical properties from 0-15 cm soil layer of different experimental fields in 1991 and 1992.

Season	pH	Electrical conductivity (dS m-1)	Organic[a] Carbon (%)	Available[a] Olsen P (mg kg^{-1} soil)	Available[a] N (mg kg^{-1} soil)	Total N[a] (mg kg^{-1} soil)
1991	7.85	0.45	0.33	4.5	44.5	502
1992	8.13	0.30	-[b]	6.1	30.9	764

[a]: Analysis methods: Organic carbon (Nelson & Sommer 1982)
Available nitrogen (Keeney & Nelson 1982)
Available phosphorus (Olsen & Sommer 1982)
Total nitrogen (Dalat *et al.* 1984)

[b]: Not determined

3.2.2. Experimental design and layout

Experiment 1: Effect of timing and duration of drought stress on extra-short-duration pigeonpea genotypes.

Experiment 1 was conducted in the rainy season of 1991 under an automatic rainout shelter (ROS) which is capable of excluding rain from an experimental area of 50 m x 25 m. A split-plot design with four replications was used. Six drought stress treatments representing individual or combinations of different crop growth stages were assigned to the main-plots.

1) Pre-flowering stress (PRFL-ST) : Stress at 40-60 DAS

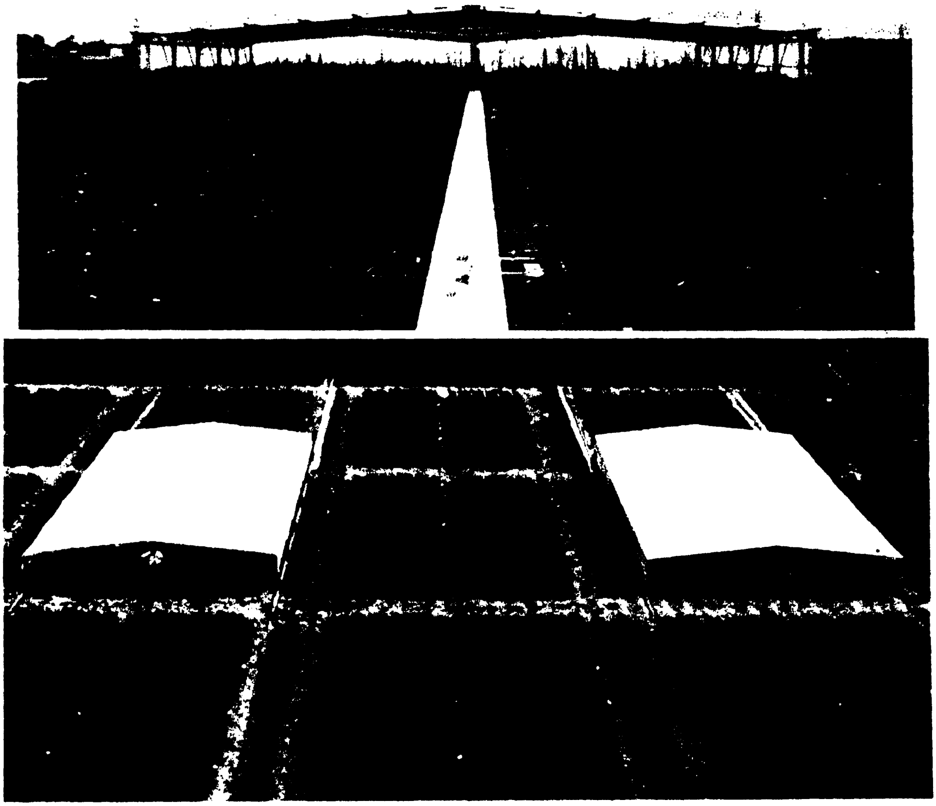


Plate 3.3.2.1: The automatic rainout shelter (above) used in the experiments of the 1991 and 1993 seasons and the manual rainout shelter (below) used in the experiment of the 1992 season.

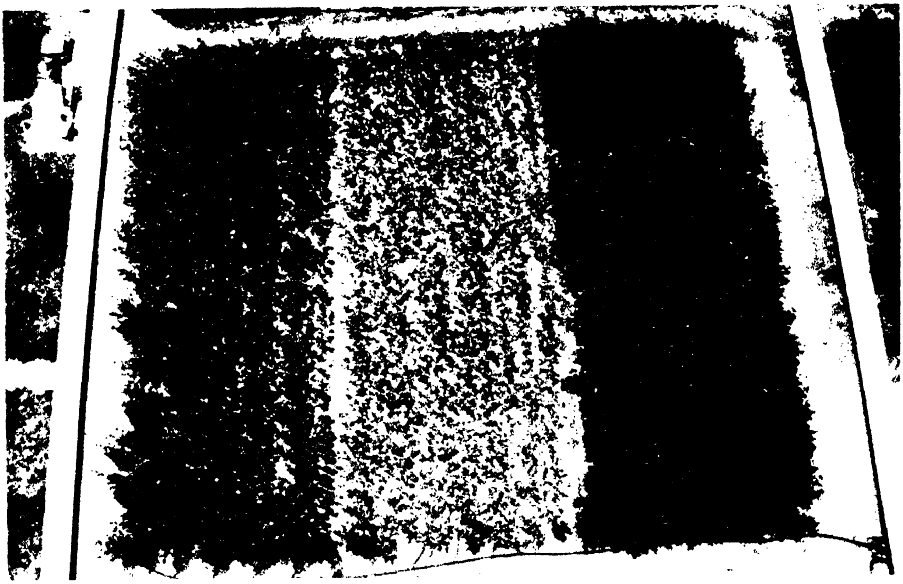


Plate 3.3.2.2: Response of extra-short-duration pigeonpea to drought stress during pre-flowering stage (left) and pre-flowering + flowering stages (middle) in comparison to the no-stress treatment (right), 1993 season.

2) Flowering stress (FL-ST) : Stress at 55-75 DAS

3) Pod-filling stress (PFILL-ST) : Stress at 75 DAS to harvest

4) Pre-flowering + flowering stress (PRFL+FL-ST)

5) Flowering + pod-filling stress (FL+PFILL-ST)

6) No-stress (N-ST)

The main-plot size was 3.0 m x 10.0 m. Two main plots were separated from each other by 1.2 m wide border strips to minimize water seepage from the adjacent main-plots.

The following four determinate (DT) or indeterminate (IDT) types of ESD pigeonpea genotypes of comparable phenology were assigned to sub-plots:

1)	ICPL 84023	(DT)
2)	ICPL 89021	(DT)
3)	ICPL 88039	(IDT)
4)	ICPL 89002	(IDT)

Each sub-plot consisted of 10 rows (3.0 m) each 2.5 m long. Sowing was done on 30 May 1991.

Experiment 2: Effect of timing of drought stress on a range of extra-short-duration pigeonpea genotypes.

This experiment was carried out during the rainy season of 1992. The stress plots were protected against rains by a set of manually-operated mini-shelters consisting of polyethylene sheets over gabled metal frames 7.5 m wide, 15 m long and 2.0 m height at the midpoint.

The experiment was laid out in a split plot design with three replications. The four main-plot treatments, comprising stress at various stages, were:

1) Pre-flowering stress (PRFL-ST): Stress at 35-55 DAS

2) Flowering stress (FL-ST) : Stress at 55-80 DAS

3) Pod-filling stress (PFILL-ST) : stress at 80 DAS to harvest

4) No stress

The main-plot size was 6.0 m wide and 12.0 m long. Two border strips along the main-plot were covered by polyethylene sheet to prevent infiltration of water to plots. Thus, water captured by the ROS during rainfall events was diverted into drains (0.30 m depth) dug at two ends of the shelter and which led away from the ROS areas.

Eight ESD pigeonpea genotypes used for comparison in the sub-plots, included the same four genotypes as used in the previous year and four additional genotypes:

1) ICPL 83015 (DT)
2) ICPL 84023 (DT)
3) ICPL 88007 (DT)
4) ICPL 89021 (DT)
5) ICPL 87111 (IDT)
6) ICPL 88032 (IDT)
7) ICPL 88039 (IDT)
8) ICPL 89002 (IDT)

The sub-plot sizes were 2.4 m x 3.0 m, comprising 8 rows 30 cm apart and 3.0 m long. Sowing was done on 16 June 1992.

3.2.3. Agronomic practices

All fields were thoroughly tilled before sowing and a basal dose of 100 kg ha^{-1} diammonium phosphate (18% N and 20% P) was incorporated before sowing. Then ridges spaced at 60 cm were established. Seeds were treated with Thiuram and Ridomil (75%) at the rate of 3 g kg^{-1} before sowing to control soil borne fungal diseases. Sowing was done by hand in shallow furrows opened on both sides of 60 cm ridges with 30 cm inter-row and 10 cm intra-row spacing between the seed hills. Two seeds per hill was sown and thinning to one plant per hill at the required density was done at 20-25 DAS.

A pre-emergence herbicide mixture containing fluchloralin (45%) at 1.5 kg ha^{-1} with prometryn (50%) at 1.5 kg ha^{-1} and paraquat (0.25%) at 4.0 kg ha^{-1} was applied one day after sowing. Two or three additional hand weedings were also given at 20-25 days intervals depending on weed infestation in each experiment. Different pesticides were used, including endosulfan (35%) at 2 kg ha^{-1} or monocrotophos (36%) at 1.0 kg ha^{-1} during the flowering stage and quinalphos (25%) or mythomyl (24%) at 2 kg ha^{-1} during the pod-filling stage to minimize losses from attack by pod borers (*Helicoverpa armigera*) and spotted borers (*Maruca testulalis*). For controlling phytophthora blight disease, Ridomil (75%) at 1.0-2.0 kg ha^{-1} was also sprayed 5 and 2 times in experiments 1 and 2, respectively. No serious problem of weeds, diseases and pests damaging the crops was recorded in either experiments.

3.2.4. Irrigation and stress treatments

After sowing, all the fields were uniformly irrigated to field capacity using perforated pipes so that soil moisture was sufficient for seed germination and good crop establishment. The Experiment 1 under the automatic ROS in 1991 was kept under rainfed conditions for the initial 15 days. After that, the shelters were activated throughout the growing period in order to exclude rains to effectively control soil moisture in each treatment. Water applied to each main-plot was through a drip irrigation system at 3-5 days interval depending on the dryness of soil surface layer. Drought stress treatments were created by closing lateral irrigation lines to the specified main-plot. In contrast, in Experiment 2 where a manual ROS was used, the experiment was kept under completely rainfed conditions and the shelter only used to cover the stressed plots. Furrow irrigation was applied when soil moisture was insufficient for N-ST plots. The stress treatment was imposed by stopping irrigation and closing the shelters during rainfall.

The total water applied at each time of irrigation to both experiments was recorded through a flow meter on the main irrigation line.

3.2.5. Observations and measurements

3.2.5.1. Meteorological observations

Weather data were obtained from the ICRISAT meteorological station located about 500 m away from the experiment sites.

Seasonal weather data of the two growing seasons (from June to October) of 1991 and 1992, in comparison with long-term average (1978-1992), recorded at ICRISAT Center is presented in Figure 3.2.5.1. The weather was substantially different between the two years of study. The total amount of rainfall during the crop growing period of 1991 and 1992 was 717 mm and 610 mm, respectively which was 5.5-19.5% less than the long-term average of 759 mm. More rainfall occurred during the reproductive stage in 1992, compared with 1991, and evaporative demand was also lower. The FL-ST treatment in 1992 appeared less affected by water stress because this period coincided with a peak of rainfall. Further, the small manual ROSs were only large enough to cover the stress plots themselves, without much provision for borders, thus water seepage from outside tended to spread into stress plots at deeper soil layers. Higher temperature during the vegetative growth period in 1992 possibly hastened flowering and all genotypes flowered 4-7 days earlier in 1992 than in 1991.

3.2.5.2. Soil moisture

Soil moisture during crop growth in each main plot of both experiments was monitored at weekly intervals. A single aluminum access tube was installed in the central row of each main plot (for the same genotype) to a depth of 120 cm and was used for soil moisture content measurement in the 15-30, 30-45, 45-60, 60-75, 75-90 and 90-105 cm layers by a neutron probe (Model 2651 Troxler Electronic Laboratories, Inc, USA). Soil moisture content in the 0-15 cm soil layer was determined gravimetrically. All soil water content values at different layers were converted into volumetric water content using a bulk density of 1.50 g cm^{-3} and a calibration curve to convert

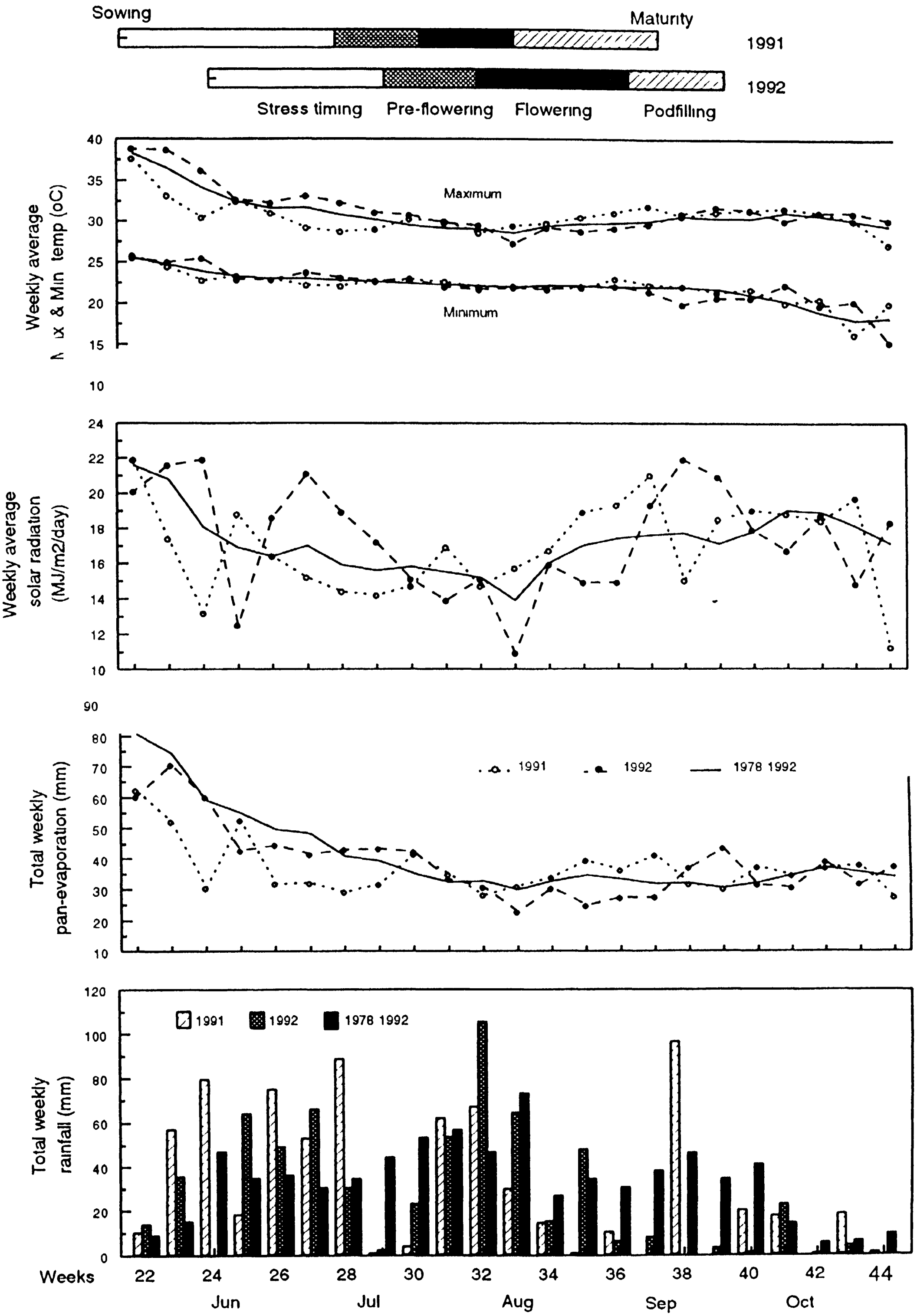


Figure 3.2.5.1: Weekly averages of daily maximum temperature, daily minimum temperature, daily total solar radiation, and daily totsl pan-evaporation, and total weekly raifall, season 1991, 1992 and long-term priod from 1978-1992.

neutron count to volumetric soil moisture content.

Total evapo-transpiration (E_t) was estimated using the following water balance equation:

$$E_t = R+I+(S_1-S_2)-R_o-D_r$$

Where, R and I are the amounts of water (cm) applied to the crop by rainfall and irrigation, S1 and S2 are the amounts of water stored in 105 cm soil profile at the crop germination and maturity stage, respectively. Deep drainage (D_r) and surface runoff (R_o) during irrigation periods was assumed to be negligible.

3.2.5.3. **Plant growth**

3.2.5.3.1. Phenology

Critical phenological stages were determined as given below:

- Days to 50% flowering: Number of days from sowing to the date when 50% of the plants in the plot have opened flowers
- Days to maturity· Number of days from sowing to the time when more than 75% of pods on the plant have a brown color (pods are dry).

3.2.5.3.2. Leaf area expansion rate

Leaf area expansion rate (LER) was estimated by tagging 5 newly unfolded leaves on 5 plants in each plot with woollen threads. The products of leaflet length and width measurements at two-day intervals were used to estimate LER using a linear regression equation for each pigeonpea genotype. The equation was determined from the area of leaves measured directly with the leaf area meter and regressed again the products of length and width of the same leaflets. The LER was calculated as mm^2/leaflet/day.

3.2.5.3.3. Growth analysis

Three plants were sampled from each plot, by destructive sampling for growth analysis at 7-10 day intervals, starting before the stress treatment. The plants were cut at the base of stem and thus roots were not included in calculating total dry matter (TDM). Plants were transferred to the laboratory in polyethylene bags and kept in a cool room at 5° C until separation into component plant parts (leaves, stem and pods and flowers) which was completed on the same day for sampling.

Leaf area was determined by using an automatic leaf area meter (Delta T Devices Ltd., Cambridge, England). Leaf area index (LAI) was calculated as:

$$LAI = LA/GA$$

where, LA is leaf area and GA is ground area.

Dry mass was determined for leaves, stem and reproductive structures (including flowers and pods) after oven-drying at 80° C to a constant weight.

3.2.5.4. **Light interception**

Canopy light interception (LI) was measured at mid-day by using a 1.0 m line quantum sensor (LI-COR, Inc.) and a quantum sensor (LI-COR, Inc., Nebraska, USA) at different growth stages in stressed and N-ST plots. The line quantum sensor was placed across crop rows below the canopy to measure the radiation transmitted to the ground (I) while the quantum sensor was placed above the canopy to measure the total incoming radiation (I_o). The output of both sensors was simultaneously recorded using a polycorder (Omnidata, International Inc., USA) and later transferred directly to a computer. The LI value (%) was calculated using following equation:

$$LI(\%) = [(I_o-I)/I_o] \times 100$$

3.2.5.5. **Leaf temperature**

Canopy temperatures were measured weekly using an infrared thermometer (Telatemp, model AG 812, USA) starting at the time when canopies fully covered the ground. The measurement was made at mid-day from 1000-1200 h on a clear day by holding the thermometer at eye level and aiming at the plot. The target area diameter was about 30 cm^2. Three measurements were performed for each plot and average leaf temperature and differential temperature with air temperature was calculated.

3.2.5.6. **Leaf water relations**

Two sets of five youngest fully expanded trifoliate leaves of pigeonpea were sampled at mid-day in stressed and N-ST plots. One set was used to determine leaf relative water content (RWC) and other was used to determine leaf water potential (LWP) and osmotic potential (OP). Sampled leaves were put in small sealed polyethylene bags and kept on ice to minimize water loss from evaporation. Measurements of leaf water status parameters was done in the same day of sampling and were determined following Kramer (1988) and Turner (1988).

3.2.5.6.2. Leaf water potential

The pressure chamber technique was used to determine LWP of pigeonpea leaves as described by Turner (1988). A leaf of pigeonpea was placed in a pressure chamber (Model B, Soil Moisture Equipment Corp., Santa Barbara, CA, USA) with the cut end of the leaf petiole protruding through a gas-tight seal of the chamber so that it could be observed for sap exudation. The pressure in the chamber was gradually increased by compressed air from a cylinder until the sap just began to exude out at the cut surface. At this point, the equilibrium established between the leaf cells and the xylem sap and the gas pressure in the chamber was considered to be exactly the water potential of the leaf cells

3.2.5.6.3. Osmotic potential

After measurement of LWP, the same leaf samples were placed in sealed polyethylene bags and transferred to a deep-freezer (-40° C). The leaf samples were then thawed and centrifuged for 5 minutes. The sap expressed from leaf samples was used to determine OP in an automatic micro-osmometer (Roebling). The OP data obtained by using the micro-osmometer were calibrated with a range of sodium chloride solutions. Osmotic potential at full turgor (OP_{100}) was calculated according to the formula of Wilson *et al.* (1979) assuming that apoplastic water content is negligible:

$$OP_{100} = \frac{OP \times RWC}{100}$$

Osmotic adjustment is the difference between the OP_{100} of N-ST and stressed pigeonpea leaves (Flower & Ludlow 1986).

3.2.5.6.4. Turgor potential

Turgor potential (TP) was computed by subtracting OP from LWP values, assuming matrix potential to be negligible.

$$TP = LWP - OP$$

3.2.5.6.1. Relative leaf water content

Fresh weight of sampled leaves was determined first and then turgid weight was obtained after soaking the leaves in distilled water for 6-8 h at room temperature. After soaking, leaves were quickly and carefully blotted dry with tissue paper prior to determining turgid weight. Dry weight was obtained after oven-drying the leaf samples to a constant weight. The RWC was calculated by the equation:

$$RWC(\%) = \frac{\text{fresh weight - dry weight}}{\text{turgid weight - dry weight}} \times 100$$

3.2.5.7 **Abscission**

One perforated plastic tray 36 cm long, 26 cm wide and 4.5 cm deep was kept under the canopy in each plot during crop growth. Abscised leaves, flowers and pods were collected at 2-3 day intervals to determine dry mass of each component. Cumulative abscission of these components was determined as g per plant for each period of drought. Total number of abscised flowers per plant was also counted.

3.2.5.8 **Total dry matter at harvest and grain yield**

Total dry matter at harvest and grain yield was determined by harvesting all plants in each net plot. For calculating TDM, total number of plants in each net plot was counted and then total fresh weight was then recorded. Then, the fresh weight of a 5-plant sub-sample, which was randomly selected, was also taken and its dry weight was recorded after oven drying at 80° C to a constant weight. Finally, TDM in each net plot was determined and expressed as t ha^{-1}.

For determining grain yield, all pods of a net plot were picked and seeds were separated by threshing in a machine after drying pods in sunlight. Grain yield was expressed as t ha^{-1} at 10% moisture basis for all genotypes.

3.2.5.9 **Yield components**

The five plant sub-samples which were used for calculation of TDM were also used for estimating yield components including: Number of pods per m^2, number of seeds per pod and 100 seed mass. Harvest index (HI) was calculated as a ratio between grain yield and total above ground dry matter (DM) at harvest in each plot.

3.2.5.10 **Water use efficiency**

Water use efficiency (WUE) was calculated as a ratio between the grain yield and total E_t

estimated for each main-plot treatment.

3.2.6 Statistical analysis

Experimental data were subjected to analysis of variance using a standard split-plot design analysis as described by Gomez and Gomez (1984) and using the GENSTAT package (Genstat Manual 1983) in a VAX mainframe computer system at ICRISAT Center. Regressions were made of the relationships among plant growth parameters against grain yield under different timings of drought stress and the N-ST treatment.

3.3 RESULTS

3.3.1 Soil Moisture Depletion and Water Extraction during Stress Periods

Under N-ST condition, available soil moisture in the soil profile (0-45 cm and 60-105 cm) was significantly greater in 1992 than in 1991 (Figure 3.3.1.1a). Seasonal available soil water of drought profiles changed more at 0-45 cm during all stress periods and little variation was noticed at the deeper layer (60-105 cm) (Figure 3.3.1.1b; c; d). Under FL-ST and PFILL-ST treatments, the soil moisture decreased to a lower level in 1991 compared to that in 1992 (Figure 3.3.1.1c & d) which indicated that the stress during these periods was more severe in 1991 than in 1992.

Soil water depletion at the end of the stress decreased with soil depth and there were significant differences in soil water between drought and N-ST treatments at the end of each stress, especially at 0-45 cm soil depth (Figure 3.3.1.2b; c; d). Total soil water extraction was higher in 1991 than in 1992 except under PRFL-ST (Figure 3.3.1.2b). The variations in available soil water at 0-45 cm depth was quite distinct with extended drought stress at pre-flowering + flowering (PRFL+FL) and flowering + pod-filling (FL+PFILL) in 1991. In both cases, total available soil water in the 0-105 cm soil profile was reduced to 45-50% of the N-ST treatment by the end of stress (Figure 3.3.1.2c; d).

3.3.2. Phenology

The time from sowing to 50% flowering of all genotypes was within 45 to 61 days. In both years, it was not significantly affected by PRFL-ST (Table 3.3.2). Genotype ICPL 89021 flowered earlier than the others by about 4-8 days. Drought stress during the flowering and pod-filling significantly hastened crop maturity from 2-3 days in both years. Drought stress during the pre-flowering significantly delayed crop maturity in 1992 because the treatment induced additional flush of flowers after stress was released by re-watering.

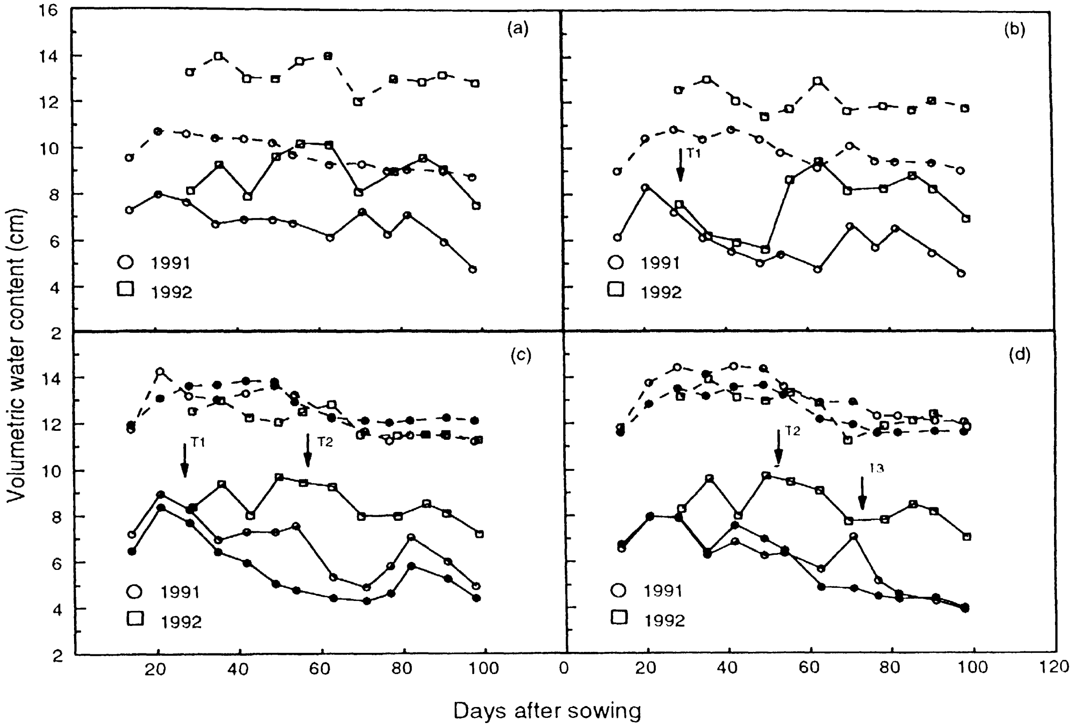


Figure 3.3.1.1: Volumetric water content pattern at 0-45 cm profile (solid line) and 60-105 cm profile (dash line) before stress imposition (a), after PRFL-ST (b) after FL-ST (c) and after PFILL-ST (d), during rainy season 1991 (open circle) and 1992 (open square). Solid circle indicate drought stress imposed at both crop growth stages. Arows indicate the beginning of stress imposed at PRFL (T1), FL (T2) and PFILL (T3) stages.

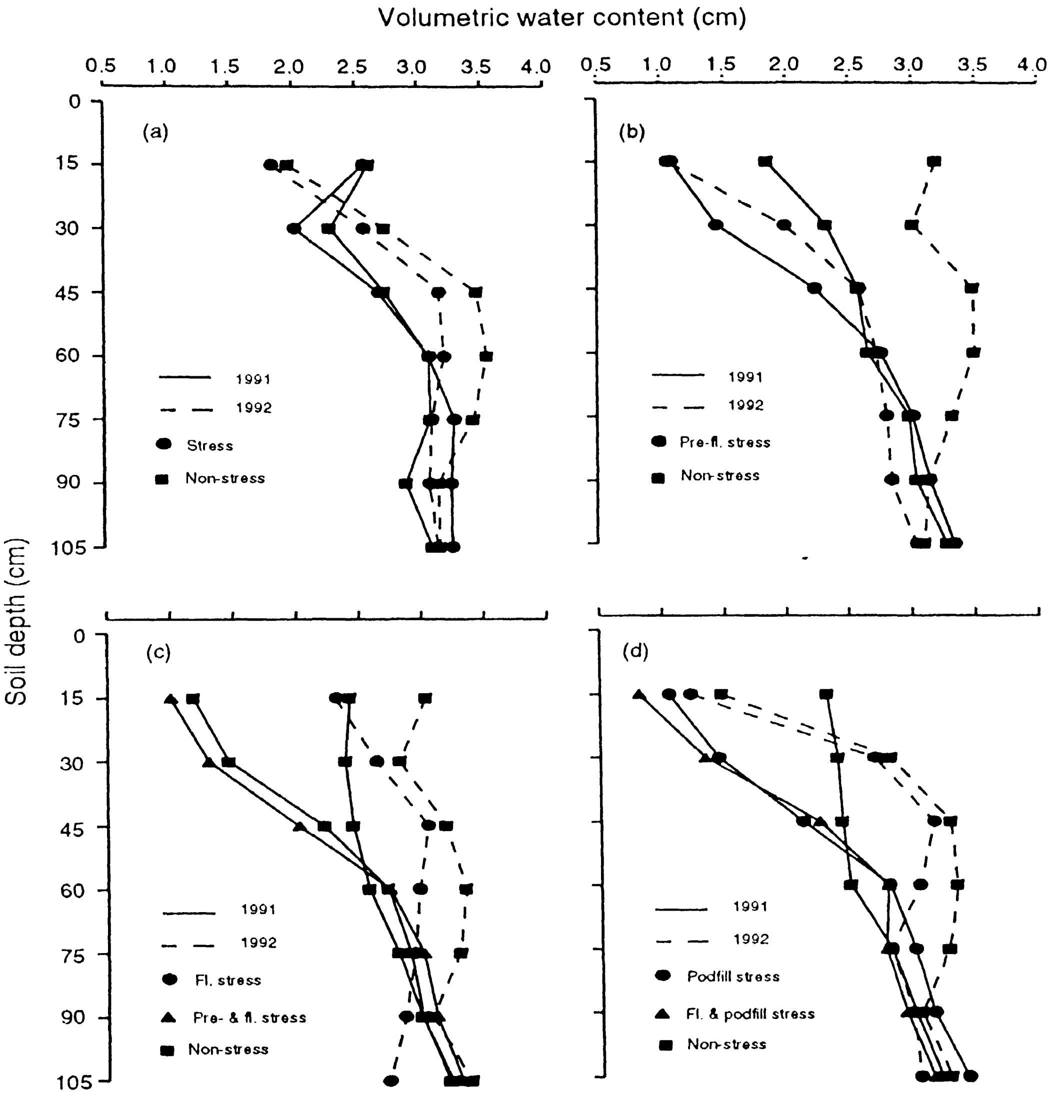


Figure 3.3.1.2: Water extraction of extra-short-duration pigeonpea before stress treatment (a), after pre-flowering stress (b), after flowering stress (c) and after pod-filling stress (d) in the seasons 1991 (solid lines) and 1992 (dash lines)

Table 3.3.2: Effect of drought stress timings on phenology of extra-short-duration pigeonpea, rainy seasons of 1991 and 1992.

	50% flowering		Physiological maturity	
	1991	1992	1991	1992
		Timing of drought stress		
- Pre-flowering	57	51	93	96
- Flowering	57	52	91	93
- Pod-fill	57	51	92	93
- Pre- and fl.	57	-[a]	92	-
- Fl. and pod-fill	57	-	91	-
- No-stress	57	51	94	94
		Genotype[b]		
- ICPL 83015	-	52	-	95
- ICPL 84023	56	50	89	93
- ICPL 86001	-	50	-	92
- ICPL 89021	52	47	85	85
- ICPL 87001	-	53	-	97
- ICPL 88032	-	54	-	97
- ICPL 88039	60	51	97	95
- ICPL 89002	61	53	98	96
SE(±) S	0.3^{NS}	0.1^{NS}	0.3^{**}	0.4^{**}
G	0.2^{*}	0.2^{**}	0.2^{**}	0.5^{**}
SxG	0.5^{NS}	0.4^{NS}	0.5^{NS}	0.9^{NS}

*,** : Significant at levels of 0.05 and 0.01 probability, respectively

NS : Non-significant

a : Not tested

b : The top four genotypes are determinate and bottom four genotypes are indeterminate.

3.3.3 Canopy Development

3.3.3.1 Leaf area expansion rate

In the N-ST treatment, LER was 3.5-4.5 cm^2 day^{-1} during 1-3 days after the leaves unfolded and 0.5-1.5 cm^2 day^{-1} after 3-5 days leaves fully unfolded (Table 3.3.3.1). Pre-flowering drought stress greatly restricted LER of all genotypes. The LER in the N-ST was 3-4 and 4-10 fold higher than that in the stress treatment during the two periods of measurement, respectively. There were highly significant differences in LER among genotypes. Generally, DT genotypes had higher LER than IDT genotypes and were also more affected by water stress. The interaction between water stress and genotype was also highly significant. The LER of genotypes ICPLs 83015, 88032 and 89002 appeared to be more sensitive to water stress while ICPL 89021 and ICPL 88039 were relatively less sensitive genotypes.

3.3.3.2 Leaf area index

At the end of PRFL-ST, drought significantly reduced LAI of all genotypes by 15-20% in 1991 and by 35-60% in 1992 (Figure 3.3.3.2.1a). The differences among genotypes under this stress were not significant in 1991 but were highly significant in 1992 (Appendix 3.1). Among genotypes tested, LAI of genotypes ICPLs 83015, 84023, 87111 and 89002 was significantly reduced by stress whereas genotypes ICPL 88039 and ICPL 88007 could retain higher LAI than the other genotypes under stress at this stage. The stress x genotype interaction, however, was not significant at this stage.

Drought stress during the flowering stage significantly reduced LAI of all genotypes in 1991 but not in 1992. There was a 30-55% reduction of LAI in the stress treatment compared with N-ST in 1991, especially when stress was imposed in PRFL+FL stages (Figure 3.3.3.2.1b and 3.3.3.2.2a). The recovery of LAI was relatively less when PRFL-ST was relieved at the flowering stage because it could only reach 50-70% of the N-ST treatment (Figure 3.3.3.2.2a).

Table 3.3.3.1: Leaf area expansion rate (cm^2 day^{-1}) of extra-short-duration pigeonpea genotypes during water stress imposed at the pre-flowering stage, rainy season of 1992.

	1-3 days after leaf fully unfolded			3-5 days after leaf fully unfolded		
Genotype	Stress	No-stress	Mean	Stress	No-stress	Mean
ICPL 83015	1.46	4.47	2.96	0.23	1.45	0.84
ICPL 84023	0.96	4.01	2.49	0.13	1.33	0.73
ICPL 86001	1.00	3.84	2.42	0.15	1.05	0.60
ICPL 89021	1.09	2.79	1.94	0.24	0.72	0.48
ICPL 87111	0.89	3.46	2.17	0.13	0.68	0.41
ICPL 88032	1.26	3.55	2.40	0.23	0.71	0.47
ICPL 88039	0.88	2.38	1.63	0.14	0.58	0.36
ICPL 89002	1.18	3.44	2.31	0.22	0.85	0.53
SE(±) S		0.198*			0.121*	
G		0.136**			0.090**	
SxG		0.268**			0.169**	
		(0.193)			(0.127)	

*,** : Significant difference at 0.05 and 0.01 probability, respectively

SE values in parenthesis are used for comparing means in same levels of stress.

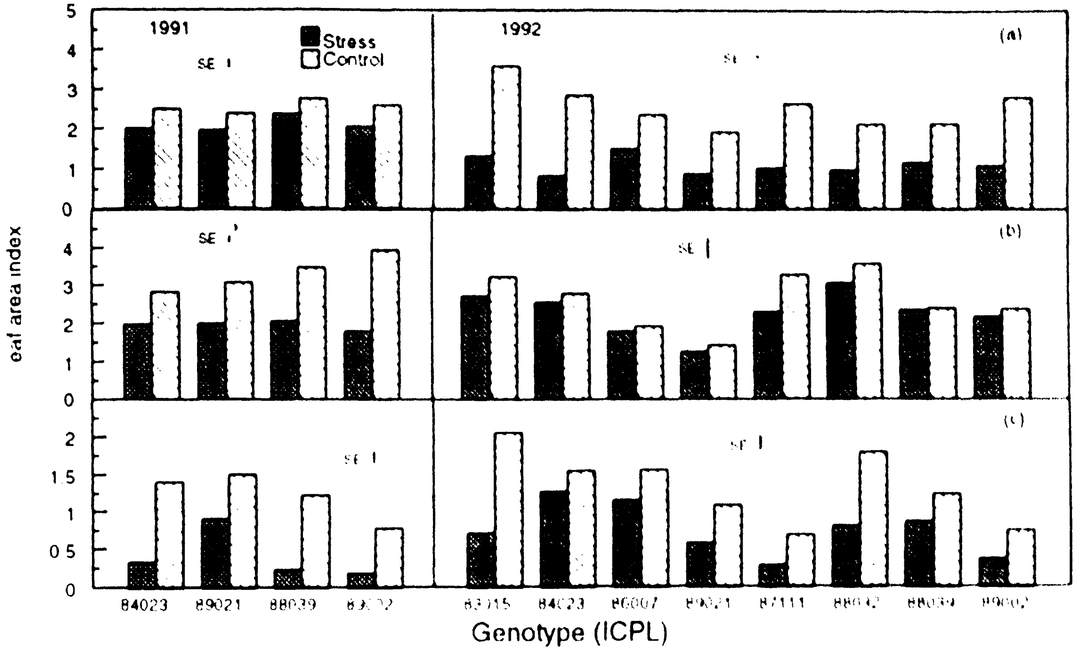


Figure 3.3.3.2.1: Leaf area index of different extra-short-duration pigeonpea genotypes after water stress imposed at PRFL (a), FL (b) and PFILL (c) stages in the seasons 1991 and 1992.
Vertical bar is SE(±) for comparing between stress treatments.

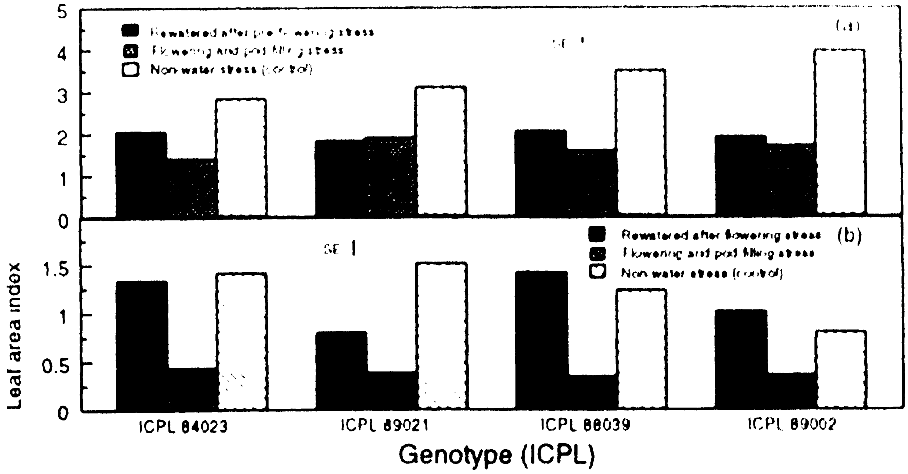


Figure 3.3.3.2.2: Comparison of leaf area index of four extra-short-duration pigeonpea genotypes under an extended period of water stress at two crop growth stages when rewatered after PRFL stress and the control at the end of FL (a) and PFILL (b) stages, rainy season 1991.
Vertical bar is SE(±) for comparing between stress treatments.

The differences in LAI among genotypes under FL-ST were significant in both years of the study (Appendix 3.1). Genotypes ICPL 84023 and ICPL 88039 showed lesser reduction in their LAI than the other genotypes under this stress.

Stress during the pod-filling stage significantly reduced LAI of all genotypes (Figure 3.3.3.2.1c). At the end of this stress in both years, the LAI of all genotypes reduced to a level less than 1.0 and 1.5 in N-ST and stress treatments, respectively. Some genotypes such as ICPL 84023 and ICPL 88039 in 1991 and ICPL 83015 and ICPL 88032 in 1992 maintained relatively higher LAI under this stress. The interaction between stress and genotype was not significant under this stress (Appendix 3.1). The LAI increased when FL-ST was relieved (Figure 3.3.3.2.2b). At the end of the pod-filling stage, the FL-ST treatment developed similar or higher LAI compared to the N-ST as re-watering favored production of new leaves while other plants dropped their leaves due to senescence. Extending the duration of drought at both Fl+pfill stages reduced LAI to 55-75% of the N-ST.

3.3.3.3 Canopy light interception

Canopy light interception (LI) of ESD pigeonpea was highly sensitive to drought as it declined steeply just after the imposition of stress and increased marginally after drought was relieved (Figure 3.3.3.3.1).

At the end of PRFL-ST, LI reduced to 30-70% in 1991 and 50-55% in 1992 compared to before stress (Figures 3.3.3.3.1a and 3.3.3.3.2a). The differences among genotypes were not significant in 1991 but were marginally significant in 1992 (Appendix 3.2). The interaction between stress and genotype was not significant at PRFL-ST treatment in both years.

Flowering stress had more effect on reducing LI of all genotypes, especially in 1991. The LI was reduced in the stress treatment to about 50% compared to N-ST at the end of stress (Figures 3.3.3.3.1b and 3.3.3.3.2b). The differences among genotypes were also highly

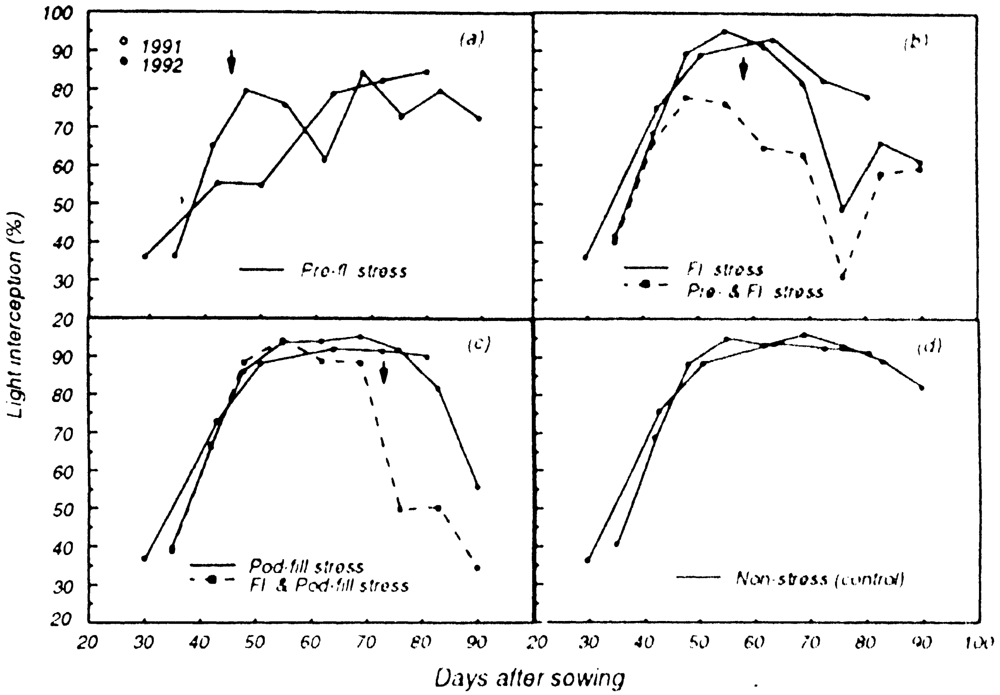


Figure 3.3.3.3.1: Light interception pattern of extra-short-duration pigeonpea under water stress imposed at pre-flowering (a), flowering (b), pod-filling (c) stages and no stress condition (d) in the seasons 1991 (open circle) and 1992 (solid circle). Dotted lines indicate drought stress imposed at two crop growth stages. Arrows indicate begining of stress imposed

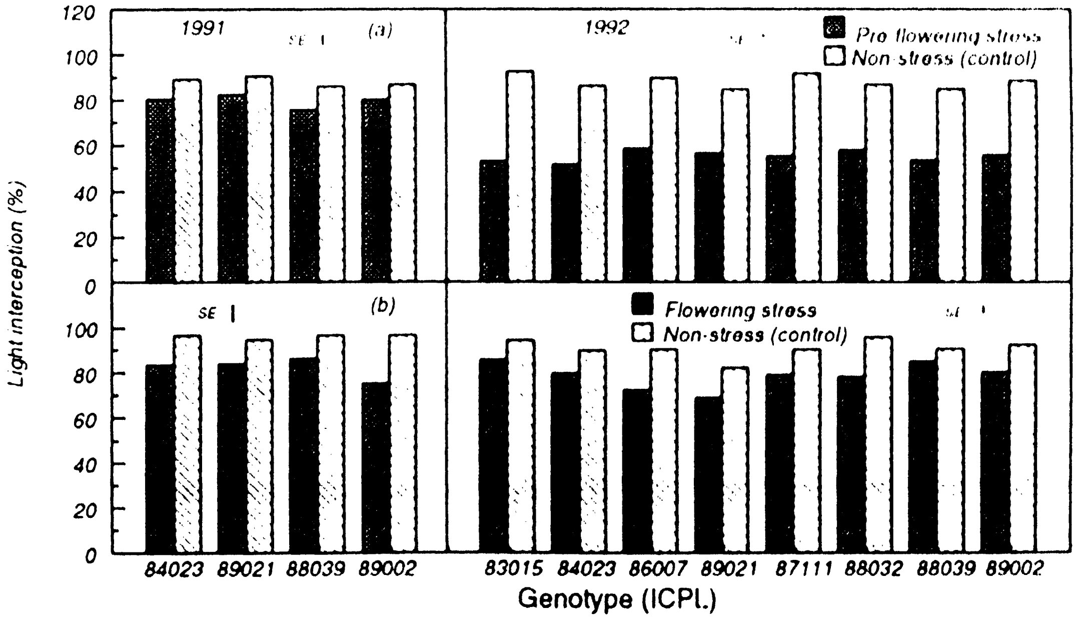


Figure 3.3.3.3.2: Comparison of light interception of different extra-short-duration pigeonpea genotypes at the end of stress imposed at pre-flowering (a) and flowering (b) stages in the seasons 1991 and 1992.
Vertical bar is SE(±) for comparing between stress treatments.

significant (Appendix 3.2) with more reduction in some genotypes such as ICPLs 86007, 88032 and 89002. Genotype ICPL 88039 was relatively less affected

At the end of PFILL-ST, LI of all genotypes attained low levels due to leaf senescence both under stress and N-ST condition. Thus the differences in LI were not significant among the stress treatments, genotypes and for their interaction (Appendix 3.2).

3.3.3.4 Leaf temperature

Leaf temperature of ESD pigeonpea significantly increased under drought stress condition and there were apparent differences in LT at different timings of drought stress (Figure 3.3.3.4). At the end of the pre-flowering and flowering stages, the difference between LT of stress and N-ST plants was about 2-3° C (Table 3.3.3.4) but it was higher under extended stress covering both pre-flowering and flowering stages. At the end of the pod-filling stage, this difference was highly significant among stress treatments, especially under stress at Fl+pfill stages. The differences among genotypes and the interaction between stress and genotype were significant for FL-ST but not for PFILL-ST (Table 3.3.3.4). After stress was relieved at the pre-flowering or flowering stages, there was a drop of about 2.0-3.5° C in leaf temperature of re-watered plants when compared with the crop which was continuously under stress treatment.

3.3.4 Dry Matter Production

3.3.4.1 Dry matter accumulation

Drought significantly reduced DM accumulation of ESD pigeonpea which largely depended on its timing and severity. However, differences among genotypes and interaction between stress and genotype were not significant in both years study (Appendix 3.3). Pre-flowering stress had the greatest effect in reducing DM accumulation and the effect of stress was more severe in 1992 than in 1991 (Figure 3.3.4.1.1a). At the end of the stress, DM was reduced by about 30-50% in

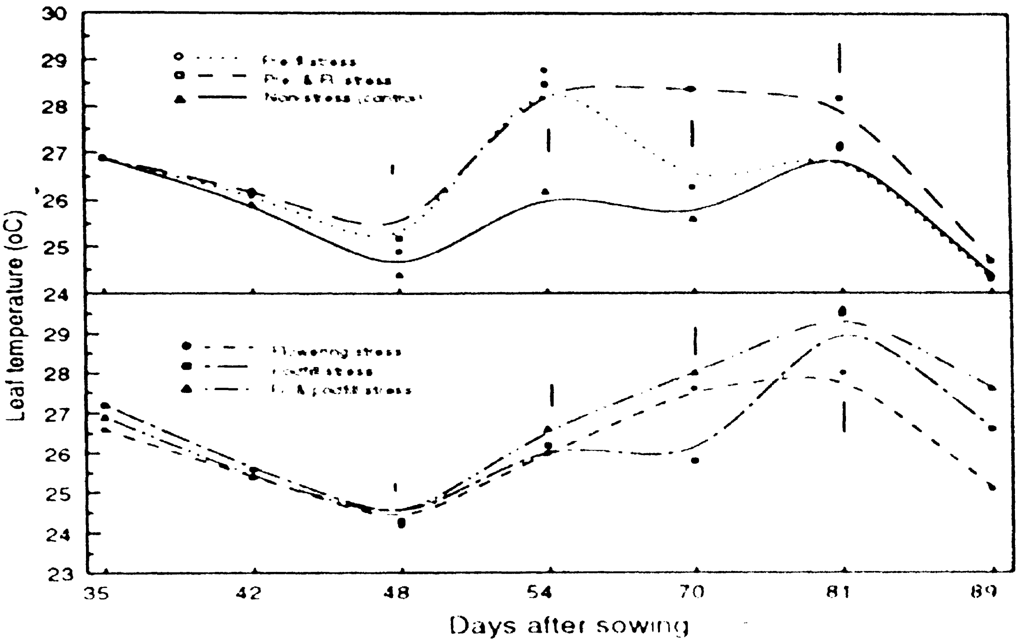


Figure 3.3 3.4. Leaf temperature patternduring the crop growth cycle of extra-short-duration pigeonpea under different timings of drought stress and no-stress condition, season 1991.
Vertical bar is SE(±) for comparing between stress treatments

Table 3.3.3.4: Leaf temperature of extra-short-duration pigeonpea under different timings of drought stress, rainy season 1991.

	54 DAS		70 DAS			89 DAS		
Genotype	PRFL stress	N-ST	PRFL+FL stress	FL stress	N-ST	FL+PFILL stress	PFILL stress	N-ST
ICPL 84023	29.3	26.6	29.0	27.5	25.6	27.3	26.5	24.7
ICPL 89021	29.7	26.4	28.4	27.9	25.9	28.6	27.1	24.4
ICPL 88039	26.8	25.6	28.5	27.6	25.3	27.3	26.4	24.0
ICPL 89002	29.3	26.0	27.5	27.7	25.7	27.2	26.2	24.4
SE (±) S	0.25**		0.30**				0.52**	
G	0.22*		0.09**				0.14NS	
S x G	0.52NS		0.35**				0.60NS	

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

different genotypes in 1992. The DM accumulation of genotypes ICPL 88039 and ICPL 89002 in 1991 and ICPLs 83015, 84023, 89021, 87111 and 88032 in 1992 was sensitivity to drought at this stage.

Stress during the flowering stage also significantly reduced DM of all genotypes in both years (Figure 3.3.4.1.1b). The DM accumulation of genotypes ICPL 89002 in 1991 and ICPLs 83015, 87111 and 88032 in 1992 was highly reduced by drought. Stress imposed at PRFL+FL stages in 1991 could reduce DM by 45-55% compared with the N-ST treatment (Figure 3.3.4.1.1c). The recovery of DM accumulation after PRFL-ST released was small except in ICPL 84023 which could increase its DM more than the other genotypes at the end of the flowering stage.

At the end of the pod-filling stage, DM accumulation declined in all genotypes under both stress and N-ST conditions due to leaf senescence, especially in IDT genotypes (Figure 3.3.4.1.1c). The recovery of DM accumulation after FL-ST released was higher than after PRFL-ST released (Figure 3.3.4.1.2). Two IDT genotypes ICPL 88039 and ICPL 89002 however, cumulated more DM than the two DT genotypes ICPL 84023 and ICPL 89021 (Figure 3.3.4.1.2b)

3.3.4.2 **Total dry matter at harvest**

Maximum TDM of ESD pigeonpea at harvest under the N-ST condition was 6.0-7.0 t ha^{-1} (Table 3.3.4.2) and there were highly significant differences in TDM at harvest for timings of stress, genotypes and stress x genotype interaction recorded in both years. The TDM at harvest was significantly reduced by all stress timings. However, drought stress during the flowering stage had the greatest effect, especially when it was preceded by PRFL-ST or was followed by PFILL-ST treatment. Total DM was reduced by more than 50% by prolonged duration of drought stress at two growth stages. Generally, genotypes ICPL 89021 and ICPL 89002 appeared most susceptible to drought at the flowering stage in both years (Table 3.3.4.2).

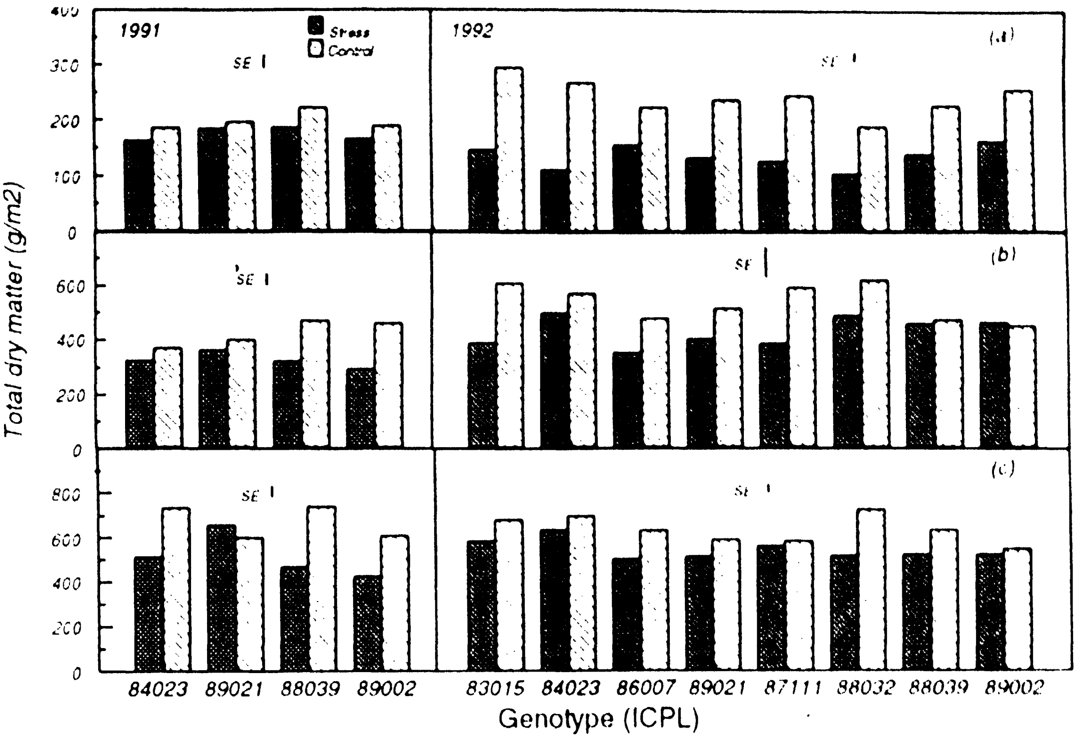


Figure 3.3.4.1.1: Total dry matter accumulation of different extra-short-duration pigeonpea genotypes after water stress imposed at PRFL (a), FL (b) and PFILL (c) stages, seasons 1991 and 1992.
Vertical bar is SE(±) for comparing between stress treatments.

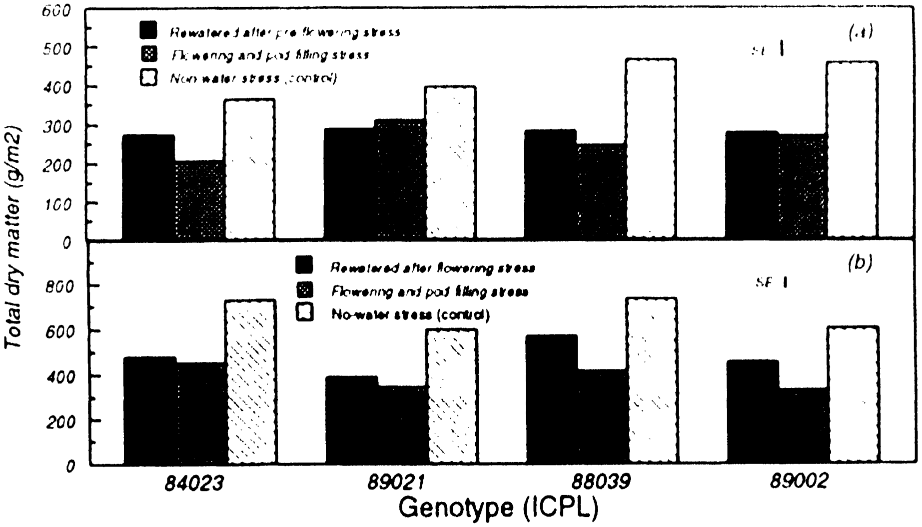


Figure 3.3.4.1.2: Comparison of dry matter accumulation of four extra-short-duration pigeonpea genotypes under extended periods of water stress at two crop growth stages, rewatered after PRFL-ST and N-ST treatments at the end of FL (a) and PFILL (b) stages, season 1991.
Vertical bar is SE(±) for comparing between stress treatments.

Table 3.3.4.2: Effect of timing of drought stress on total dry matter at harvest (t ha^{-1}) of extra-short-duration pigeonpea genotypes during the rainy seasons 1991 and 1992.

Genotype	PRFL stress	FL stress	PFILL stress	PRFL+FL stress	FL+PFILL stress	N-ST (control)
			Timing of drought stress			
			Rainy season 1991			
ICPL 84023	5.49	4.59	5.00	3.47	3.27	7.19
ICPL 89021	5.13	3.87	5.73	3.42	3.27	6.60
ICPL 88039	5.31	4.60	4.86	3.45	3.24	6.30
ICPL 89002	4.49	4.41	4.04	3.48	2.91	6.13
Mean	5.10	4.37	4.91	3.46	3.17	6.55
SE(±) S			0.269^{**}			
G			0.081^{**}			
SxG			0.320^{**} (0.200)			
			Rainy season 1992			
ICPL 83015	5.82	4.79	6.21	-		7.13
ICPL 84023	5.35	5.41	5.81	-		7.13
ICPL 86001	5.02	5.06	5.37	-		6.53
ICPL 89021	4.14	4.09	4.96	-		5.47
ICPL 87111	5.19	4.93	5.29	-		5.93
ICPL 88032	5.26	5.18	5.81	-		6.85
ICPL 88039	4.16	5.31	5.60	-		5.70
ICPL 89002	4.33	3.38	4.60	-		6.90
Mean	4.91	4.77	5.48	-		6.46
SE(±) S			0.180^{**}			
G			0.136^{**}			
SxG			0.311^{**} (0.272)			

** : Significant at levels of 0.01 probability

a : Not tested

SE values in parenthesis are used for comparing means at same levels of stress

3.3.4.3 Dry matter abscision

Abscision of TDM was highly variable depending on different timings of stress and different genotypes (Appendix 3.4). There were highly significant differences in dry weight of leaves and flowers dropped from stress treatments. The effect of stress treatment on number of pods dropped was not significant in any of the seasons. In general, IDT genotypes dropped more flowers than DT genotypes (Tables 3.3.4.3). The interaction between stress timing and genotype was not significant for DM abscision components in both years of the study.

During the flowering stage in 1991, flowers accounted for about 60-65% of total abscised DM under drought stress while leaves contributed 75-80% of that in the N-ST condition (Figure 3.3.4.3.1). In 1992, although leaf drop contributed most to abscised DM in both stress and N-ST treatments, the amount of dropped flowers remained high under stress compared to the N-ST condition. Pod drop made the lowest contribution to abscised DM in both years. During the pod-filling stage, leaf drop contributed to about 70-80% and 85-90% total abscised DM in 1991 and 1992, respectively (Figure 3.3.4.3.2). Flowers contributed to about 12-30% in 1991 and only 3-4% in 1992.

3.3.5 Leaf water status

3.3.5.1 Leaf water potential

Leaf water potential was lower under drought in all genotypes (Figure 3.3.5.1). Stress during the pre-flowering stage had less effect on LWP and the treatment effects of stress, genotype and stress x genotype interaction were not significant (Appendix 3.5). Flowering stress caused significant differences among stresses, genotypes and stress x genotype interaction effects in 1991 and the differences among genotype were also significant in 1992. Stress at this stage reduced LWP of all genotypes. Genotypes ICPL 84023 and ICPL 89002 in 1991 and ICPLs 84023, 86001 and 88032 in 1992 were among the genotypes most affected by this stress (Figure

Table 3.3.4.3: Number of dropped flowers plant^{-1} of extra-short-duration pigeonpea genotypes after water stress imposed at flowering and pod-filling stages, rainy seasons 1991 and 1992.

	Season 1991			Season 1992	
Genotype	PRFL+FL stress	FL stress	N-ST (control)	FL stress	N-ST (control)
		After flowering stress			
ICPL 83015	-^{a}	-	-	146	134
ICPL 84023	53	77	168	113	121
ICPL 86001	-	-	-	143	151
ICPL 89021	45	89	148	106	88
ICPL 87111	-	-	-	179	187
ICPL 88032	-	-	-	129	163
ICPL 88039	81	171	273	233	224
ICPL 89002	54	111	206	157	156
SE(±) S		11.8^{**}		5.2^{NS}	
G		7.5^{**}		14.4^{**}	
SxG		17.6^{NS}		19.8^{NS}	
		(15.1)		(20.4)	
		After pod-filling stress			
ICPL 83015	-	-	-	1	2
ICPL 84023	0	15	11	2	1
ICPL 86001	-	-	-	1	1
ICPL 89021	0	3	0	0	0
ICPL 87111	-	-	-	19	11
ICPL 88032	-	-	-	7	6
ICPL 88039	5	30	41	1	2
ICPL 89002	3	32	37	5	3
SE(±) S		4.7^{**}		0.4^{NS}	
G		3.1^{*}		2.1^{**}	
SxG		8.1^{NS}		2.8^{NS}	
		(7.7)		(3.0)	

*,** : Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

^{a}: Not tested

SE values in parenthesis are used for comparing means in same levels of stress.

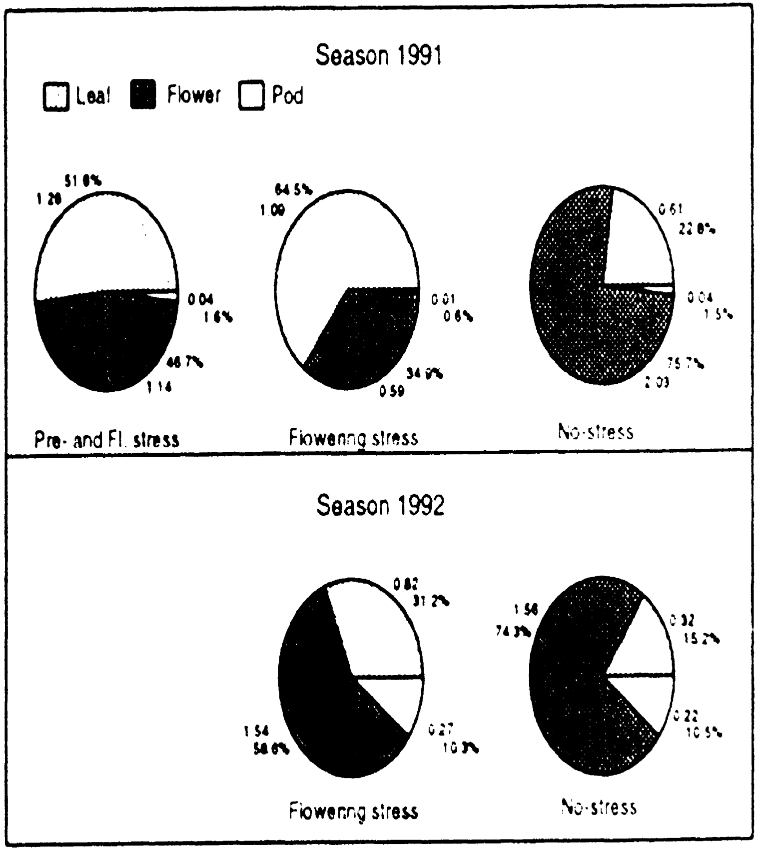


Figure 3.3.4.3.1 Relative contribution of leaf, flower and pod drop to abscised dry matter (g/plant) of extra-short-duration pigeonpea after water stress imposed at flowering stages in the seasons 1991 and 1992.

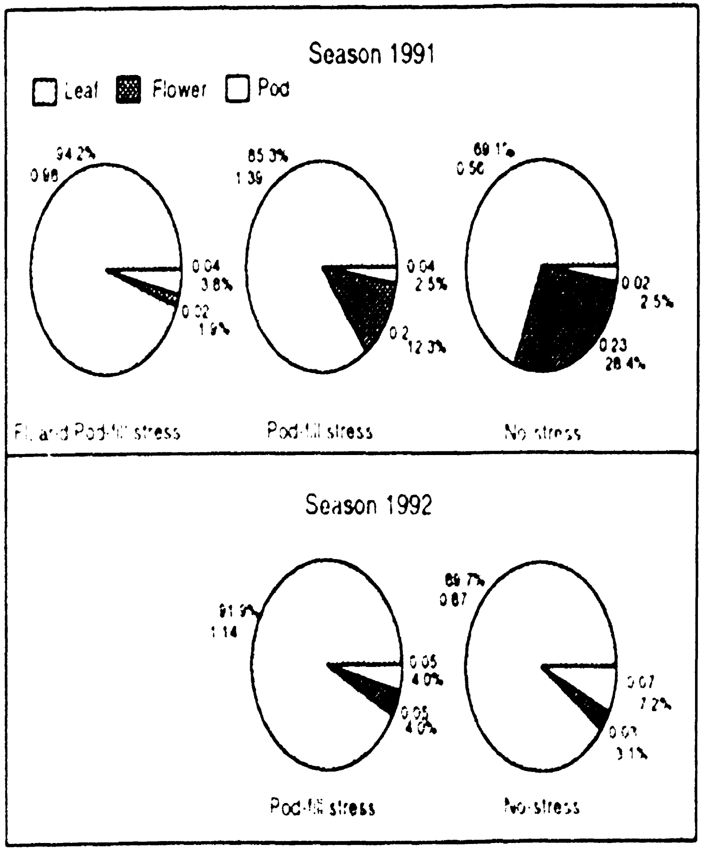


Figure 3.3.4.3.2. Contribution of leaf, flower and pod drop to abscised dry matter of extra-short-duration pigeonpea under water stress imposed at pod-filling stage in the seasons 1991 and 1992

3.3.5.1b). Stress during the pod-filling stage in 1991 had a greater effect in reducing LWP than in 1992 (Figure 3.3.5.1c). Under prolonged duration of drought at both PRFL+FL or Fl+pfill stages, LWP was reduced to very low levels, -2.2 to -3.0 MPa, in different genotypes (Figures 3.3.5.1b; c).

3.3.5.2 Leaf osmotic potential and osmotic adjustment

Leaf OP did not differ significantly under drought stress at the pre-flowering and pod-filling stages in 1992. Stress during the flowering and pod-filling stages in 1991 significantly caused a decline of OP in all genotype tested (Appendix 3.6 and Figure 3.3.5.2). The difference between genotypes was not significant and the interaction between stress and genotype was significant only for the FL-ST in 1991 and for the PRFL-ST in 1992. Among genotypes tested, OP of ICPL 89002 and ICPL 84023 in 1991 and ICPLs 83015, 87111, 88032 and 88039 in 1992 declined more than the other genotypes (Figure 3.3.5.2b). Leaf OP of ESD pigeonpea declined to very low values (-3.5 to -4.0 MPa) due to extended drought stress at PRFL+FL stages or at FL-PFILL stages (Figures 3.3.5.2b; c).

The degree of osmotic adjustment (OA) varied in the range 0.17- 0.40 MPa under PRFL-ST, 0.40-0.56 MPa under FL-ST, and 0.16-0.37 MPa under PFILL-ST for the two years. The differences among genotypes were not significant in 1992 but when stress was more severe during FL+PFILL in 1991, differences among genotypes were significant (Table 3.3.5.2). Genotype ICPL 89021 showed the lowest OA but a very high level of 1.0-1.2 MPa was apparent in ICPL 84023 and ICPL 88039, respectively for stress during the PRFL+FL stages and of 1.0 MPa in ICPL 89002 for stress during the FL+PFILL stages.

3.3.5.3 Leaf turgor potential

Leaf TP increased significantly under stress during the flowering stage in both years (Appendix 3.7 and Figure 3.3.5.3). The differences in TP among genotypes were only significant during

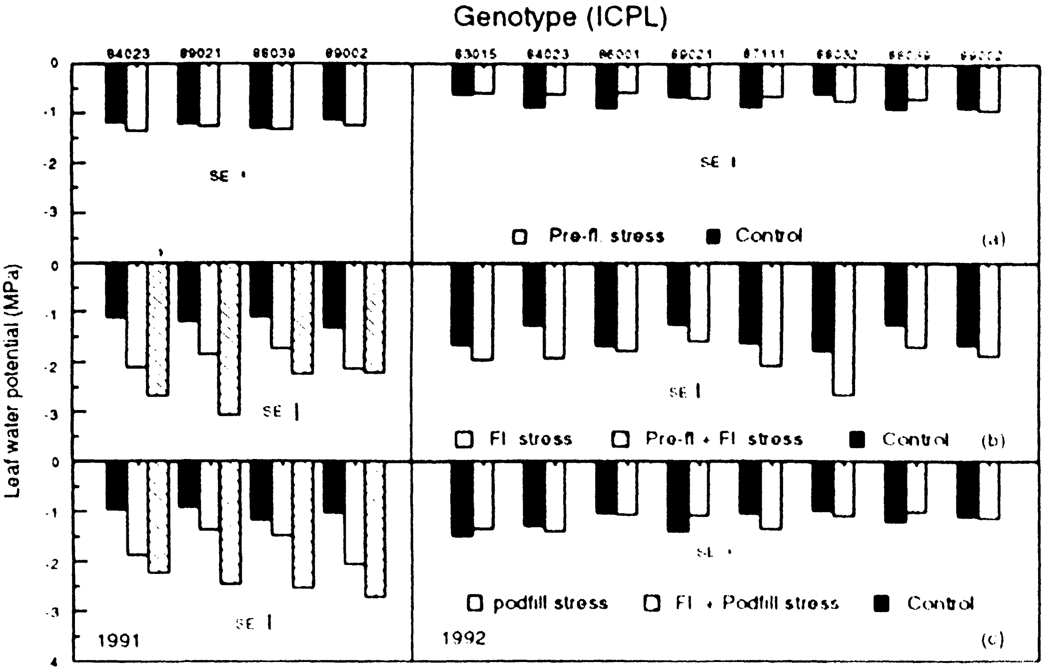


Figure 3.3.5.1: Leaf water potential of different extra-short-duration pigeonpea genotypes at the end of stress imposed at pre-flowering (a), flowering (b), and pod-filling (c) stages in the seasons 1991 and 1992. Vertical bar is SE(±) for comparing between stress treatments.

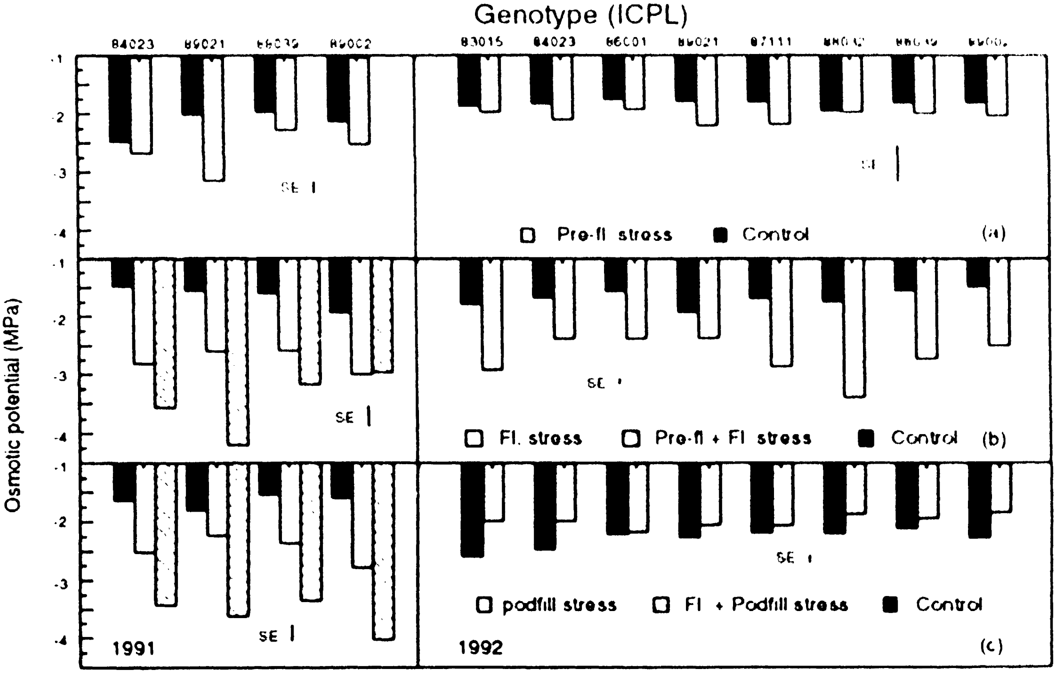


Figure 3.3.5.2: Osmotic potential of different extra-short-duration pigeonpea genotypes at the end of stress imposed at pre-flowering (a), flowering (b), and pod-filling (c) stages in the seasons 1991 and 1992. Vertical bar is SE(±) for comparing between stress treatments.

Table 3.3.5.2: Osmotic adjustment of extra-short-duration pigeonpea genotypes after water stress imposed at pre-flowering and flowering stages, rainy seasons 1991 and 1992.

	Season 1991			Season 1992	
Genotype	PRFL stress	PRFL+FL stress	FL stress	PRFL stress	FL stress
ICPL 83015	-[a]	-	-	0.08	0.27
ICPL 84023	0.51	1.08	0.71	0.26	0.29
ICPL 86001	-	-	-	0.10	0.33
ICPL 89021	0.37	0.88	0.19	0.39	0.15
ICPL 87111	-	-	-	0.23	0.53
ICPL 88032	-	-	-	0.00	0.90
ICPL 88039	0.53	1.26	0.64	0.17	0.41
ICPL 89002	0.37	0.80	0.70	0.13	0.27
SE(±)		0.090^{NS}	0.191^{*}	0.144^{NS}	0.305^{NS}

* : Significant at levels of 0.05 probability
NS : No significant
a : Not tested

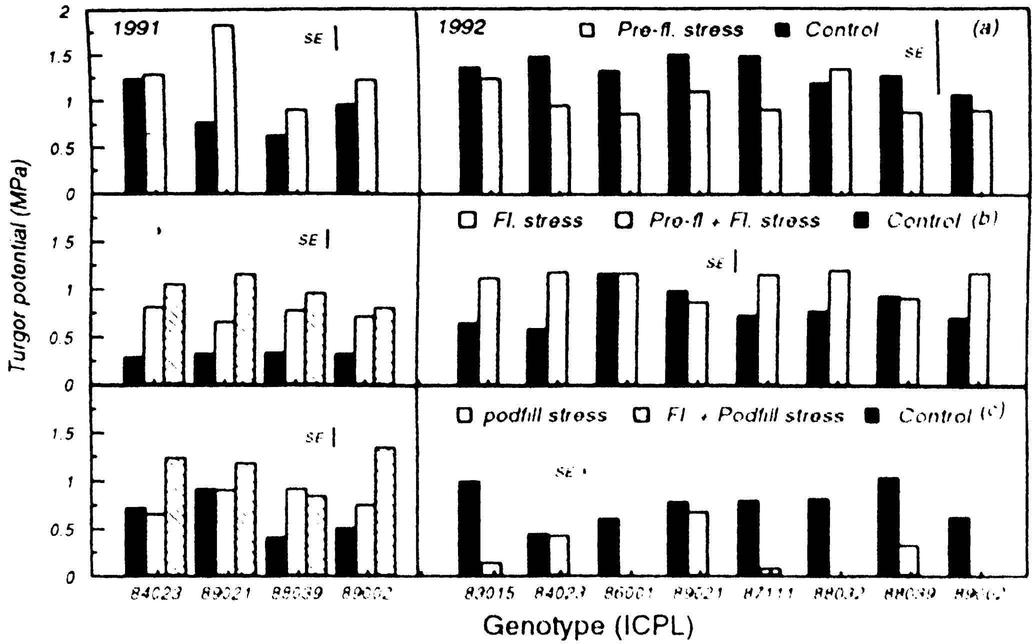


Figure 3.3.5.3: Leaf tugor potential of different extra-short-duration pigeonpea genotypes at the end of stress imposed at PRFL (a), FL (b) and PFILL (c) stages, seasons 1991 and 1992.
Vertical bar is SE(±) for comparing between stress treatments.

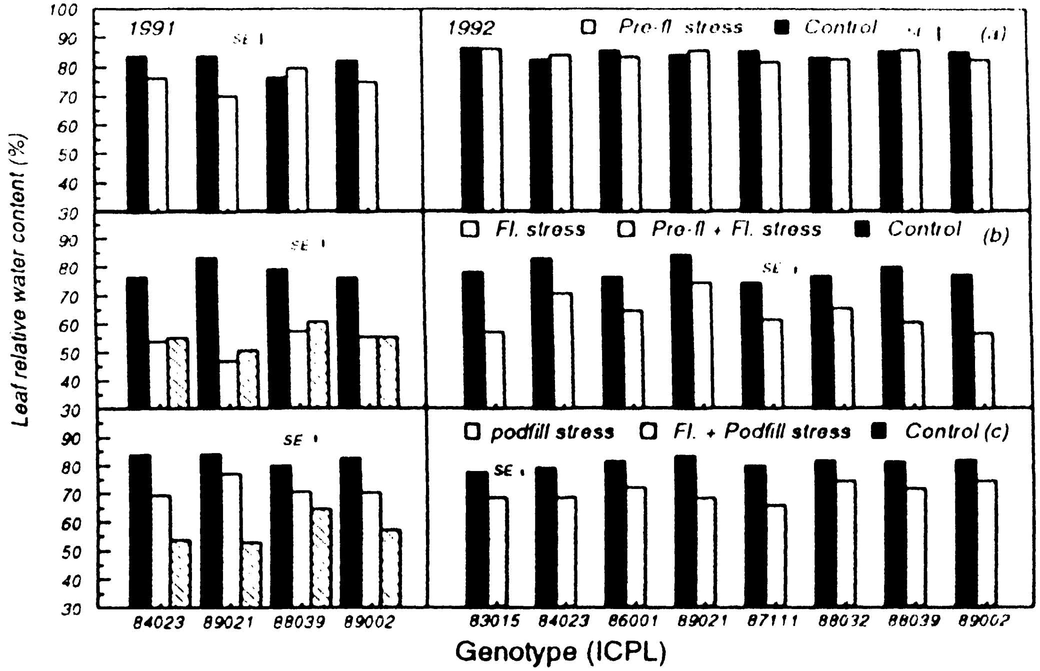


Figure 3.3.5.4: Leaf relative water content of different extra-short-duration pigeonpea genotypes at the end of stress imposed at PRFL (a), FL (b) and PFILL (c) stages, season 1991 and 1992.
Vertical bar is SE( ) for comparing between stress treatments.

PRFL-ST and PFILL-ST in 1991. Genotype ICPL 89021 had greatest leaf TP potential at the end of PRFL-ST while ICPL 89002 had higher leaf TP at the end of PFILL-ST treatment The interaction between stress and genotypes was not significant for any stress timings in both years

3.3.5.4 Leaf relative water content

At the end of PRFL-ST, leaf relative water content (RWC, %) of stressed plants was lower in the stress treatment, especially in 1991 (Figure 3.3.5.4a). However, the differences for the stress treatment as well as genotype were not significant in both years (Appendix 3.8) Stress during flowering had the greatest effect in reducing leaf RWC of all genotypes (Figure 3.3.5.4b). Leaf RWC was reduced by about 20-30% in stressed plants in 1992 and 1991, respectively The most affected genotypes were ICPL 89002 in 1991 and ICPLs 83015, 88039 and 89002 in 1992 At the end of FL-ST, there were significant differences in leaf RWC between stress and genotype in both years but interaction between stress and genotype was significant only in 1991 Stress during the pod-filling stage had less effect in reducing leaf RWC than during FL-ST (Figure 3.3.5.4c). However, leaf RWC has been reduced to a low level when stress was imposed at FL-PFILL stages in 1991. The difference among genotypes was not significant at the end of this stress.

3.3.6 Grain Yield and Yield Components

3.3.6.1 Grain yield

With adequate supply of soil moisture, all ESD pigeonpea genotypes produced yields more than 2 t ha^{-1} (Table 3.3.6.1). Some genotypes such as ICPLs 83015, 84023, 88032 and 88039 could be considered as high yielding genotypes under favorable conditions.

Drought stress at any growth stage resulted in significant reductions in grain yield of all genotypes in both years. However, the degree of yield reduction varied in relation to timing of

Table 3.3.6.1: Effect of timing of drought stress on grain yield (t ha^{-1}) of extra-short-duration pigeonpea genotypes, rainy seasons 1991 and 1992.

	Timing of drought stress					
Genotype	PRFL stress	FL stress	PFILL stress	PRFL+FL stress	FL+PFILL stress	N-ST (control)
			Season 1991			
ICPL 84023	2.12	1.12	2.04	0.77	1.02	2.61
ICPL 89021	1.77	1.33	2.53	0.96	1.23	1.23
ICPL 88039	2.11	1.41	1.91	0.95	1.19	2.44
ICPL 89002	1.85	1.25	1.22	1.08	0.78	2.28
Mean	1.96	1.28	1.92	0.94	1.05	2.48
SE(±) S				0.134^{**}		
G				0.034^{**}		
SxG				0.153^{**} (0.084)		
			Season 1992			
ICPL 83015	2.12	1.50	2.35	-[a]	-	2.40
ICPL 84023	1.68	1.64	2.20	-	-	2.46
ICPL 86001	1.89	1.60	2.02	-	-	2.13
ICPL 89021	1.60	1.72	2.05	-	-	2.02
ICPL 87111	1.67	1.48	1.88	-	-	1.97
ICPL 88032	1.38	1.35	2.06	-	-	2.50
ICPL 88039	1.69	1.76	2.09	-	-	2.19
ICPL 89002	1.61	1.32	1.76	-	-	2.07
Mean	1.70	1.55	2.05	-	-	2.22
SE(±) S				0.083^{**}		
G				0.062^{**}		
SxG				0.142^{*} (0.123)		

*,** : Significant at levels of 0.05 and 0.01 probability, respectively

a : Not tested

SE value in parenthesis is used for comparing means at same levels of stress drought stress, its duration and severity. Drought stress coinciding with the pre-flowering stage reduced grain yield by 15-30% and 10-40% in 1991 and 1992, respectively (Table 3.3.6.1). Drought stress during the flowering was most lethal, causing 40-55% and 15-40% reduction in yield in 1991 and 1992, respectively. Stress imposed during the pod-filling stage was less important as about 80-95% of the maximum yield was being realized under this stress. Nevertheless, there was considerable reduction in the yield of two IDT genotypes ICPL 88032 and ICPL 89002 under the PFILL-ST treatment. Under the extended stress at PRFL+FL or FL-PFILL stages in 1991, grain yield of ESD pigeonpea genotypes was reduced to 50-70% of the N-ST treatment (Table 3.3.6.1).

3.3.6.2 Yield components and harvest index

The number of pods per unit area was greatly affected by the timing and duration of stress (Appendix 3.9). Drought stress imposed at the pre-flowering stage differentially affected pod set of different genotypes. Genotypes ICPLs 83015, 89021, 88032 and 89002 had lesser number of pods showing sensitivity to this stress, but other genotypes such as ICPLs 86001, 87111 and 88039 were relatively less affected (Figure 3.3.6.2a). All genotype were more affected by FL-ST and under this stress, number of pods reduced by 25-40% in 1991 and by about 10-40% in 1992. The differences among genotypes for number of pods per unit area were also significant. The most susceptible genotypes were ICPLs 83015, 89021, 87111, 88032 and 89002 while genotype ICPL 88039 showed relatively better pod setting ability under FL-ST in both years. Pod-filling stress was least harmful in reducing the number of pods produced in all genotypes except ICPL 89002 in 1991.

Number of seeds per pod of ESD pigeonpea was less affected by drought stress in 1991 but was significantly reduced by FL-ST in some genotypes such as ICPLs 83015, 86001, 89021 and 88039 in 1992 (Appendix 3.9 and Figure 3.3.6.2b). The differences in number of seeds per pod among genotypes were significant only in 1992. The interaction between stress and

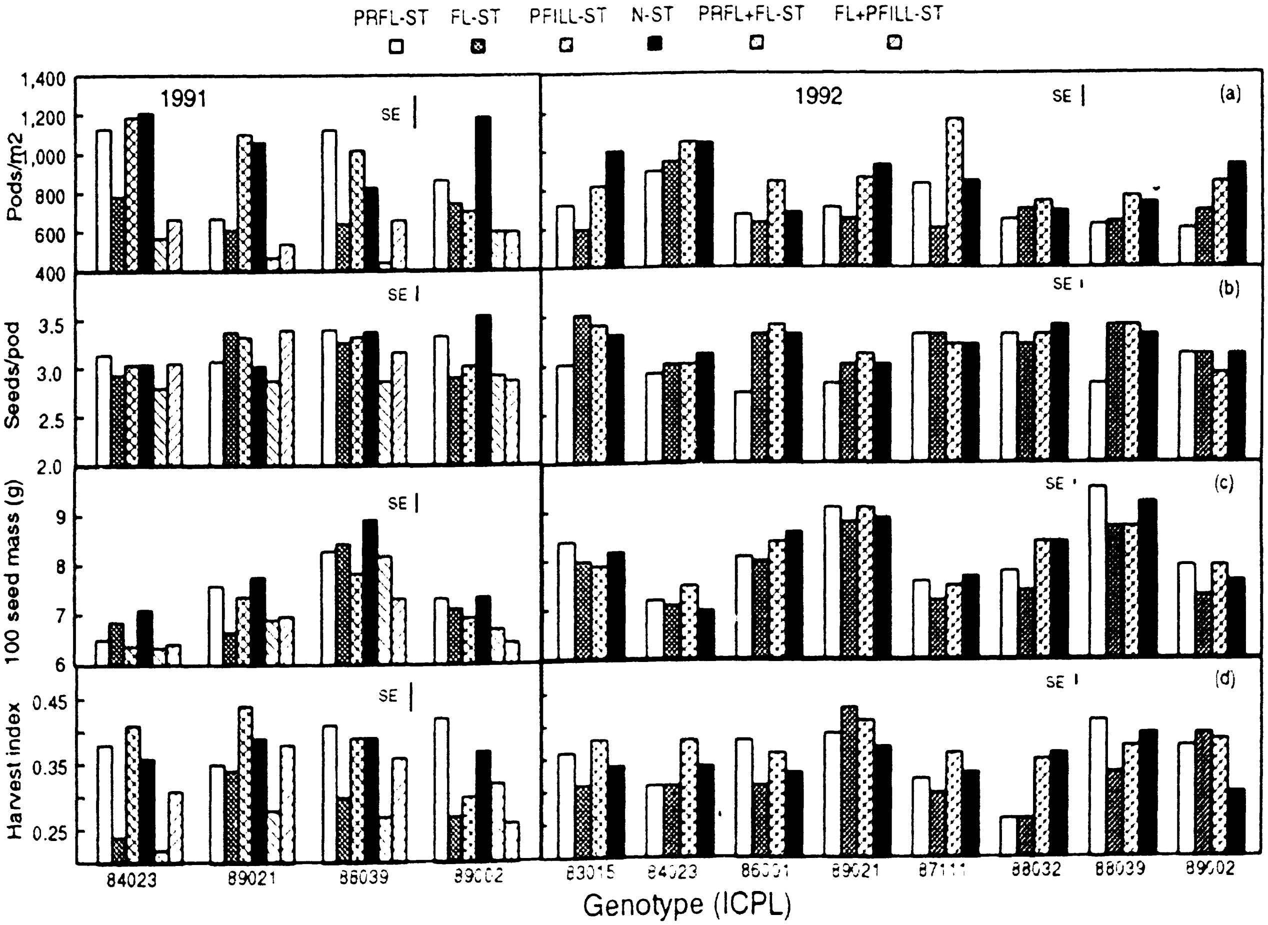


Figure 3.3.6.2: Yield components of different extra-short-duration pigeonpea genotypes under different timings of drought stress, seasons 1991 and 1992. Vertical bar is SE( ) for comparing between stress treatments.

genotypes was not significant in either year.

Hundred seed mass was greatly affected by drought and there were highly significant differences due to stress timings as well as among genotypes in both years (Appendix 3.9 and Figure 3.3.6.2c). In both years, drought during the pre-flowering did not reduce hundred seed mass but stress at the reproductive phase generally reduced hundred seed mass of all genotypes, especially when stress commenced from the flowering stage and continued up to the pod-filling stage.

Harvest index of ESD pigeonpea was greatly affected by drought stress timing. There were highly significant differences in HI due to stress, genotypes and their interaction in both years (Appendix 3.9). In gereral, drought stress during the pod-filling or extended drought stress at both crop growth stages reduced HI in most genotypes (Figure 3.3.6.2d).

3.3.7 Water use efficiency

Total water used in stress treatments was reduced by 15-27% when compared with N-ST treatment in both years (Figure 3.3.6.3). The water used was reduced by 45% under extended duration of drought covering PRFL+FL stages and FL+PFILL stages in 1991.

Water use efficiency of ESD pigeonpea was in the range 52-59 kg cm^{-1} ha^{-1} under the N-ST condition in 1991 (Table 3.3.6.3). There were significant differences between stress timing, genotypes and stress x genotype interaction in WUE in both seasons. Drought stress at the pre-flowering gave a similar WUE compared with the N-ST treatment. Genotypes ICPL 84023 and ICPL 88039 had higher WUE values under this stress. Drought stresses during flowering or extended duration of stress reduced WUE by 20-40% when compared with N-ST. Stress during the pod-filling had least effect on WUE. However, WUE of genotype ICPL 89002 was more affected by this stress. There was a highly significant positive correlation between grain yield and WUE of ESD ($r = 0.874$) under N-ST and different water stress timings.

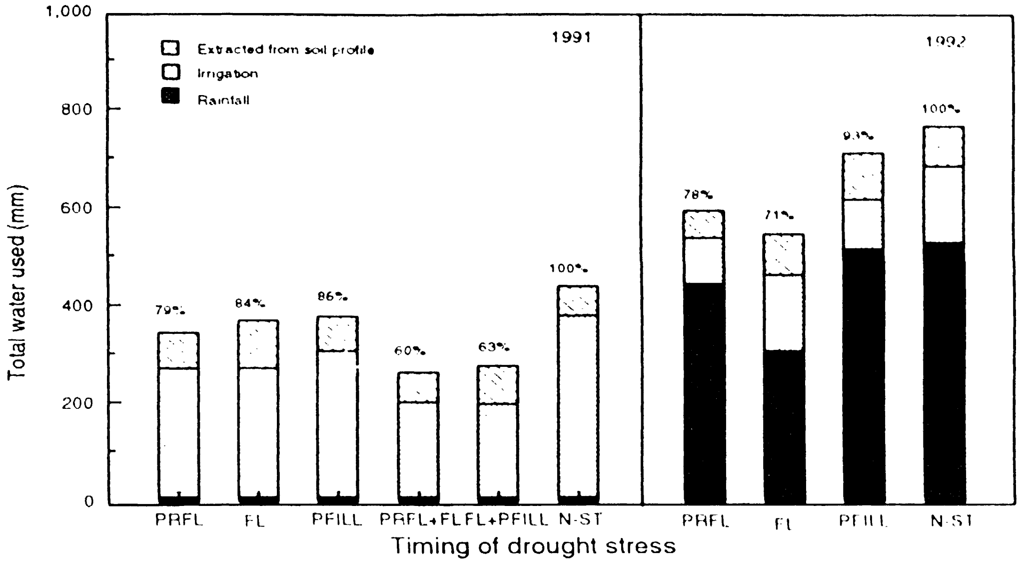


Figure 3.3.6.3: Total water used of extra-short-duration pigeonpea under different timings of drought stress and no stress conditions in the seasons 1991 and 1992.

Table 3.3.6.3: Effect of timings of drought stress on water use efficiency (kg cm^{-1} ha^{-1}) of extra-short-duration pigeonpea genotypes, rainy seasons 1991 and 1992.

	Timing of drought stress					
Genotype	PRFL stress	FL stress	PFILL stress	PRFL+FL stress	FL+PFILL stress	N-ST (control)
			Season 1991			
ICPL 84023	61	30	54	29	36	59
ICPL 89021	51	36	67	37	45	59
ICPL 88039	61	38	50	36	43	56
ICPL 89002	53	34	32	41	31	52
Mean	57	34	51	36	39	56
SE(±) S			4.3^{**}			
G			1.0^{**}			
SxG			$4.8\ (2.4)^{*}$			
			Season 1992			
ICPL 83015	35	27	33	-	-	30
ICPL 84023	28	30	31	-	-	31
ICPL 86001	29	29	27	-	-	27
ICPL 89021	27	32	29	-	-	25
ICPL 87111	28	27	26	-	-	25
ICPL 88032	23	25	29	-	-	32
ICPL 88039	28	32	29	-	-	28
ICPL 89002	27	24	25	-	-	26
Mean	28	28	29	-	-	28
SE(±) S			1.4^{NS}			
G			1.0^{**}			
SxG			$2.3\ (1.9)^{*}$			

*, ** : Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

SE values in parenthesis are used for comparing means at same levels of stress

3.4 DISCUSSION

The depletion of soil water content after a stress period was high in the upper soil layer (0-45 cm) and was progressively reduced with the depth of soil profile (Figure 3.3.1.2) which indicated that ESD pigeonpea had a shallow root system and could only extract most of its required water in the upper soil layer, as generally observed in other early maturing cultivars (Fereres *et al.* 1986; Arihara *et al.* 1991b; Chauhan 1992). This differs from the situation in long duration pigeonpea which has been reported as a deep-rooted, with extensive root penetration and with water extraction to deeper layers to 120-180 cm (Sheldrake & Natarayannan 1979; Singh & Russell 1981; Whiteman *et al.* 1985). For improving drought resistance of ESD pigeonpea, exploiting difference in rooting depth and extraction of soil water among genotypes is necessary.

Water stress during the pre-flowering stage did not affect the time to flowering. This is in agreement with the results reported by Muchow (1985a) in pigeonpea and other grain legumes. In the present study, all the genotypes flowered about one week earlier in 1992 than in 1991. This was probably because temperatures during vegetative period in 1992 were higher than in 1991 (Figure 3.2.5.1), although sowing time in 1991 was earlier than in 1992. The predominant environmental factor influencing flowering time of ESD pigeonpea seemingly therefore was temperature, rather than water or photoperiod as has been observed in SD soybean and mung bean (Lawn 1982) or in longer duration pigeonpea genotypes (Troedson *et al.* 1990). Drought during the flowering and pod-filling stages hastened maturity but the variation was less when compared with SD genotypes (Lopez *et al.* ICRISAT, unpublished data). Stress relieved by rewatering at the end of PRFL+FL stages increased plant regrowth by producing new branches and leaves and other flushes of flowers which prolonged duration of flowering and delayed maturity. Reduced phenology plasticity of ESD pigeonpea under drought observed in this study may make it more sensitive to drought than cowpea which is able to shorten its flowering period according to the amount of water available (Muchow 1985a).

The grain yields of ESD pigeonpea under the N-ST condition ranged from 2.0 to 2.5 t ha^{-1} in both years, which were similar to the highest yield levels in normal sowing on Alfisol recorded by Chauhan *et al.* (1993) and Nam *et al.* (1993). It represented the high yield potential of ESD pigeonpea which can be comparable with medium- or SD pigeonpea in the same environments. However, large variation in the grain yield under different timings of drought recorded in this experiment reflected the sensitivity of ESD pigeonpea to water supply. Drought at any growth stage reduced grain yield compared with the N-ST treatment. This indicates that ESD pigeonpea is more sensitive to drought than the longer duration types. No differences in yield stability under water stress associated with growth habit in ESD pigeonpea has been found, in which the IDT growth habit was seemingly an advantage in drought resistance in medium- or SD pigeonpea genotypes (ICRISAT 1989). Nevertheless, significant differences in grain yield between genotypes and stress x genotype interaction indicated that genotypic differences in drought resistance at particular stress timings existed among the genotypes tested.

During two years of the study, soil water deficit occurring prior to the flowering substantially reduced grain yield at average levels of 20-25% relative to the N-ST condition. These levels of yield reduction were relatively higher compared to soybean (Bartels & Caesar 1987; Eck *et al.* 1987) or with cowpea (Turk *et al.* 1980; Akyeampong 1985), but were similar or relatively lower than in green gram (Sadarivam *et al.* 1988). However, grain yield response to drought at this stage also varied among different genotypes. Generally, genotypes such as ICPL 84023 and ICPL 88039 in 1991 and ICPL 83015 and ICPL 86001 in 1992, which had vigorous early growth, were seemingly more resistant to the PRFL-ST treatment. Several studies have suggested that the better shoot growth is related to better root growth (Sponchialo *et al.* 1989; Ketring 1984; Wright *et al.* 1991; Chapmant *et al.* 1993a; Cortes & Sinclair 1986) which helps extraction of more soil water during drought stress period. Genotypes ICPL 89021 and ICPL 88032 were considered relatively sensitive to stress at the pre-flowering stage.

Drought stress during the flowering stage has been found to be more damaging for almost grain legumes such as soybean (Pahalwan & Tripathi 1984; Brown *et al.* 1985; Eck *et al.* 1987; Kpoghomon *et al.* 1990), cowpea (Turk *et al.* 1980; Shouse *et al.* 1981), groundnut (Boote *et al.* 1992) and SD pigeonpea (Lopez *et al.* ICRISAT, unpublished data). In the present study, ESD pigeonpea also showed high sensitivity to drought during the flowering stage. Reductions of grain yield up to 40-55% were recorded in both years, which supported the earlier results in SD pigeonpea that flowering was the most critical stage. Furthermore, grain yield reductions by this stress in different genotypes depended on stress degree in each year. Stress during 1991 appeared just after 2 weeks of withholding irrigation and symptoms of vertical orientation and wilting of leaves were observed. Stressed plants abscised most of their lower leaves and flowers. In contrast, stress in 1992 developed slowly due to the soil moisture in stress plots being higher than in 1991 (Figure 3.3.1.2c), which was caused by higher rainfall during the stress period. At the end of the flowering period, stress was less severe in the stressed treatment with a resulting yield reduction of only 15-40% of the no-stress yield although stress duration was longer by about one week compared to 1991. Genotypic differences were apparent among genotypes under this stress with ICPLs 83015, 84023, 88032 and 89021 suffering more by this stress while genotype ICPL 88039 appeared relatively resistant in both years.

Drought stress during the pod-filling stage was considered less damaging to grain yield of ESD pigeonpea than that at the earlier stages. Grain yields were reduced more in 1991 than 1992 because the duration of stress was longer. Sensitivity of ESD pigeonpea genotypes to this stress also dependent on genotype. Genotype ICPL 89021 had shorter duration and thus could escape from the effect of stress while genotype ICPL 89002, which had longest duration of the pod-filling, suffered more by this stress.

The reduction of grain yield of ESD pigeonpea under the extended period of stress spanning two crop growth stages was most severe because the duration of stress was long relative to the crop growth cycle. Thus, the crops did not have adequate time for recovery. The experimental results also indicated that droughts during PRFL+FL and FL+PFILL were equally effective in reducing yield, without any superior genotypes apparent.

Grain yield of ESD pigeonpea had a very close relationship with TDM at harvest (Figure 3.4.1). The variation of grain yield therefore, can be explained by the variation of their DM accumulation under different timings of drought stress. The genotypic differences in response to drought can be due to both DM production and DM partitioning under stress. Drought stress during the pre-flowering stage restricted shoot dry mass primarily by reducing crop growth rate, while stress during later stages mostly caused increased abscission of shoot dry mass components. There was an increased proportion of abscised flowers during FL-ST and an increased proportion of abscised leaves during PFILL-ST treatment. Although the capacity for producing flowers is high in pigeonpea most flowers are shed without setting pods (Sheldrake *et al.* 1979; Sumerfield & Roberts 1985). This appears necessary to keep a balance between demands of sink capacity and assimilate supply. The higher proportion of abscised flowers under stress could favor a reduction in the capacity of the source relative to that of the reproductive sink which was an unfavorable condition for pod setting. Thus maintenance of source capacity (by reducing leaf abscission) and diminishing the imbalances between source capacity and reproductive sink (by sustaining photosynthesis capacity and increasing pods set) during stress period were seemingly critical to improve drought tolerance of ESD pigeonpea. This will be discussed in more detail in Chapter IV.

The ability to recover after stress during PRFL-ST when irrigation was resumed was relatively low in ESD pigeonpea although it has been seen as an important trait to support drought resistance in cowpea (Wien *et al.* 1979; Turk *et al.* 1980), soybean (Hoogenboon *et al.*

1987) and groundnut (Nageswara Rao *et al.* 1985). Stress released after the pre-flowering nearly doubled the yield of all genotypes compared with continuing stress during the flowering stage but the final yield was approximately 80% of the N-ST treatment. Re-watering after FL-ST was not so effective in increasing grain yield because there was only an approximate 10% increased yield compared with continuing stress at the pod-filling stage. Although plants could produce new leaves and flushes of flowers they had less time to recover and the pods which formed late did not contribute to yield as harvesting was done before these pods matured. Moreover, HI declined because of increasing competitiveness of the new vegetative growth with the earlier formed pods.

Vegetative drought restricted growth of ESD pigeonpea by significantly reducing LA development and finally its DM accumulation. Pigeonpea generally has a lower initial plant growth rate than other grain legumes (Brakke & Gardner 1987). Leaf area development of ESD pigeonpea has been observed attaining only 40-50% of that of horse gram or cowpea at the late vegetative stage (Nam *et al.* 1993). The 15-60% reduction in LAI recorded after PRFL-ST in both years which was reflected in the reduction of DM. Genotypes ICPLs 83015, 84023, 87111, 88032 and 89002 had low LAI at the end of stress and also had low total DM accumulation. The grain yields of genotypes such as ICPL 84023 and ICPL 88039 in 1991 and ICPLs 83015, 86001 and 88039 in 1992 which had higher LAI at the end of this stress had higher yield than the others. Reduction of LAI under stress at this stage was mainly dependent on restriction of leaf expansion rather than by reduction number of leaves.

The decline in the rate of LA expansion increased with duration of drought and it was higher in broad leaves DT genotypes (ICPL 83015 and ICPL 84023). Genotype ICPL 88039 had lower LA expansion and was less affected by this stress, possibly because this genotype has smaller leaf size than the others (Table 3.3.3.1). This character has been reported as an advantageous trait in drought resistance in some other grain legumes (Blum 1980; Nageswara Rao 1992). Low LER in crop plants is considered associated with lower LWP (Boyer 1968;

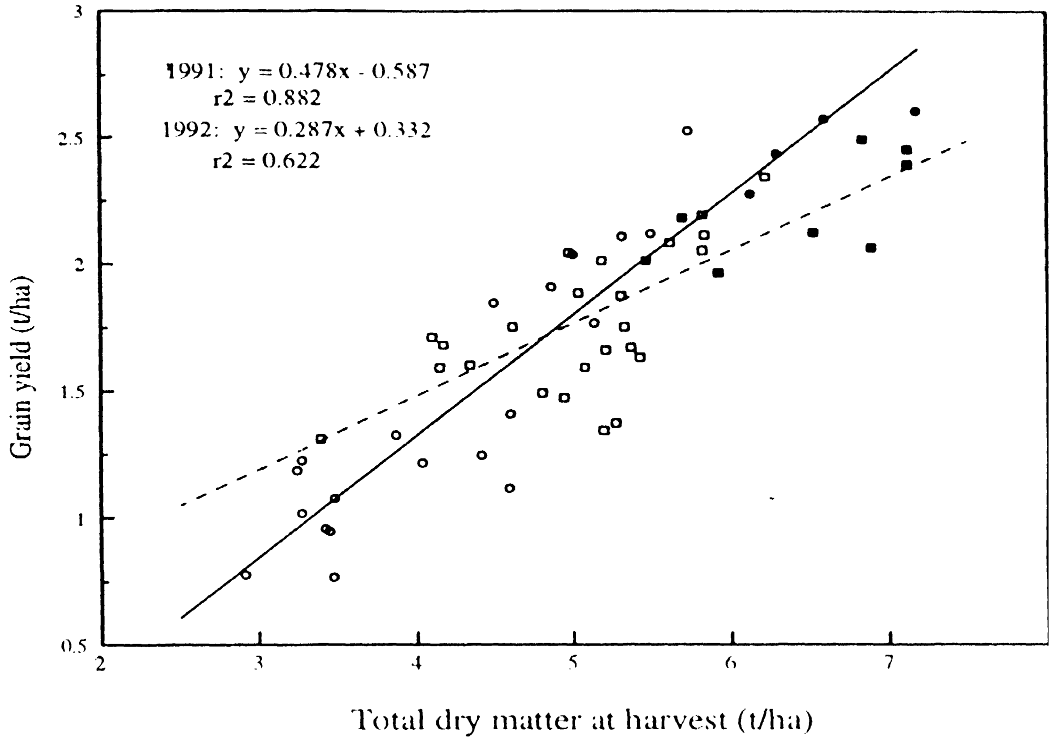


Figure 3.4.1: Relationship between total dry matter at harvest and grain yield of extra-short-duration pigeonpea under different timings of drought stress and no-stress condition, seasons 1991 (solid line, circle symbol) and 1992 (dashed line) (solid symbols indicate no-stress condition)

Bradford & Hsiao 1982; Hsiao *et al.* 1985) and in this experiment a positive correlation between LER and LWP observed during stress period was an evident ($r = 0.33$; $n = 16$) although the r value was not significant due to limited number of observations. At the end of the stress imposed at this stage, a significant positive correlation between LAI level and final grain yield was observed in both years (Figure 3.4.2a) which indicated the important role of this trait, while such relationship was not observed under the N-ST condition. The ability to retain LA during stress was thus, necessary for the maintenance of growth function and recovery after the stress was removed. The same conclusion has been reported by Lopez *et al.* (ICRISAT, unpublished data) for the effect of stress during the pre-flowering stage in SD pigeonpea. Another effects of drought during the vegetative stage was to reduce stem development in length and diameter. The symptom of lodging at the pod-filling stage which was caused by the weakness of the stems in all genotypes was observed in 1991.

Stress during the flowering caused a significant reduction of LAI in all genotypes which was mostly through faster leaf senescence. Non-significant correlation between grain yield and LAI under N-ST condition (Figure 3.4.2b) but less and non significant were observed under this stress in 1991 and 1992, respectively. This indicated that the levels of LA retention at the end of stress did not explain the variation of the final grain yield which was not the same at PRFL-ST treatment. Heavy loss of LAI due to stress at this stage indicated that drought stress had a considerable effect on reducing the efficiency of conversion of intercepted photosynthetically radiation to biomass. The reduction in the efficiency of conversion of LI into biomass could be related to reduction of both photosynthetic area and photosynthetic capacity of leaves by closing stomata under stress. Leaf area index of ESD pigeonpea under N-ST condition started declining after reaching a critical level during the flowering at 60 DAS due to leaf senescence, but the heavy losses of leaves under stress were mainly determined by shortage of water supplied. The acceleration of leaf abscission caused significant reduction in source capacity which was reflected in lower DM contribution of leaf and stem at the end of stress. The size of the reproductive sink

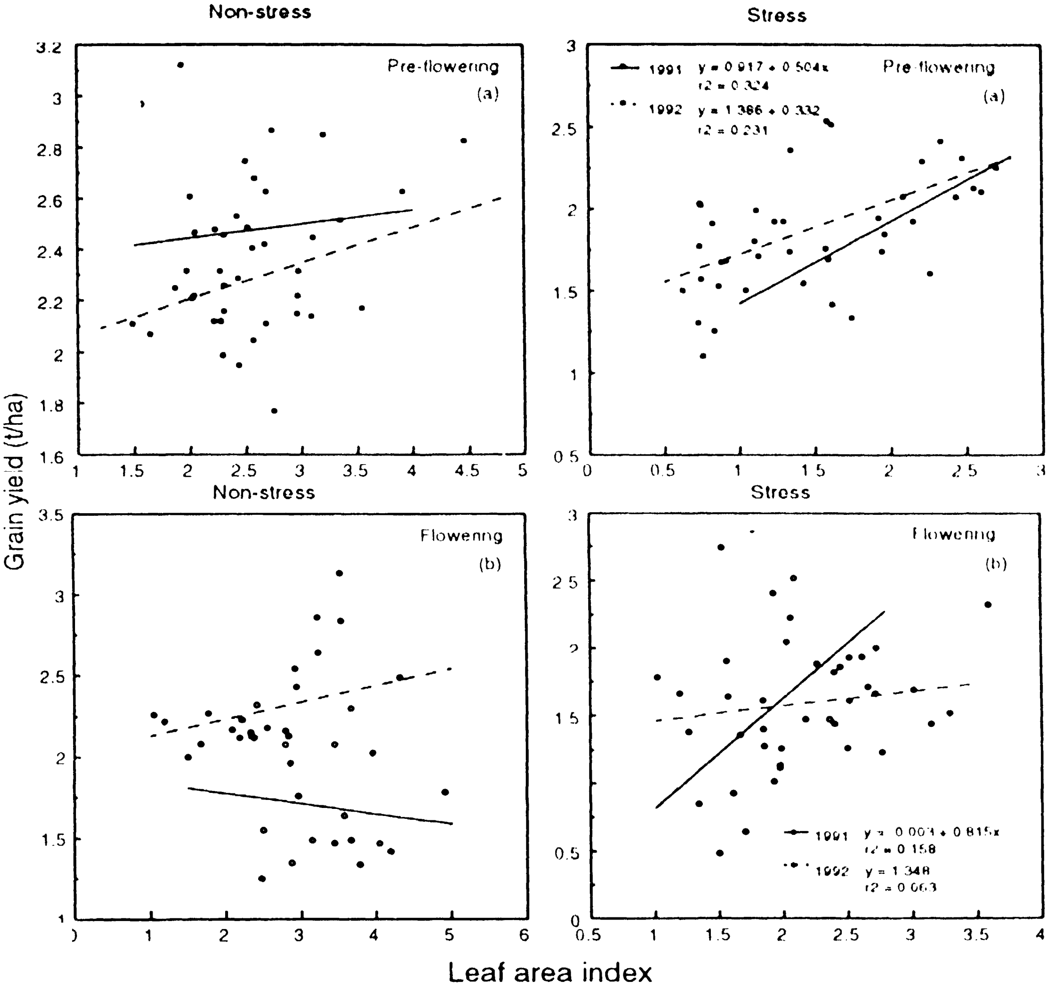


Figure 3.4.2: Relationship between LAI at the end of PRFL-ST (a), and the end of FL-ST (b) with grain yield under water stress and no-stress conditions, seasons 1991 (solid line) and 1992 (dashed line).

was also decreased by the reduction in number of flowers produced in stressed plants and the increasing fraction of abscised flowers.

Dry matter accumulation in pigeonpea is essentially a linear function of LAI development (Hughes *et al.* 1981; Hughes & Keatinge 1983) and LI by the canopy because the relationship between LAI and LI was closely correlated under both PRFL-ST and FL-ST, and N-ST conditions during both years of the study (Figure 3.4.3). This indicated that total cumulative LI by the canopy will increase with increasing LAI level as well as LA duration. High levels of LAI during vegetative drought increases efficiency of LI, as has been seen in pigeonpea (Muchow 1985b), and has association with soil water extraction capacity as has been seen in groundnut (Wright *et al.* 1991) which enables the crop to maintain leaf water status and leaf function despite reduced water availability. Critical LAI level for attaining 95% total solar light intercepted observed in this study was in a range 3.8-4.0 (Figure 3.4.4) which was similar to that reported by Muchow (1885a) but lower than the level described by Rowden *et al.* (1981). However, LI was sensitive to drought for almost all genotypes at all the stages. It was reduced to a great extent by leaflet paraheliotropy, by wilting or finally by leaf drop. The magnitude of reduction of LI depended on the duration of stress imposed but LI tended to recover after stress released. Because sensitivity of LI to drought was evident at all the crop growth stages, resulting from many plant responses to stress such as plant survival, leaf orientation, leaf angle, leaf abscission and vegetative as well as reproductive growth, it could be considered as an ideal trait which integrates most of the impact of water stress influencing grain yield and thus as a "criterion in drought resistance screening for ESD pigeonpea improvement".

When soil moisture becomes limiting, stomatal closure occurs resulting in reduced transpiration, increased heat load on the canopy and a consequent rise in leaf temperature. The changes in the leaf temperature of ESD pigeonpea undergoing drought stress indicated lack of transpirational cooling caused by low level of ET. Different ESD pigeonpea genotypes showed differential response in increased leaf temperature, especially during stress at the flowering stage where both genotype and stress x genotype interaction effects were highly significant. This may be related to different drought resistance ability of these genotypes at particular stress timings. Differences of about 2.5-3.0° C between stressed and N-ST plants were recorded. However, there was apparent reduction to normal canopy temperature when stress was relieved, which was the result of the increased ET of the rewatered plants. This indicated that measurements of canopy temperature as well as the differences between the canopy and the air temperature facilitate comparison of the effect of water deficit between ESD pigeonpea genotypes.

It is recognized that plant water status strongly influences plant growth and biomass production through its effect on leaf and root extension (Beadle *et al.* 1993) and biomass production is directly proportional to the water used. Thus, plant water status plays an important role in physiological activity of the crop as water moves through the soil-plant-atmosphere system along gradients of water potential. Drought resistance can be achieved through drought avoidance by maintaining water status under drought stress and drought tolerance by maintaining plant functions under drought (Hall *et al.* 1979).

The ESD pigeonpea showed extreme drought avoidance during PRFL-ST because the leaf RWC and LWP at the end of stress did not exhibit significant differences from the N-ST treatment, although these parameters tended to decline under stress treatments. Lower LWP at this stage has been seen to restrict LA expansion, as discussed earlier. The ability to maintain leaf RWC and LWP under stress is related to ability to extract and use more water in the soil during stress (Turner & Begg 1981). Ability of cowpea to avoid drought by maintaining relatively high LWP during stress period was reported by Turk and Hall (1980). In the present study leaf RWC of all genotypes declined significantly compared to the N-ST treatment during stress at flowering stage. This was consistent with the sensitivity of seed yield to water stress at this stage, as mentioned above. Leaf RWC could reduce to a level of 50-55% of the control under

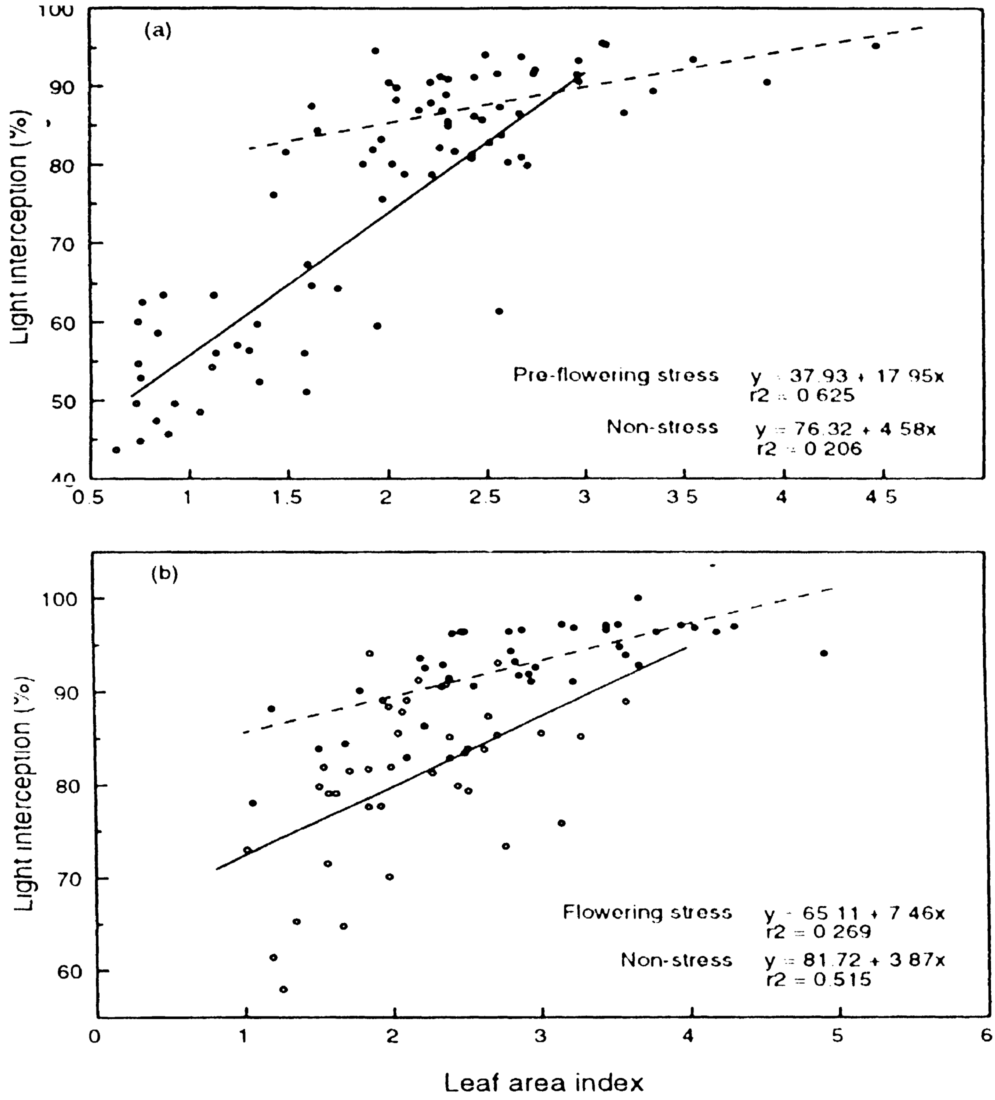


Figure .3.4.3: Relationship between LAI at the end of pre-flowering stress (a) and at the end of flowering stress (b) with grain yield under water stress and no stress conditions, seasons 1991 (solid lines) and 1992 (dash lines)

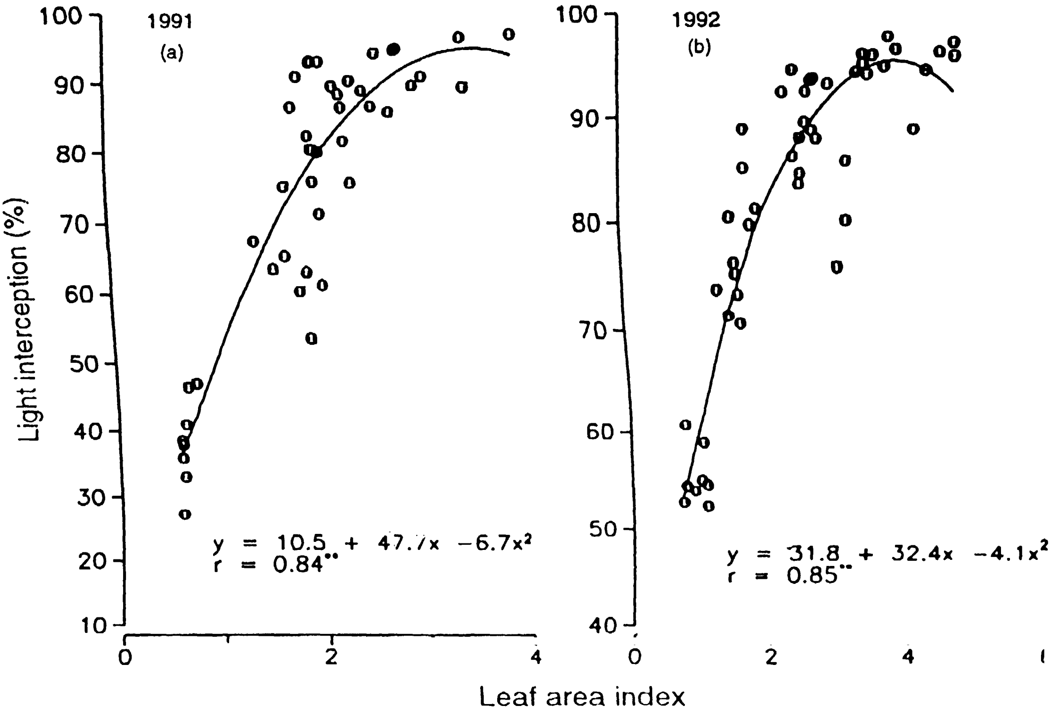


Figure 3.4.4: Relationship between light interception and leaf area index of extra-short-duration pigeonpea under water stress and no-stress condition, seasons 1991 (a) and 1992 (b).

severe drought in 1991 which is close to the lethal limits of 32% for pigeonpea (Flower & Luddlow 1986). Most susceptible genotypes, such as ICPL 89002 and ICPL 83015, also had lower RWC under drought stress. This was in agreement with the relationship observed between the ability to maintain higher leaf RWC and drought tolerance of soybean (Sloane *et al.* 1990) or wheat (Schonfeld *et al.* 1988; Ritchie *et al.* 1990).

Similarly, LWP and OP were also greatly reduced during FL-ST but OP was reduced more than LWP so as to maintain leaf turgor. A similar trend was observed in other stressed plants (Hsiao *et al.* 1976; Turner & Jones 1980). Between the two years of study, both LWP and OP were higher in 1992 than in 1991 which was due to higher evaporative demands in 1991 and more available water being present in the soil profile during the stress period of 1992 season. The lowest values of LWP of ESD pigeonpea could reach -2.8 to -3.0 MPa under severe drought. Similar values have been reported for cowpea by Wien *et al.* (1979) and Turk & Hall (1980).

It is recognized that OA, which is defined as a lowering of OP due to net solute accumulation in response to water stress, can play a significant role in maintaining the turgor relations of crop plants subjected to water deficits (Begg & Turner 1976; Jones & Turner 1978). The benefit of OA is the maintenance of root growth during the stress period that enables the crop to explore more water in deeper soil layers and continue to grow (Wright *et al.* 1983; Turner 1986b). Greater OA is associated with improved drought resistance in wheat (Morgan 1983; Johnson *et al.* 1984) and chickpea (Morgan *et al.* 1991). The ESD pigeonpea was able to realize a high level of OA during the stress period, especially under prolonged duration of stress at both crop growth stages. High levels of TP under all drought stress timings in 1991 and FL-ST in 1992 were seemingly contributed to by OA in all genotypes. Maintaining TP under drought stress has been seen as an adaptation to water deficit in grain legume crops. The maximum value of OA recorded in this experiment was 1.3 MPa, which is consistent with observations in longer duration pigeonpea (Flower & Ludlow 1986). At this level, pigeonpea which is considered having high dehydration tolerance compared with other grain legumes (Flower & Ludlow 1987), could to withstand low LWP and RWC without leaf death.

Among yield components, the number of pods m^{-2} was the main factor which could explain the grain yield differences between genotypes under drought for many grain legumes (Muchow 1985a). A highly positive correlation between pod number m^{-2} with grain yield was observed in this study under drought at the flowering stage in both years (Figure 3.4.5) but no such correlation was observed under PRFL-ST or PFILL-ST treatment. This suggested that enhanced ability to set pods under drought stress at the flowering was an important trait in drought resistance for ESD pigeonpea. Besides the number of pods m^{-2}, a significant reductions in 100 seed mass and HI were also observed, especially under stress at the pod-filling and under stress at FL+PFILL stages in 1991 whereas seeds pod^{-1} was the most stable yield component. Lower 100 seed mass was probably caused by limited remobilization of assimilates stored in roots and stems to developing seeds (see Chapter IV). Early stress improved HI mostly by reducing vegetative growth relative to grain yield produced. However, drought during the flowering or with prolonged duration of stress at both growth stages caused a reduction in HI by causing a greater relative reduction in DM production than in yield. It is clear that each of the yield components was affected differentially by stress at different stages of growth due to the sequential development of each component as well as the timing and duration of stress imposed. Thus, for improving stability of grain yield of ESD pigeonpea under drought conditions, improving stability of pods number m^{-2} as well as 100 seed mass should be exploited.

The maximum WUE value (calculated on a grain yield basis) of 60 kg cm^{-1} ha^{-1} was observed under non stress and PRFL-ST in 1991. This level was significantly higher than in 1992 as well as the WUE level of pigeonpea reported by Rana and Malhotra (1992), which was probably due to better control of water supply under ROS and water supplied by drip irrigation. Drought decreased crop evapotranspiration compared with the N-ST and thus increased or

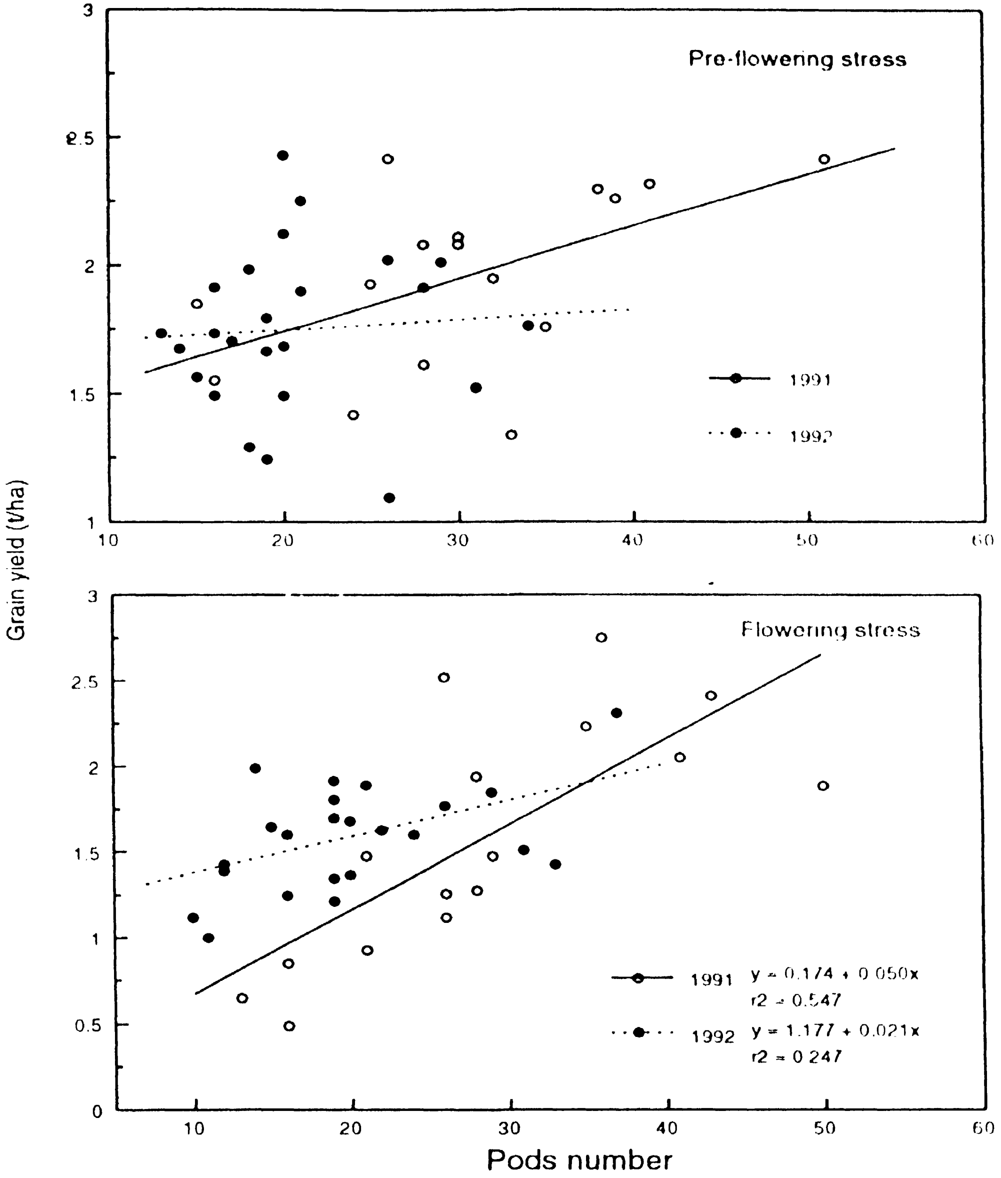


Figure 3.4.5: Relationship between grain yield and number of pods per plant of extra-short-duration pigeonpea under water stress imposed at the pre-flowering stage (a) and flowering stage (b), seasons 1991 and 1992.

maintained WUE of ESD pigeonpea under PRFL-ST treatment. However, drought stress at the flowering stage or for extended duration of stress reduced WUE because the reduction in ET of all ESD pigeonpea genotypes under these severe stresses was at the expense of their grain yield. Under these severe droughts, ESD pigeonpea had lower LWP, LAI, LI and finally the net rate of photosynthesis. This may cause a greater adverse effect on yield contributing characters leading to greater reduction in final grain yield relative to ET.

CHAPTER IV

PHYSIOLOGICAL TRAITS AND GRAIN YIELD RESPONSE OF EXTRA-SHORT-DURATION PIGEONPEA UNDER REPRODUCTIVE DROUGHT STRESS AND PARTIAL LEAF AREA REMOVAL

4.1 INTRODUCTION

The results of the experiments on the effect of timing of drought stress on ESD genotypes conducted in the rainy seasons of 1991 and 1992 showed that grain yield was dramatically reduced by drought stress at the flowering stage, especially when preceded by drought during the vegetative stage or followed by drought at the pod development stage (Chapter III). A 30-50% reduction in grain yield under the flowering stage stress and more than 60% reduction under the both flowering and pod-filling stages stress was observed. There were highly significant timing of drought stress x genotype interactions for grain yield in both seasons. Genotype ICPL 88039 gave relatively better yield under drought stress during the flowering stage, indicating its superior drought resistance compared to the other genotypes (Chapter III).

Early growth vigor and better ability to retain LA of ESD genotypes could be considered as an important trait contributing to drought resistance during pre-flowering stress. The role of LA retention under drought stress was also apparent in MD and SD pigeonpea in previous studies. The MD pigeonpea generally suffers from drought stress during the reproductive growth period at the end of the rainy season and the variation in sensitivity to drought was found to be closely correlated with the extent of LA retained at the end of drought (Legumes Program 1990). Similarly, LAI retained in SD pigeonpea explained nearly 97% and 58% of total variation in yield at the end of pre-flowering and flowering drought stress, respectively (Legumes Program 1991). Leaf retention during the pre-flowering stress is thus an important indicator of drought resistance because it allows plant growth and partitioning during and after a drought event (Lopez *et al.*

ICRISAT, unpublished data).

Food legume crops generally produce excess LAI when moisture is not limiting. This may result in excessive transpiration, without any improvement in radiation use efficiency. Extra-short-duration pigeonpea can develop a LAI of about 5 (Chauhan *et al.* 1993; Nam *et al.* 1993) which is substantially in excess of the critical level required for 95% light interception (Chapter III). When water supply becomes limiting, reducing LA is an important adaptive mechanism to reduce transpiration (Hussain *et al.* 1990).

Pigeonpea leaves can withstand a considerable degree of dehydration before death occurs (Flower & Ludlow 1986). Nonetheless, a large amount of leaf loss due to FL-ST and PFILL-ST treatments suggests that LAI is appropriately adjusted to minimize water transpired. In ESD pigeonpea, drought stress naturally caused reduced LA expansion, increased leaf thickness and caused severe leaf shedding, which was evidence of minimizing water loss (Chapter III). However, the impact of conservation of transpiration loss of water through reducing LA must keep balance with maintenance of a degree of retention of LA necessary for photosynthesis, especially during reproductive growth. A very low yield inspite of a heavy loss of LAI under PRFL+FL stress and FL+PFILL stress, which was exhibited by all genotypes in the 1991 experiment, indicated that this balance was not achieved and the reduction in grain yield was a result of decreasing assimilate availability. Partial defoliation during early reproductive growth of pigeonpea caused a reduction of seed yield (Pandey & Singh 1981; Tayo 1982). The extent to which LAI reduction at the reproductive stage affects to yield need to be determinated.

In this study, an effort was made to manipulate the LAI of ESD pigeonpea genotypes by reducing their LAI by 50% before flowering when a drought treatment was beginning, in order to understand the effect of different levels of LA retention under water limiting and non-limiting conditions. Such information may lead to a better understanding of how LA traits ultimately affect grain yield and then guide genetic improvement efforts for droughted environments.

4.2. MATERIALS AND METHODS

4.2.1. Site of the experiment

This experiment (experiment 3) was conducted at ICRISAT Center during the rainy season of 1993 under an automatic ROS at same site of experiment 1 as described in Chapter III. Soil chemical properties are given in Table 4.2.1.

Table 4.2.1: Soil chemical properties from 0-15 cm soil layer of this experiment.

pH	Electrical conductivity (dS m-1)	Organic[b] Carbon (%)	Available[b]		Total N[b] (mg kg^{-1} soil)
			Olsen P	N	
			(mg kg^{-1} soil)		
8.02	0.22	0.35	10.5	27.2	526

[a]: Analysis methods of soil chemical properties followed are as cited in Chapter III)

4.2.2. Experiment design and layout

A split-split-plot design with four replications was used. Stress treatments imposed at the reproductive growth stage (from 50 DAS to harvest) and no-stress were assigned to main-plots. The LA removal treatments were assigned to sub-plots, as follows:

Main plot: 1) No-stress (control or N-ST)

2) Drought stress (D-ST)

Sub-plot: 1) Full LA development (F-LA)

2) 50% LA removal before stress (R-LA)

To impose the 50% LA removal (R-LA) treatment, leaves from alternate nodes on the main stem and branches of each plant were removed from top to bottom, thereby ensuring that the degree of reduction of LA in each genotype was uniform.

The following six ESD pigeonpea genotypes, 5 of which were used in Experiment 2 of 1992 and an additional genotype (ICPL 85010), were assigned to sub-sub-plots:

1) ICPL 83015 (DT)
2) ICPL 84023 (DT)
3) ICPL 85010 (DT)
4) ICPL 88032 (IDT)
5) ICPL 88039 (IDT)
6) ICPL 89002 (IDT)

Each sub-sub-plot consisted of 5 rows (1.5 m plot width) each 4.5 m long. Sowing was done on 14 June 1993.

4.2.3. Agronomic practices

All agronomic practices used were the same as described in Chapter III.

4.2.4. Irrigation and stress treatments

Irrigation to field capacity through perforated pipes was applied just after sowing so that soil moisture was sufficient for seed germination and good crop establishment. The automatic ROS was activated from 10 DAS until harvest and further irrigations were applied to each main-plot by a drip irrigation system at 3-5 days intervals depending on the dryness of soil surface layer. Drought stress treatments were imposed by removing irrigation lines from the stressed main plots.

4.2.5. Observations and measurements

4.2.5.1. Soil moisture

Soil moisture in the 0-105 cm soil profile was monitored at weekly intervals using a neutron probe as described in Chapter III. An access tube was installed in each sub-plot and soil moisture was measured in three replications.

4.2.5.2. Crop growth and physiological traits

4.2.5.2.1 Growth analysis

The LA, TDM and the partitioning of DM into component plant parts were determined using the same methods as described in Chapter III. Different growth analysis parameters were calculated as follows (Beadle 1993):

- Relative Growth rate (RGR)

RGR ($gg^{-1}week^{-1}$) = $(\ln W_2 - \ln W_1)/(T_2 - T_1)$

- Crop growth Rate (CGR)

CGR ($gm^{-2}day^{-1}$) = $1/GA \times (W_2 - W_1)/(T_2 - T_1)$

- Net Assimilation Rate (NAR)

NAR ($gm^{-2}day^{-1}$) = $(W_2 - W_1)/(T_2 - T_1) \times (\ln LA_2 - \ln LA_1)/(LA_2 - LA_1)$

- Leaf Area Index (LAI)

LAI = LA/GA

where, LA is leaf area (m^2), GA is ground area (m^2), T is time (day) and W is dry weight (g).

4.2.5.2.2 Transpiration rate and stomatal conductance

Transpiration rate (TR) and stomatal conductance (CD) were measured using a Steady State Porometer (LI-1600, LI-COR Inc., Nebraska, USA). Measurements were made at weekly intervals before and during water stress periods on the abaxial surface of the last fully expanded leaf on the main stems between 0930 and 1500 h of sunny days.

4.2.5.2.3 Non-structural carbohydrate

Non-structural carbohydrates such as glucose, fructose, sucrose and starch stored temporarily in stems in the water stress and LA removal treatments were quantified at the beginning of and during the period of stress. The method of analysis followed was the UV-method with an enzyme-kit from Boehringer Mannheim (1993). The procedure to prepare samples for analysis is briefly described below:

Stems samples were collected from each 10 cm stem length at the center of 3 plants and were cut into small pièces with scissors. Approximately 1 g of fresh stem sample was taken and ground by a mortar with 5 ml of deionized distilled water (DW) plus a small spoonful of quartz sand. The homogenate was transferred to a plastic centrifuge tube with screw cap and an additional 5 ml of DW was added. The tube was immediately placed in a water bath at 95°C for 3 minute to stop biological activity. A further extraction was carried out by vigorously shaking the tube for 30 min. at 60 °C. The supernatant was used for analysis of glucose, fructose and sucrose. The precipitate was twice washed with 10 ml of acetone and then dried at 60° C. The starch was extracted by shaking the sample with 1 ml of HCl (8 mol/l) and 4 ml of dimethylsulfoxide for 30 min. at 60° C. The starch extract was mixed with 2M acetate buffer (pH 5.0) in 3 to 10 ratio for neutralization prior to analysis.

4.2.5.2.4 **Other observations**

All other observations such as light interception, leaf water relations, TDM at harvest, grain yield and yield components were recorded as described in the Chapter III.

Radiation use efficiency (RUE) was calculated as the ratio of total DM accumulation to the cumulative radiation intercepted at different crop growth stages.

4.2.6 Statistical analysis

The experimental data were analyzed by using the GENSTAT package in the VAX mainframe computer system at ICRISAT Center, as described in Chapter III.

4.3 RESULTS OF EXPERIMENT

4.3.1 Soil Moisture Pattern during Crop Growth

Soil water in the 0-15 cm profile showed a considerable depletion during the stress period imposed (Figure 4.3.1.1). This difference was less conspicuous in deeper layers and very little difference was noted below 60 cm soil depth. The differences between soil water of F-LA and R-LA treatments were not significant.

As reported in Chapter III, ESD pigeonpea extracted more water from 0-45 cm, which showed significant differences between D-ST and N-ST at 51 and 86 DAS, while it was relatively constant during the stress period below 60 cm (Figure 4.3.1.1). In the N-ST treatment, soil water was relatively higher in R-LA than in F-LA treatment but this difference was not apparent in the D-ST treatment (Figure 4.3.1.1).

4.3.2 Response of grain yield

There were very highly significant differences in grain yield due to the D-ST and N-ST treatments, the R-LA and F-LA treatments and among the different genotypes (Figure 4.3.2; Appendix 4.1). However, all the interaction effects among these treatments were not significant. The highest grain yields ranging from 1.7-2.4 t/ha were obtained with N-ST and F-LA. Drought stress reduced grain yield by 30-45% in the F-LA and 30-50% in the R-LA treatments. Generally, partial R-LA caused reduction in grain yield by 5-10% in the N-ST and 5-15% in the D-ST treatments. However, only genotype ICPL 89002 gave higher grain yield under R-LA than F-LA under N-ST treatment.

There were highly significant genotypic differences in grain yield between the N-ST and D-ST treatments (Appendix 4.1). Genotype ICPL 88039 showed least yield reduction under drought stress while ICPL 83015 exhibited the largest reduction of yield.

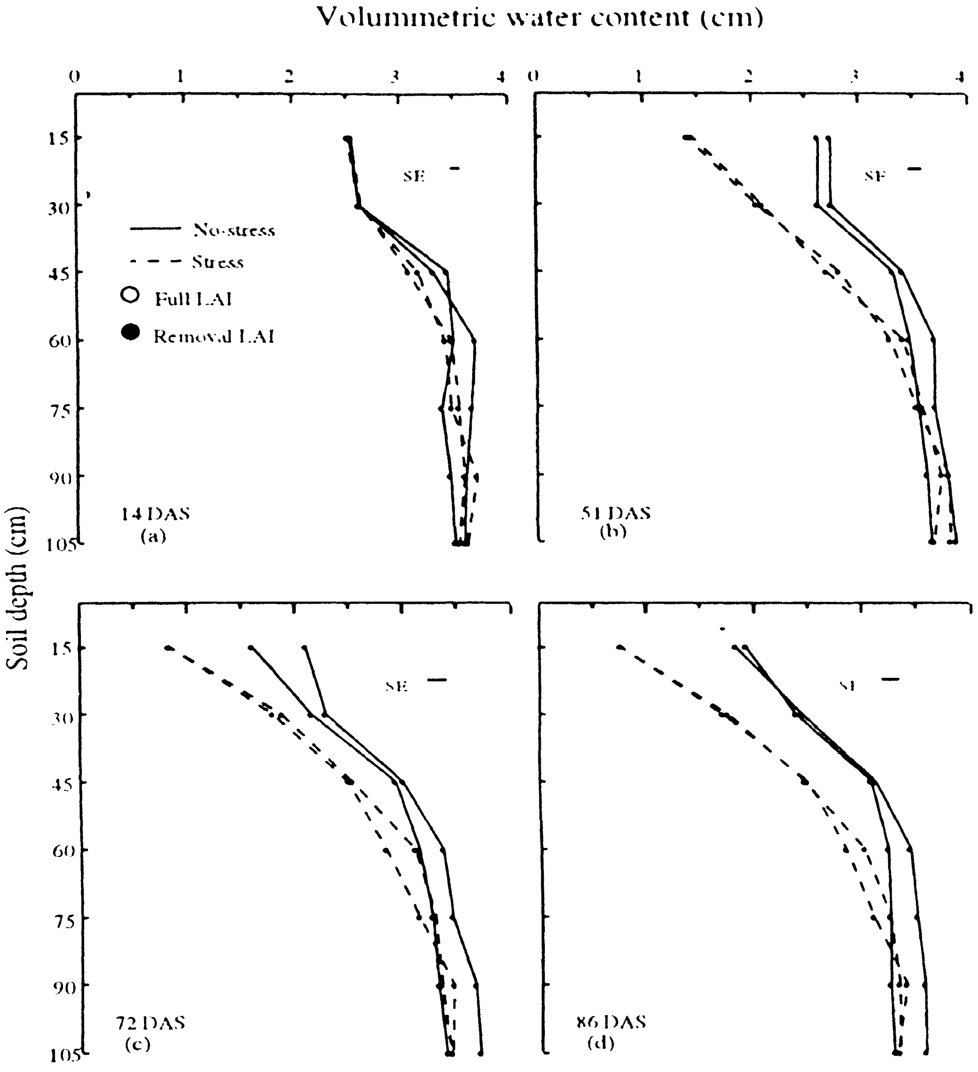


Figure 4.3.1.1: Water extraction of extra-short-duration pigeonpea before stress imposition (14 DAS, a) and during the stress period: 51 DAS (b), 72 DAS (c) and 86 DAS (d). Horizontal bar is SE( ) for comparing between stress treatments

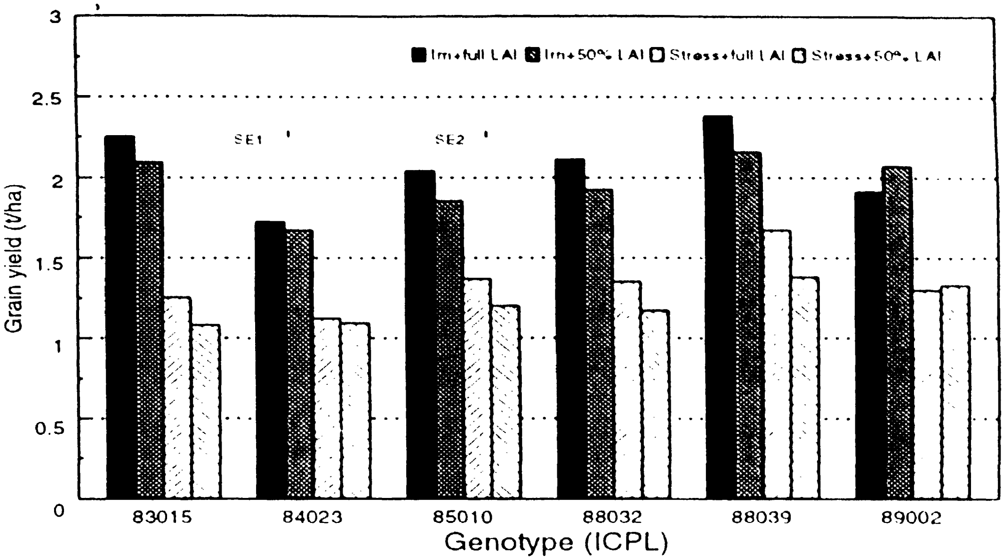


Figure 4.3.2: Grain yield of different extra-short-duration pigeonpea genotypes under different drought stress and leaf area removal treatments.
(SE1 is used for comparing between stresses and SE2 for comparing between leaf area removal treatments)

4.3.3 Canopy development and radiation interception

4.3.3.1 Leaf area index

The canopy development patterns of different genotypes as affected by both D-ST and by partial LA removal treatments are given in Figure 4.3.3.1. Generally, all the genotypes attained a maximum LAI at 60-65 DAS in the F-LA treatment but it was delayed about 5-7 days in the R-LA treatment. In the N-ST treatment, genotype ICPL 83015 developed the highest LAI which was more than 5.0 whereas LAI of ICPL 84023 was lowest, at about 3.5.

The differences in LAI were highly significant between D-ST and N-ST treatments (Appendix 4.2). Drought stress reduced maximum LAI to 3.0-3.5 in different genotypes (Figure 4.3.3.1). The highest LAI that could be attained in the drought treatment was 62-82% and 52-71% of the controls under F-LA and R-LA, respectively.

The R-LA treatment resulted in a sharp drop of LAI. It also caused changes in the accumulation pattern of LAI under both D-ST and N-ST treatments (Figure 4.3.3.1). The differences in LAI between the F-LA and R-LA treatments were significant during the drought stress period but these differences became smaller towards maturity (Appendix 4.2). The interactions among different treatments were not significant (Appendix 4.2).

4.3.3.2 Light interception

In the N-ST treatment, different genotypes could intercept a maximum of 98% total incident radiation by 60-65 DAS when LAI was at maximum level (Figure 4.3.3.2.1). Drought stress significantly reduced radiation interception over the entire duration of stress with the maximum value being only about 80%. The R-LA treatment significantly reduced LI in all genotypes just after the treatment was imposed. However, the differences were not significant during the pod-filling stage (Figure 4.3.3.2.1). The relationship between LAI and LI was highly significant in both

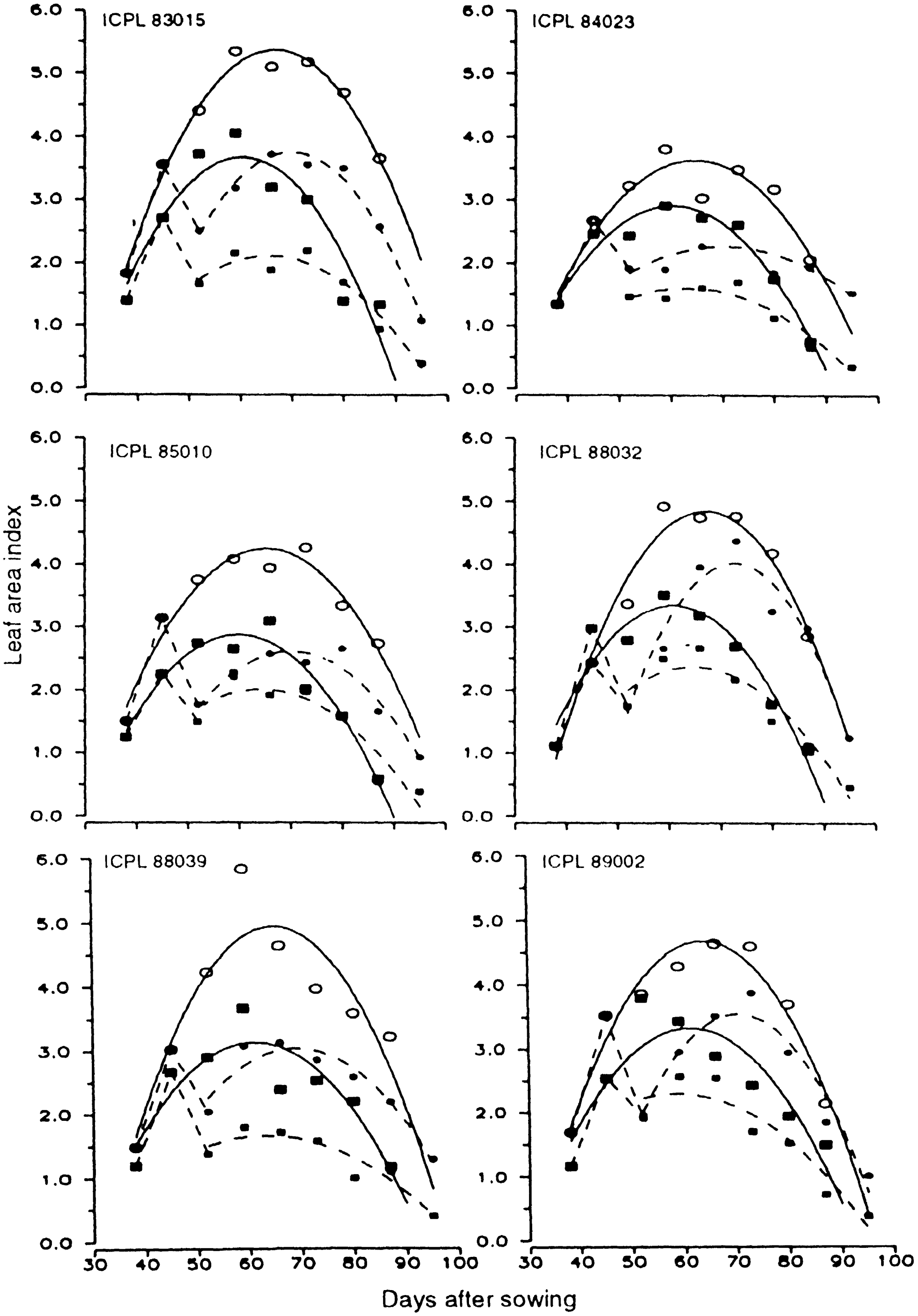


Figure 4.3.3.1: Canopy development pattern of six ESD pigeonpea genotypes under water stress (dashed line) and no-stress (solid line) treatments, and under LA removal (square symbol) and full LA (circle symbol) treatments, season 1993.

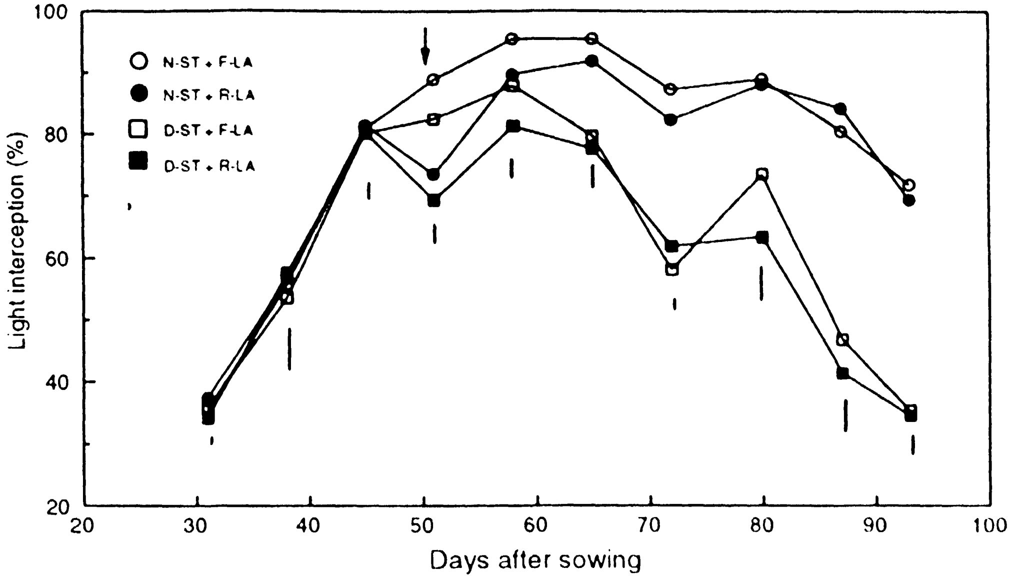


Figure 4.3.3.2.1: Light interception pattern during crop growth in different stress and leaf area removal treatments.
Vertical bar is SE(±) for comparing between stress treatments.

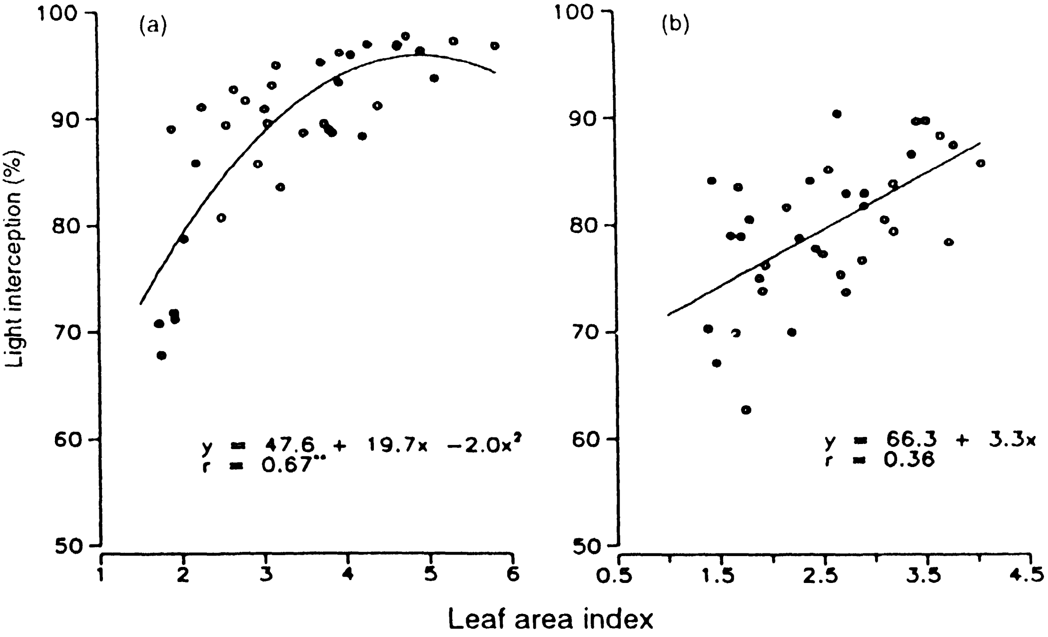


Figure 4.3.3.2.2: Relationship between light interception and leaf area index of extra-short-duration pigeonpea in the no-stress (a) and the stress (b) treatments.

D-ST and N-ST treatments (Figure 4.3.3.2.2). The critical LAI level to intercepted 95% radiation was about 4.0 in the N-ST treatment, which was relatively higher than the levels in 1991 and 1992 (Figure 4.3.3.2.2a). In the drought stress treatment, LAI did not reach the critical level (Figure 4.3.3.2.2b).

4.3.4 Biomass accumulation and radiation use efficiency

In the N-ST treatment, DM accumulation increased rapidly when LAI was maximum (55-65 DAS) and also during the pod development stage (75-85 DAS). Differences in DM accumulation due to drought stress were significant from 65 DAS onward (Figure 4.3.4.1; Appendix 4.2). The DM accumulation immediately slowed down (20-30%) after applying the LA removal treatment. The difference was significant because a portion of DM held in leaves was removed by the leaf removal treatment. The reduction was higher in the D-ST treatments than in the N-ST treatment. The differences in DM between LA removal treatment were not significant at maturity. All interaction effects were not significant.

For all genotypes, there were highly significant relationships between accumulated DM production and cumulative LI in all the treatments (Figure 4.3.4.2). The LI accounted for 89-99% of total variation in DM under N-ST and for 79-99% under D-ST treatments. The radiation use efficiency (RUE) as determined from the slopes of the regressions varied over the range 0.77-1.00 g MJ^{-1} in the N-ST and in the range 0.58-0.74 g MJ^{-1} in the D-ST treatments. The RUE was considerably lower in the R-LA treatment (Figure 4.3.4.2). Mean radiation use efficiency (RUE) of all ESD pigeonpea genotypes during the stress period was lower in the D-ST and R-LA treatments than in the N-ST and F-LA treatments (Figure 4.3.4.3).

The differences in DM were highly significant between stress treatments; between R-LA treatments and among genotypes (Appendix 4.1). The interaction effects of these factors were not significant. Total DM at harvest was significantly reduced by the D-ST and by the R-LA

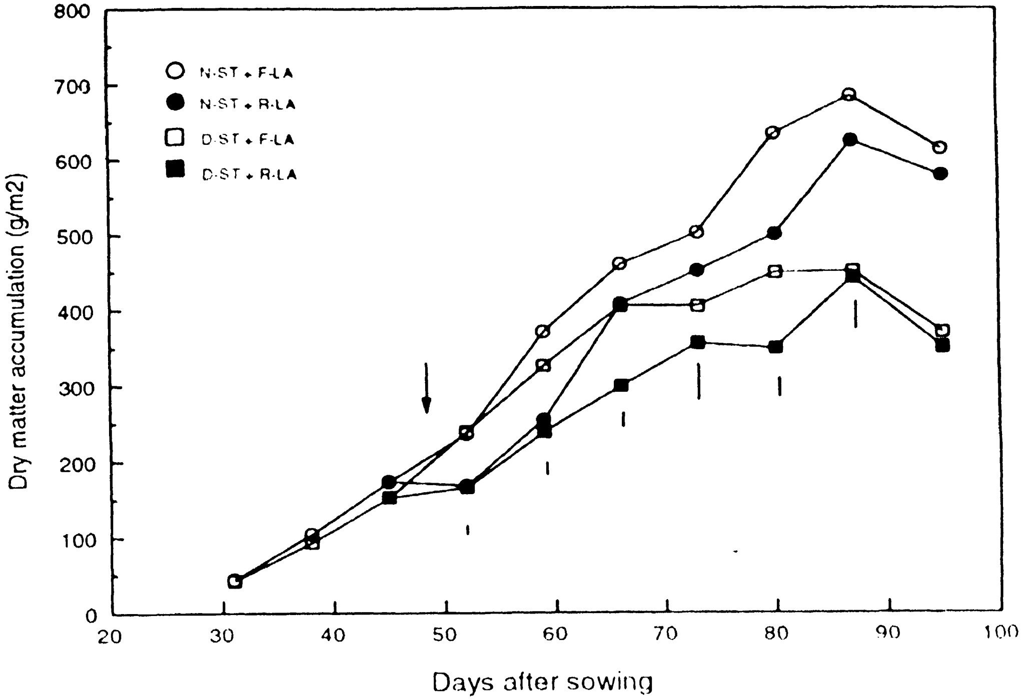


Figure 4.3.4.1: Dry matter accumulation pattern of extra-short-duration pigeonpea during crop growth cycle under the drought stress and the leaf area removal treatments.
Vertical bar is SE(±) for comparing between stress treatments.

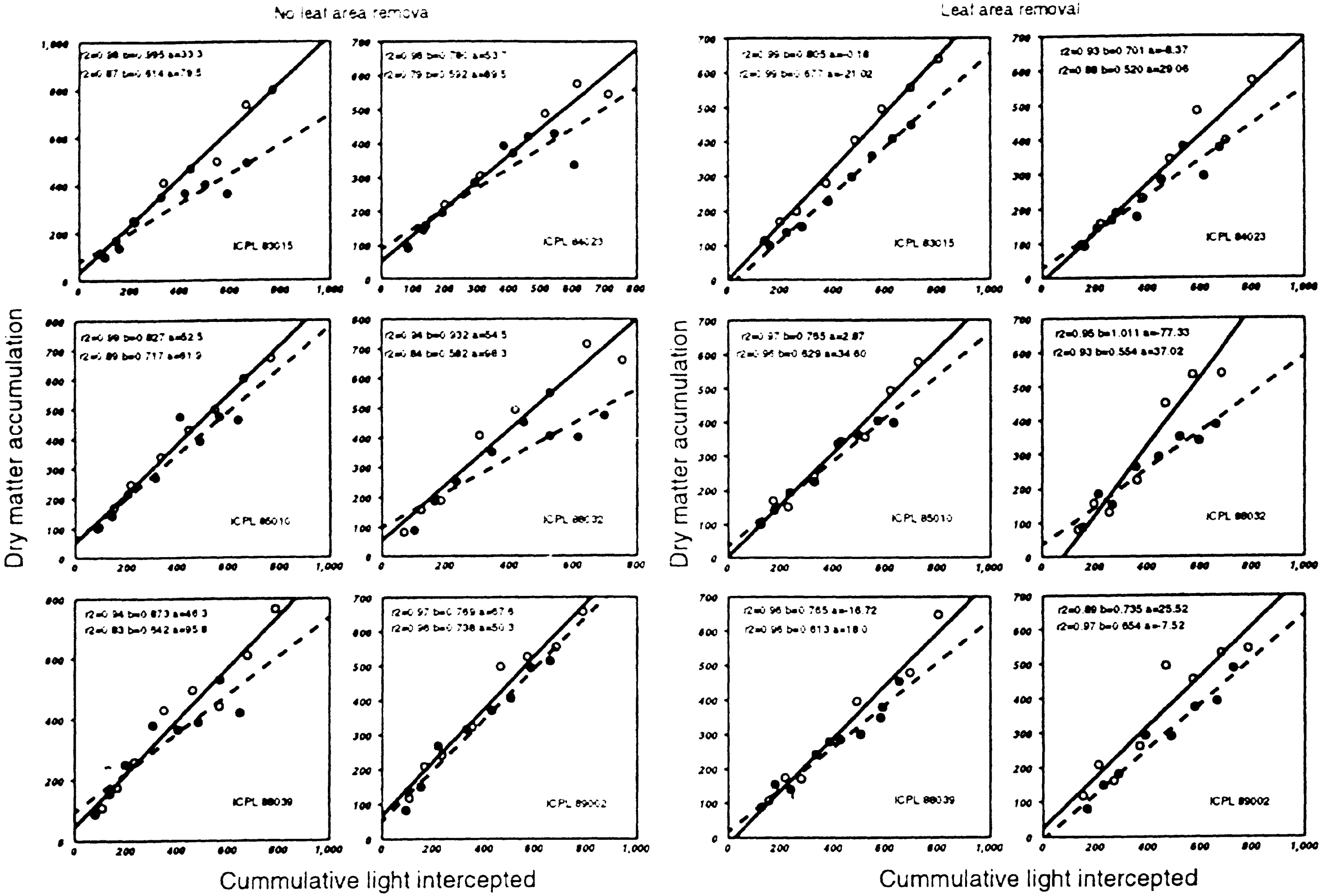


Figure 4.3.4.2: Relationship between total dry matter accumulation and cumulative light intercepted of six ESD pigeonpea genotypes under drought stress and leaf area removal treatments, season 1993. The slope values indicate the radiation use efficiency (g/MJ).

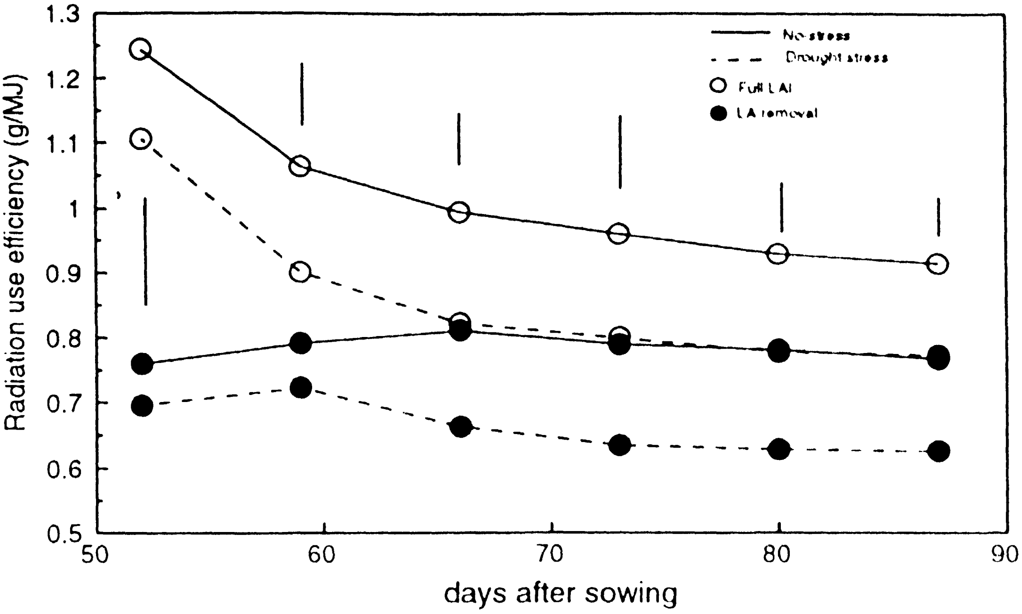


Figure 4.3.4.3: Radiation use efficiency of extra-short-duration pigeonpea as affected by the water stress (dashed line) and no-stress (solid line), and by leaf area removal (solid circle) and full leaf area (open circle) treatments. Vertical bar is SE(±) for comparing between stress treatments.

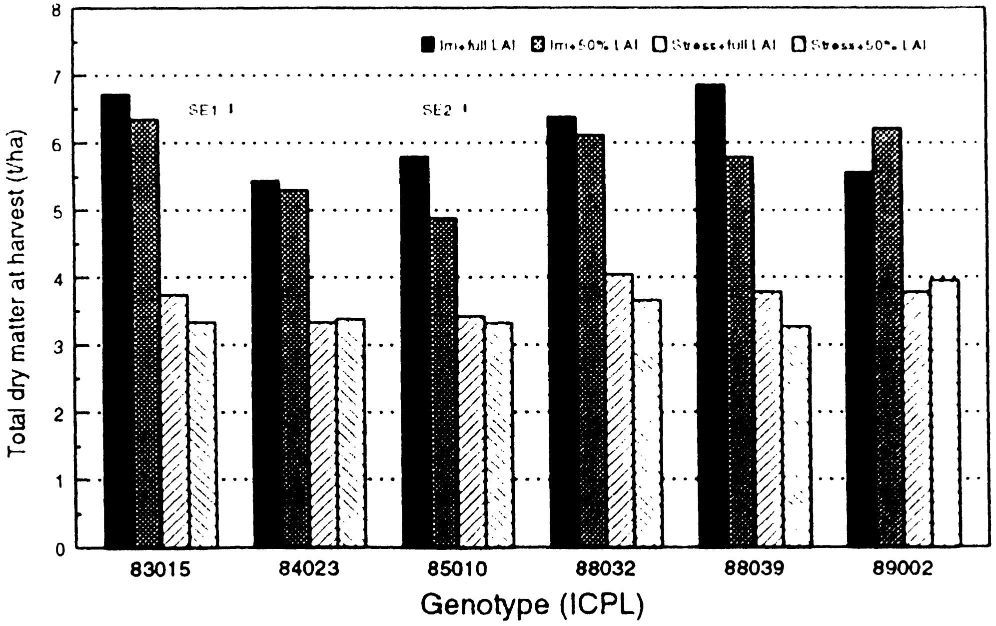


Figure 4.3.4.4: Total dry matter at harvest of six extra-short-duration pigeonpea genotypes under water stress and LA removal treatments. (SE1 is used for comparing between stresses and SE2 for comparing between leaf area removal treatments)

treatments (Figure 4.3.4.4). The D-ST as well as R-LA treatment caused greatest reduction in TDM of genotypes ICPL 83015 and ICPL 88039 but genotype ICPL 89002 showed higher TDM in the R-LA treatment under the N-ST condition (Figure 4.3.4.4).

4.3.5 Transpiration 'rate

Transpiration rates (TR) increased from early crop growth to the pod-filling stage (70 DAS) and then declined during seed development and maturity (Figure 4.3.5a). Drought stress reduced TR throughout the period and the differences were highly significant at the end of pod-filling stage (Table 4.3.5). The R-LA treatment did not affect the TR in the N-ST treatment but it slightly increased the TR under the D-ST treatment (Figure 4.3.5a), particularly during the period of high transpiration demand. Genotypic differences in TR were significant at the end of flowering stage but not significant at the end of the pod-filling stages. Susceptible genotype ICPL 83015 had lower TR than resistant genotype ICPL 88039 under D-ST as well as the R-LA treatments and the differences were only significant during the flowering stage (Table 4.3.5). All interaction effects were not significant during the stress period (Table 4.3.5).

4.3.6 Stomatal conductance

In the N-ST treatment, stomatal conductance (CD) increased with increasing TR during the flowering stage (Figure 4.3.5b). Drought stress caused greater decrease in CD than TR and the differences were highly significant throughout the stress period. Removal of LA increased CD but the differences was not significant (Figure 4.3.5b). The differences among genotypes were significant at the end of pod-filling stage, with ICPL 83015 having significantly lower values than other genotypes, especially in the F-LA treatment (Table 4.3.6).

4.3.7 Leaf water status

Leaf water potential (LWP), which was similar between treatments at the time the stress was

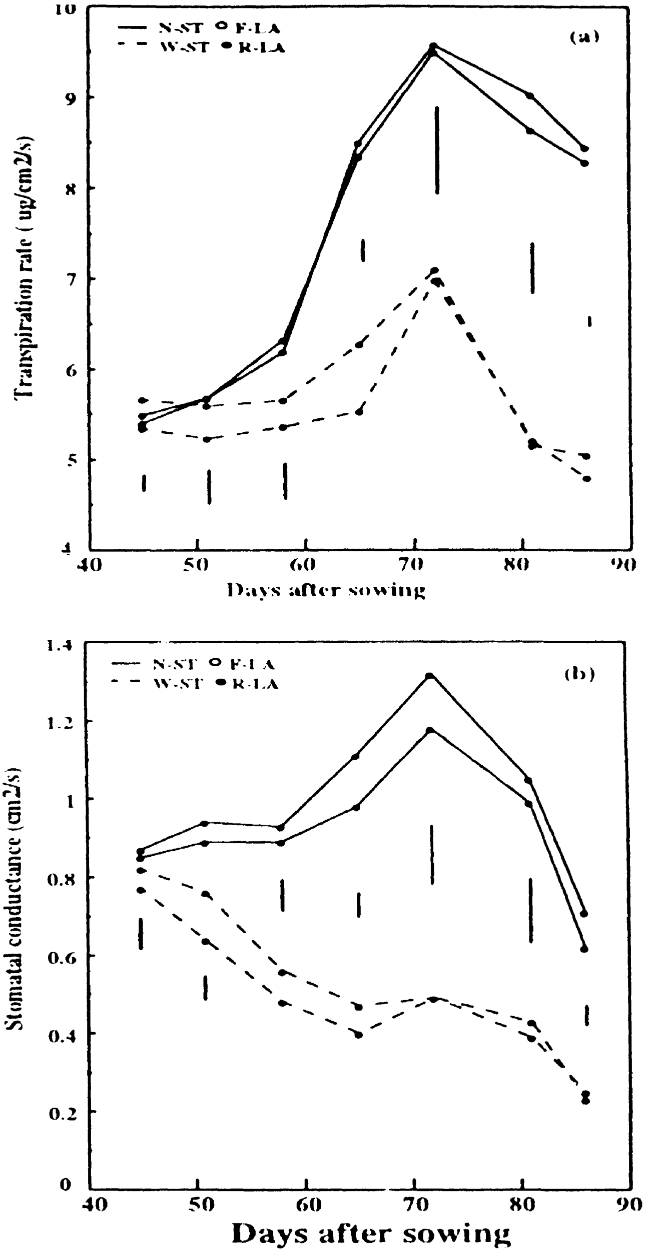


Figure 4.3.5: Effect of drought stress and leaf area removal treatments on transpiration rate (a) and stomatal conductance (b) of extra-short-duration pigeonpea. Vertical bar is SE(±) for comparing between stress treatments.

Table 4.3.5: Effect of drought stress and leaf area removal treatments on transpiration rate (mg cm^{-2} s^{-1}) at the end of flowering and pod-filling stages in six extra-short-duration pigeonpea genotypes, rainy season 1993.

Genotype	No-stress		Drought stress	
	Full LA	LA removal	Full LA	LA removal
	Flowering stage			
ICPL 83015	9.84	9.52	6.55	7.40
ICPL 84023	9.35	9.89	6.92	6.51
ICPL 85010	9.45	9.20	7.36	6.78
ICPL 88032	9.30	9.14	6.26	6.15
ICPL 88039	9.65	10.01	7.27	8.35
ICPL 89002	9.33	9.65	7.35	7.34
Mean	9.49	9.57	6.97	7.09
SE (±)	Stress (S)		0.615^{NS}	
	Treatment (T)		0.215^{NS}	
	Genotype (G)		0.228*	
	S x T		0.651 (0.304)^{NS}	
	S x G		0.681 (0.322)^{NS}	
	T x G		0.364^{NS}	
	S x T x G		0.772 (0.515)^{NS}	
	Pod-filling stage			
ICPL 83015	7.36	8.07	4.04	4.81
ICPL 84023	8.44	8.52	5.09	5.29
ICPL 85010	8.44	8.12	4.64	6.02
ICPL 88032	8.84	8.02	4.57	4.74
ICPL 88039	8.53	8.94	5.20	4.61
ICPL 89002	8.06	8.94	5.20	4.80
Mean	8.28	8.44	4.79	5.04
SE (±)	Stress (S)		0.084**	
	Treatment (T)		0.183^{NS}	
	Genotype (G)		0.237^{NS}	
	S x T		0.201 (0.258)^{NS}	
	S x G		0.318 (0.336)^{NS}	
	T x G		0.357^{NS}	
	S x T x G		0.478 (0.504)^{NS}	

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

SE value in parenthesis is used for comparing means in the same level of stress

Table 4.3.6: Effect of drought stress and leaf area removal treatments on stomatal conductance (cm^2 s^{-1}) at the end of flowering and pod-filling stages in six extra-short-duration pigeonpea genotypes, rainy season 1993.

Genotype		No-stress		Drought stress	
		Full LA	LA removal	Full LA	LA removal
		Flowering stage			
ICPL 83015				1.251.260.460.62	
ICPL 84023				1.201.410.690.78	
ICPL 85010				1.191.210.630.65	
ICPL 88032				1.151.170.690.61	
ICPL 88039				1.211.460.660.76	
ICPL 89002				1.081.380.620.87	
Mean				1.181.320.620.71	
SE (±)	Stress (S)			0.075**	
	Treatment (T)			0.025^{NS}	
	Genotype (G)			0.053^{NS}	
	S x T			0.079 (0.036)^{NS}	
	S x G			0.101 (0.074)^{NS}	
	T x G			0.072^{NS}	
	S x T x G			0.124 (0.102)^{NS}	
		Pod-filling stage			
ICPL 83015		0.46	0.62	0.18	0.24
ICPL 84023		0.69	0.78	0.25	0.27
ICPL 85010		0.63	0.65	0.22	0.32
ICPL 88032		0.69	0.61	0.21	0.22
ICPL 88039		0.66	0.76	0.27	0.22
ICPL 89002		0.62	0.87	0.23	0.22
Mean		0.62	0.71	0.23	0.25
SE (±)	Stress (S)			0.024**	
	Treatment (T)			0.008**	
	Genotype (G)			0.029*	
	S x T			0.025 (0.012)*	
	S x G			0.044 (0.040)^{NS}	
	T x G			0.038^{NS}	
	S x T x G			0.058 (0.053)^{NS}	

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

SE value in parenthesis is used for comparing means in the same level of stress imposed was reduced during the stress period (Figure 4.3.7a). The difference between the stress treatments was highly significant at the end of pod-filling stage (Appendix 4.3). The effect of LA removal treatment was not significant in LWP at the flowering stage but was significant at the end of the flowering stage. All the interaction effects were not significant at any of the stages.

Drought stress caused a greater reduction in osmotic potential (OP) than LWP and the differences were significant throughout the period of stress imposition (Figure 4.3.7b; Appendix 4.3). Leaf removal treatment increased OP slightly but the differences were not significant during stress period (Figure 4.3.7b). The differences among genotypes were significant at the beginning of stress but were not significant at the end of stress (Appendix 4.3). All interaction effects of OP were not significant. The range of osmotic adjustment (OA) varied from 0.2 to 0.5 MPa in different genotypes during the stress period (Table 4.3.7). Genotypes ICPLs 83015, 88032 and 88039 showed relatively high OA. However, the differences between the LA removal treatments and among genotypes tested were not significant.

Turgor potential increased rapidly after stress imposition (Figure 4.3.7c). The D-ST treatment increased TP and the R-LA treatment decreased TP at the end of stress. The differences were significant between the stress and between the R-LA treatments but not among the genotypes (Appendix 4.3). All the interaction effects were not significant.

Leaf RWC was reduced by drought stress and the differences were significant between stress treatments at the end of stress (Figure 4.3.7d). The LA removal treatment did not affect the leaf RWC. The genotypic differences in leaf RWC under different treatments were not significant (Appendix 4.3). The interaction between the stress and LA removal treatments, and between the LA removal treatment and genotypes were significant only at 71 DAS. The other interaction effects were not significant.

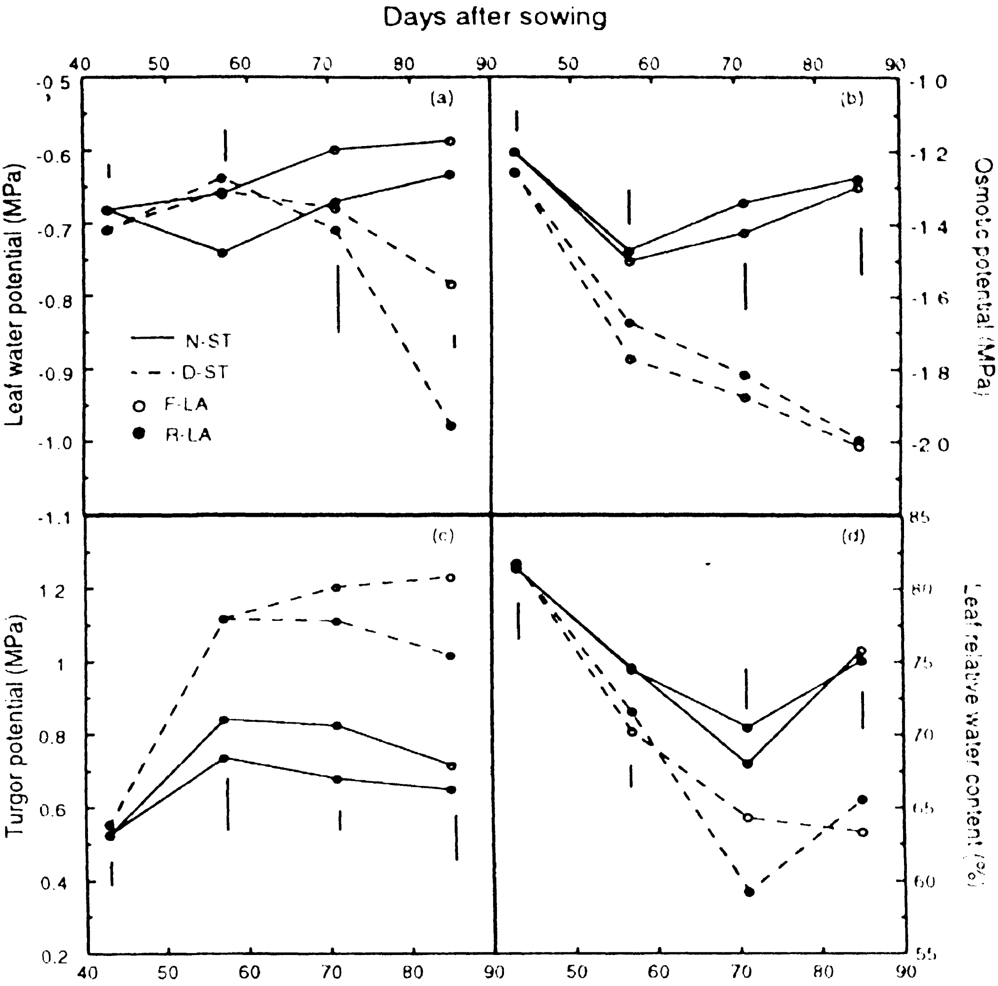


Figure 4.3.7: Leaf water potential (a), osmotic potential (b), turgor potential (c) and leaf relative water content (d) of extra-short-duration pigeonpea as affected by drought stress (dashed line), no-stress (solid line), and by LA removal (solid circle) and full LA (open circle), season 1993.
Vertical bar is SE(±) for comparing between stress treatments.

Table 4.3.7: Osmotic adjustment (MPa) of extra-short-duration pigeonpea genotypes affected by partial removal of leaf area before water stress imposed at different stages of stress, rainy season 1993.

genotype	71 DAS		85 DAS	
	Full LA	LA removal	Full LA	LA removal
ICPL 83015	0.30	0.18	0.44	0.22
ICPL 84023	0.21	0.13	0.14	0.33
ICPL 85010	0.16	0.07	0.40	0.23
ICPL 88032	0.25	0.26	0.26	0.40
ICPL 88039	0.29	0.19	0.22	0.43
ICPL 89002	0.25	0.16	0.47	0.48
Mean	0.24	0.16	0.32	0.35
SE (±) T	0.030NS		0.032NS	
G	0.059NS		0.091NS	
T x G	0.081NS		0.121NS	

NS: Non significant difference

4.3.8 Non-structural carbohydrates

Drought stress and LA removal treatments had a profound effect on total soluble sugars (including glucose) and starch content which was temporarily stored in the stems during stress (Figure 4.3.8.1). Drought stress significantly increased glucose, total sugar and starch content in the stem (Appendix 4.4), especially during the peak flowering period (65-70 DAS). During the pod-filling stage to maturity (after 73 DAS), the differences between stress treatments were not significant. In contrast, LA removal treatment caused a reduction in glucose as well as total sugar content at beginning of stress (50-65 DAS) but the differences were not significant at later stages (Appendix 4.4). The R-LA treatment did not affect the starch content during the stress period.

A comparison of total sugar and starch content pattern in stem of two contrasting genotypes indicated that the drought susceptible genotype ICPL 83015 generally had higher sugar and starch content in the stem than the resistant genotype ICPL 88039, especially under stress treatment (Figure 4.3.8.2). The differences between the two genotypes were particularly more conspicuous during the pod development stage (from 65 DAS to harvest).

4.3.9 Yield components and harvest index

The differences in total pods m^{-2} were significant between stress treatments and among genotypes (Appendix 4.1). Drought stress reduced number of pods m^{-2} in all genotypes (Figure 4.3.9a). The LA removal treatment reduced pod set in all the determinate genotypes irrespective of drought stress while it appeared to increase number of pods set in the indeterminate genotypes, especially in ICPL 89002. However, these differences were not statistically significant (Appendix 4.1).

Seed number pod^{-1} was not affected by the D-ST and R-LA treatments (Figure 4.3.9b) but the differences among the genotypes were significant (Appendix 4.1).

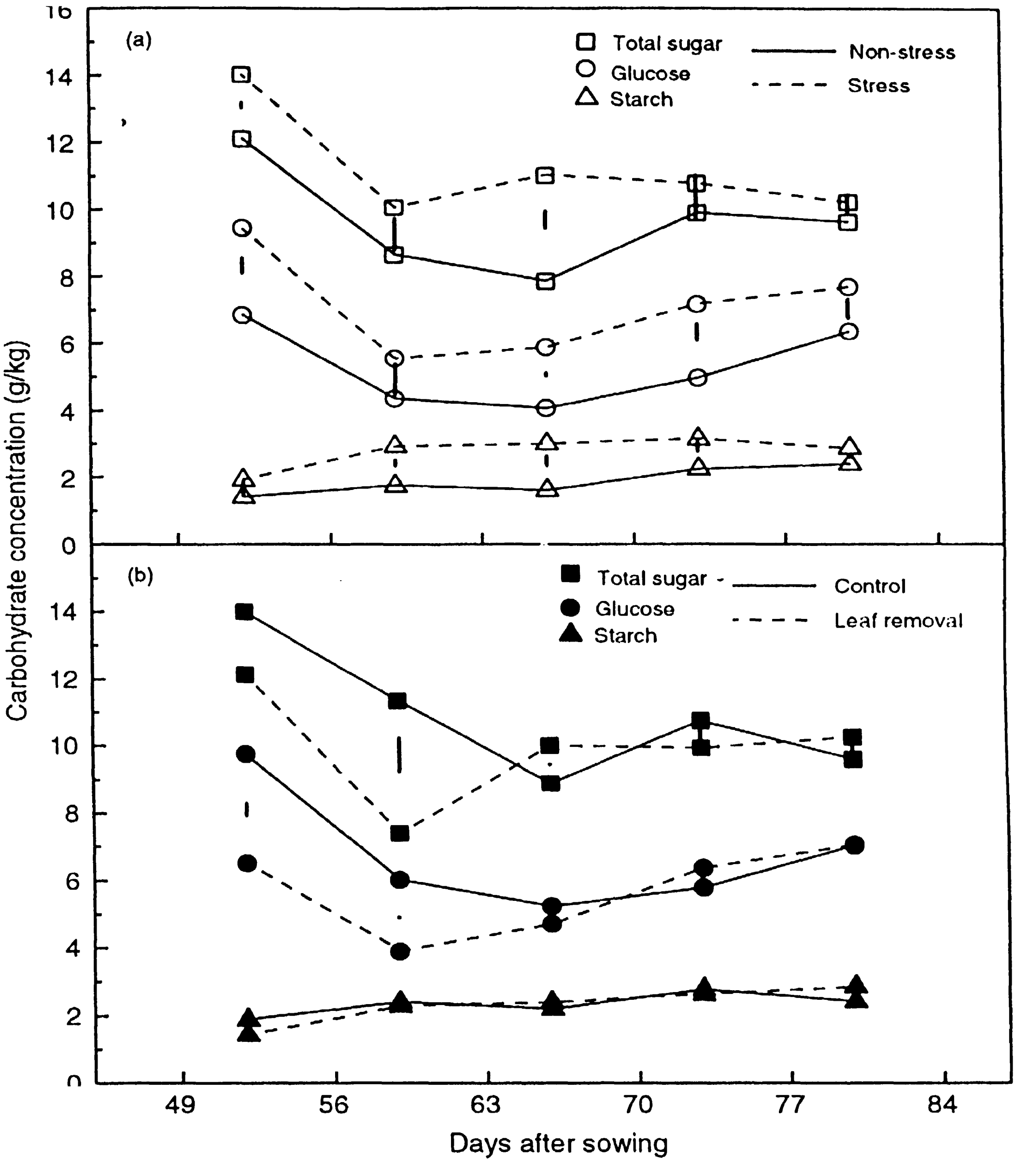


Figure 4.3.8.1: Effect of drought stress (a) and leaf area removal (b) treatments on non-structural carbohrydrate concentration in stem at different times during drought stress imposed.
Vertical bar is SE(±) for comparing between stress treatments.

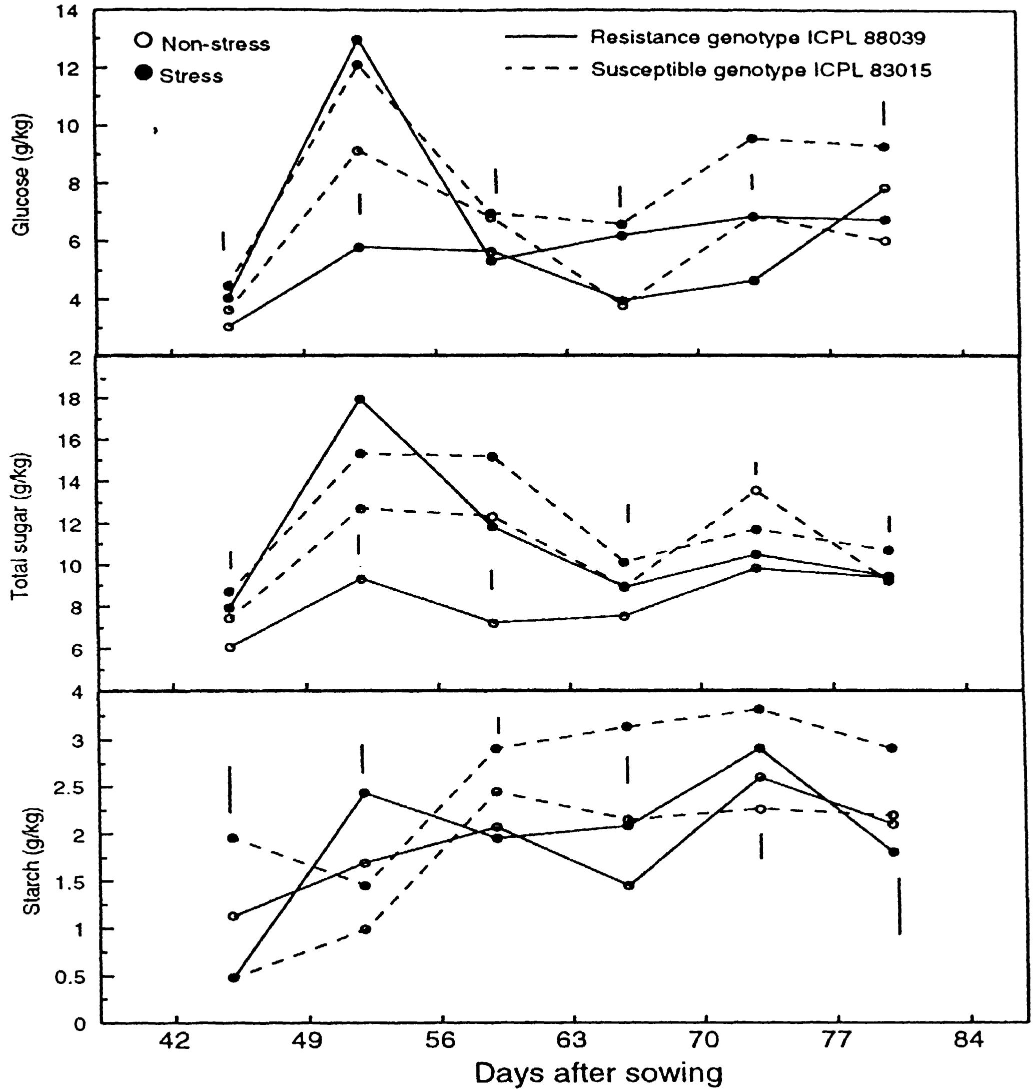


Figure 4.3.8.2: Carbohrydrate concentration in stem of two contrasting extra-short-duration pigeonpea genotypes ICPL 88039 (solid line) and ICPL 83015 (dashed line) under no-stress (open circle) and drought stress (solid circle).
Vertical bar is SE(±) for comparing between stress treatments.

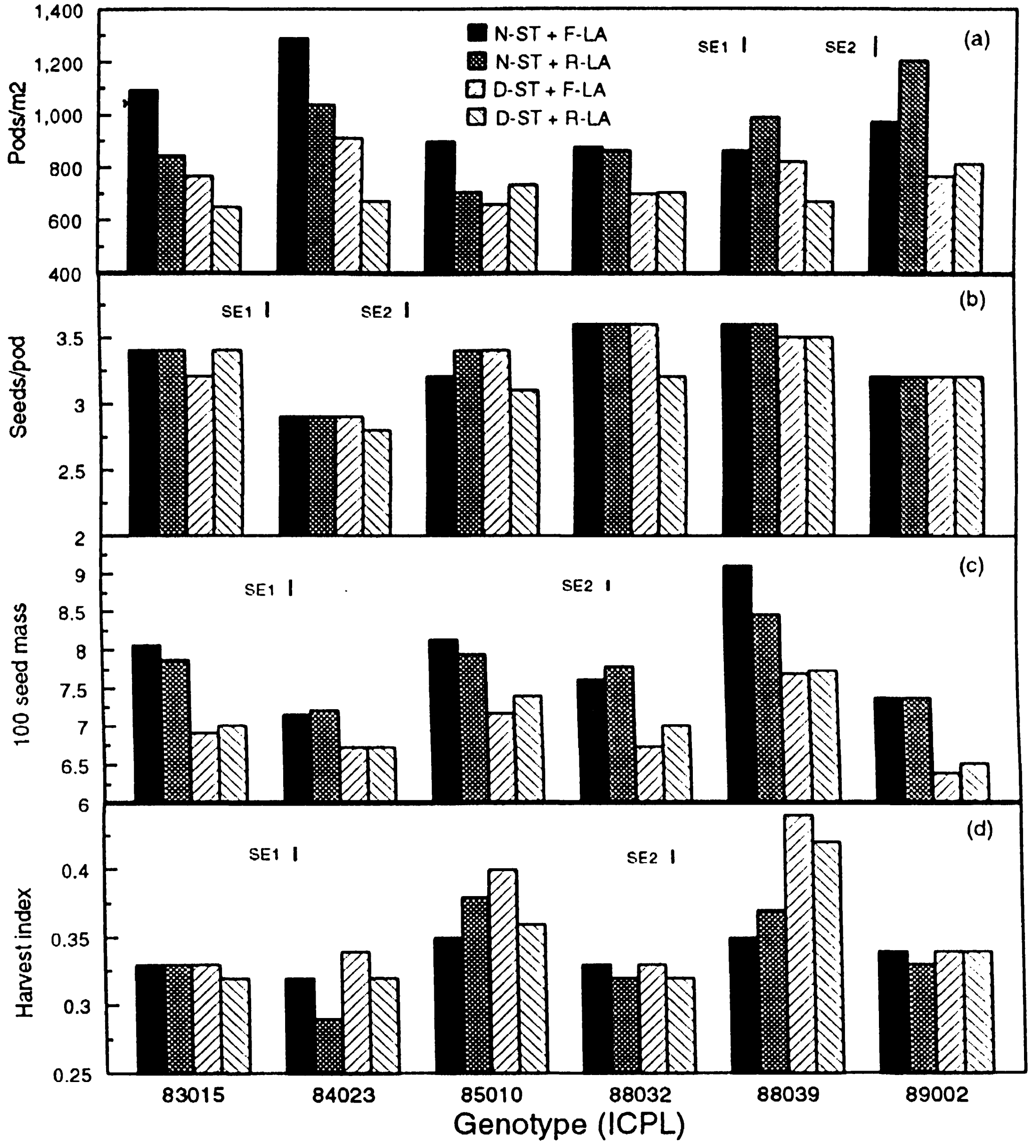


Figure 4.3.9: Yield components and harvest index of extra-short-duration pigeonpea genotypes under drought stress and leaf area removal treatments. (SE1 is used for comparing between stresses and SE2 for comparing between leaf area removal treatments)

Hundred seed mass of all genotypes showed a significant reduction due to drought stress and the differences were highly significant between stress treatments and among genotypes but not due to the LA removal treatments (Appendix 4.1). Genotype ICPL 89002 was the most affected by the drought stress treatment (Figure 4.3.9c).

The drought stress and LA removal treatments had a little effect on HI of ESD pigeonpea but differences among genotypes were significant (Appendix 4.1). The LA removal treatment slightly increased HI in genotypes ICPLs 85010 and 88039 in the non-stress treatment but decreased HI of almost genotypes in the drought stress. Genotype ICPL 88039 increased HI by 30-40% in the D-ST treatment compared with the N-ST treatment (Figure 4.3.9d). Genotypes ICPLs 85010 and 88039 had relatively higher HI than the others under both the D-ST and the R-LA treatments.

All the interaction effects for yield components and HI were not significant. Drought stress x genotype interaction for HI was, however, highly significant (Appendix 4.1).

4.4 DISCUSSION

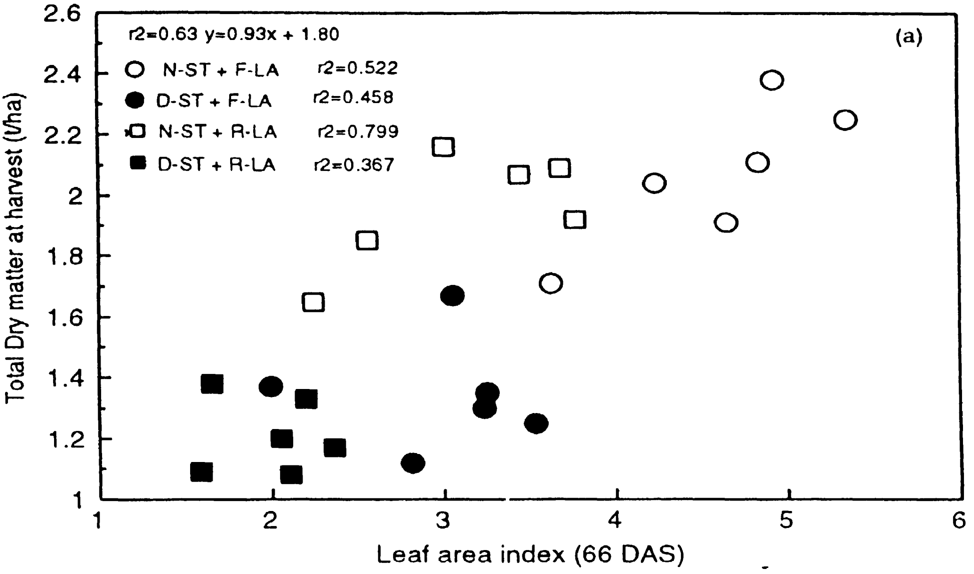
In Chapter III, the ability of ESD pigeonpea to give more than 2 t ha^{-1} yield under N-ST condition and its relatively high sensitivity to drought, especially during the flowering stage was highlighted. There were, nevertheless, significant differences among genotypes in response to drought at different crop growth stages. In order to further understand the bases of these differential responses, six ESD pigeonpea genotype were subjected to drought from the beginning of flowering to physiological maturity. To asses the implications of the leaf abscision that usually accompanies a drought stress situation, the drought stress treatments were combined with the partial defoliation treatments.

The responses in grain yield of different genotypes to drought stress were consistent with those reported in chapter III with ICPL 83015 showing high sensitivity and ICPL 88039 showing a high degree of drought resistance (Figure 4.3.2). This confirms that there are subtle differences in drought resistance among the ESD pigeonpea genotypes.

The deep rooting ability is a characteristic feature of traditional pigeonpea which helps it to extract water from deeper soil layers (Singh & Russell 1981). However, in the present study, ESD pigeonpea genotypes showed acute drought symptom even when there was considerable moisture present below 45 cm soil depth. The crops were unable to extract water beyond the 60 cm layer, which may be due to their shallow rooting ability. An access to water held in deeper soil layers can reduce sensitivity of crops to drought (Gregory 1988; Jordan et al. 1983). For example, drought resistant bean cultivars could extract water held up to 120 cm depth, whereas susceptible genotypes could not exploit beyond 80 cm in the soil profile (Sponchiado et al. 1989). A positive relationship between rooting depth and drought resistance has also been reported in groundnut (Wright et al 1991; Chapman et al. 1993) and in soybean (Cortes & Sinclair 1986). As root traits are seemingly important for drought resistance (Gregory 1988; Jordan et al. 1983), there is a need for further work in ESD pigeonpea on this aspect.

To optimize crop production in a given environment, in addition to a well developed-root system, it is important to match canopy size with duration of moisture availability and radiation. Whenever transpiratory demand of water exceeds the water availability, crops tend to adjust LA by shedding leaves and other plant parts. This process may not always be beneficial for yield as some sensitive genotypes may loose more leaves than necessary for achieving high yield. A positive association between LA retained at the pre-flowering stage and grain yield has been discussed in Chapter III. In the present study, artificial defoliation helped in conserving soil moisture only in the no-stress situation and was of no use under the stress condition. This was probably because a reduced LAI in the drought treatment could have increased exposure of soil to sunlight and thus increase soil evaporation. In the N-ST situation, reduced LA probably was still enough to cover the soil surface. However, leaf removal resulted in a decline in yield which varied in the range 5-10% in the no-stress situation and 15-20% in the stress situation. Tayo (1985), using a dwarf pigeonpea variety, observed up to a 55% yield loss with 33% defoliation and 60% with 66% defoliation. Lack of a similar response in the present study could be because of a higher LAI which may be well above the critical limits. Absence of a large decrease in yield with defoliation even under stress may suggest that genotypes which may be conservative in LAI development may not necessary prove to be more drought resistant. In chickpea, artificial defoliation to adjust the pattern of canopy development increased WUE, HI and yield under water limiting conditions during the reproductive period (Siddique & Sedgley 1985).

In general, TDM and yield of ESD pigeonpea was determined by the level of LAI and LAD during reproductive stage (Figure 4.4.1; 4.4.2). However, this relationship was changed under particular drought stress and LA modification treatments. There was a positive correlation between DM production with LAI (r^2=0.52) and LAD (r^2=0.54), and grain yield with LAI (r^2=0.70) and LAD (r^2=0.61) under N-ST without LA removal, but these relationships became less significant for grain yield under N-ST with LA removal. All these relationships became insignificant under drought both with or without LA removal. The differences in LAI and LAD



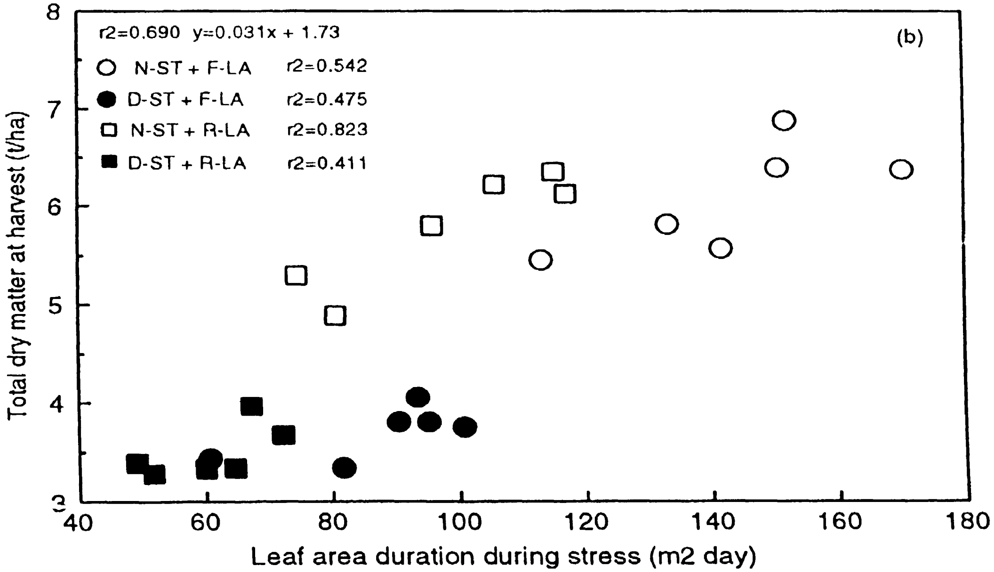


Figure 4.4.1: Relationship between total dry matter and leaf area index at the end of flowering stage (a) and leaf area duration during stress period (b) under different treatments.

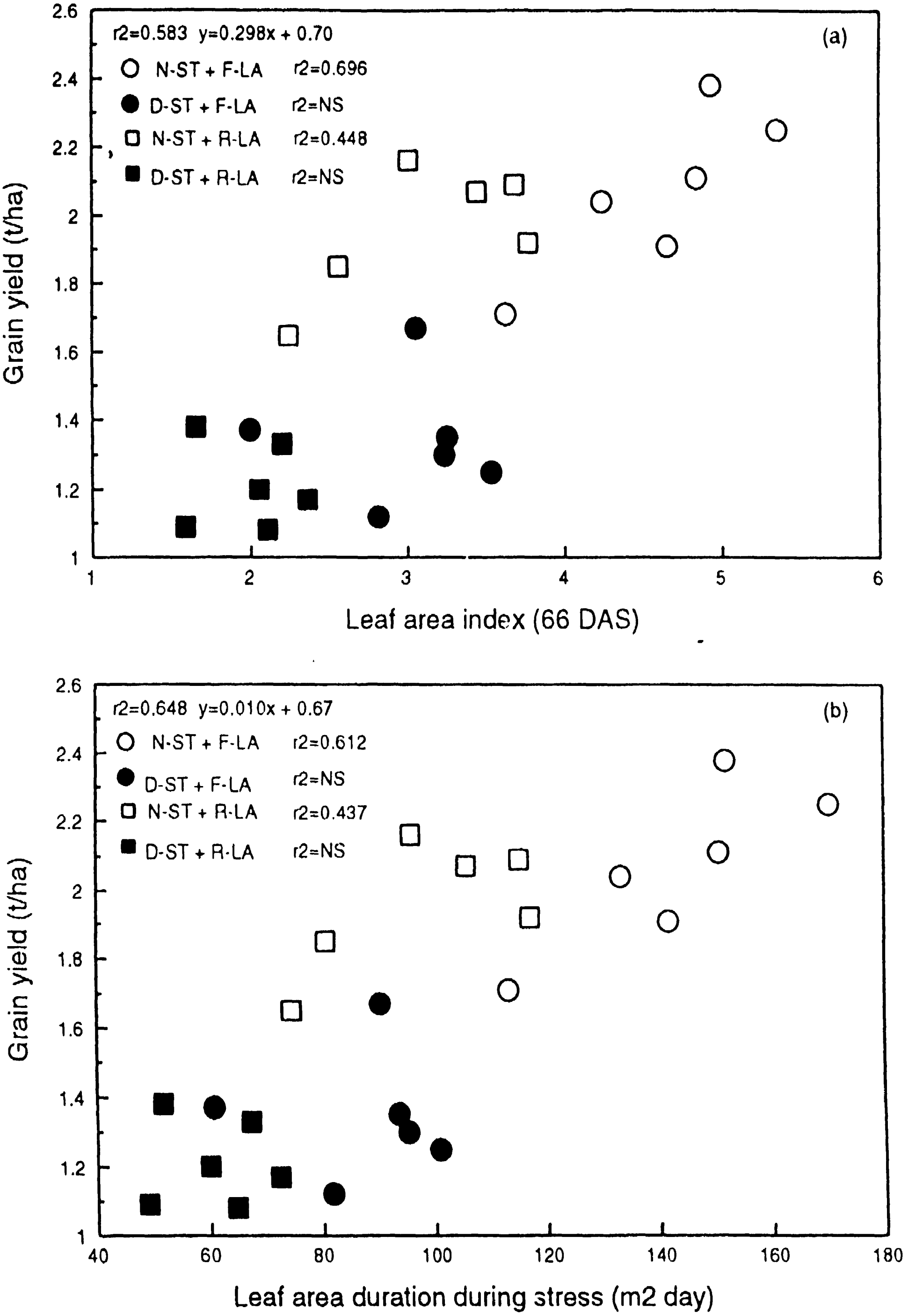


Figure 4.4.2: Relationship between grain yield and leaf area index at the end of flowering stage (a) and leaf area duration (b) under different treatments. N-ST (open symbol), D-ST (solid symbol), F-LA (circle symbol) and R-LA (square symbol).

could contribute more than 80% of the difference in DM and in grain yield of different ESD pigeonpea genotypes under no-stress but not under drought in this experiment. These changes indicated that the role of LAI and LAD which could contribute to DM production and final grain yield of ESD pigeonpea was different under stress and N-ST conditions.

Crop growth is a function of light interception and radiation use efficiency (Gifford 1984). The productivity of many crops has been closely linked with light interception (Monteith 1977). In the present study, drought significantly reduced both LAI and LAD, and hence light interception. By contrast, artificial defoliation had a relatively small effect on the pattern of light interception (Figure 4.3.3.2.1). The slope values of the relationship between cumulative DM production and cumulative radiation intercepted, which represent radiation use efficiency (RUE), differed among genotypes and between drought treatments. The RUE is a measure of photosynthetic performance of field grown crop and is dependent on canopy attributes such as light extinction coefficient, biochemical conversion efficiency and CO_2 exchange efficiency (Monteith 1977). It is considered to be a conservative trait (Squire 1990). In the present study, however, up to 30% variation in RUE was revealed in both stress and no-stress situations. The values of RUE observed here were comparable with those reported in pigeonpea by Hughes & Keating (1983) and for other grain legumes by Muchow et al. (1993). The highest RUE was obtained under N-ST condition without LA removal and it was significantly reduced by drought stress (Figure 4.4.3). Surprisingly, reduction in DM production under drought was better explained by a decline in RUE rather than LAI or LAD (Figure 4.4.4). This was not true for N-ST condition where both LAI and LAD explained a large amount of variation in DM (Figure 4.4.1). Low RUE was concerned with low LAI in stressed and reduced LA treatments but loss in DM production was mainly due to lower RUE than radiation intercepted (Figure 4.4.3). The relationship between RUE and CGR in ESD pigeonpea was also significant under both stress and no-stress conditions (Figure 4.4.4). This indicated that the differences in RUE could explain the differences in DM production of ESD pigeonpea under drought and may be an important factor

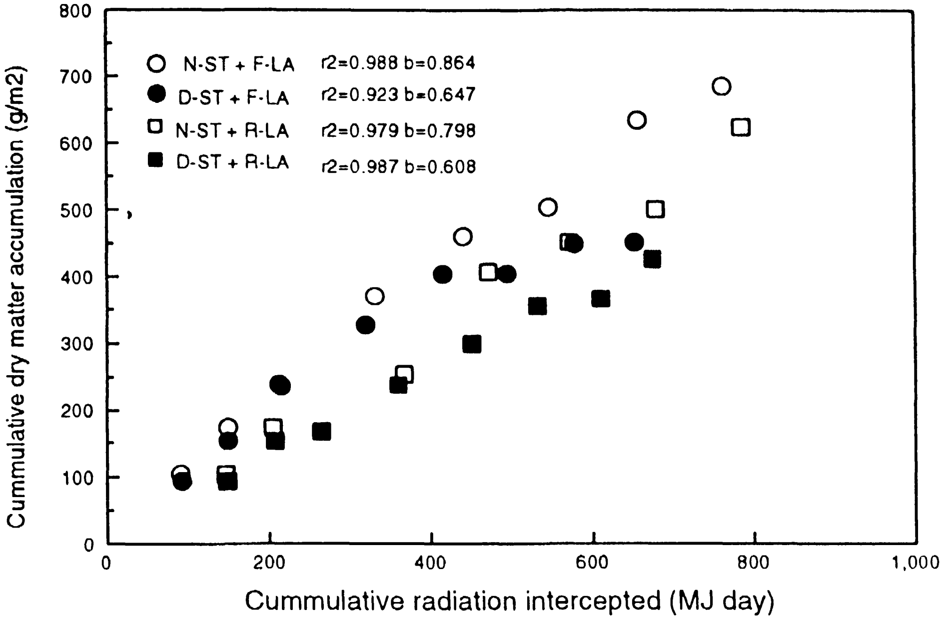


Figure 4.4.3: Relationship between cumulative light intercepted and cummulative dry matter accumulation of extra-short-duration pigeonpea under different treatments.
The slope values of the regression are presenting the radiation use efficiency.

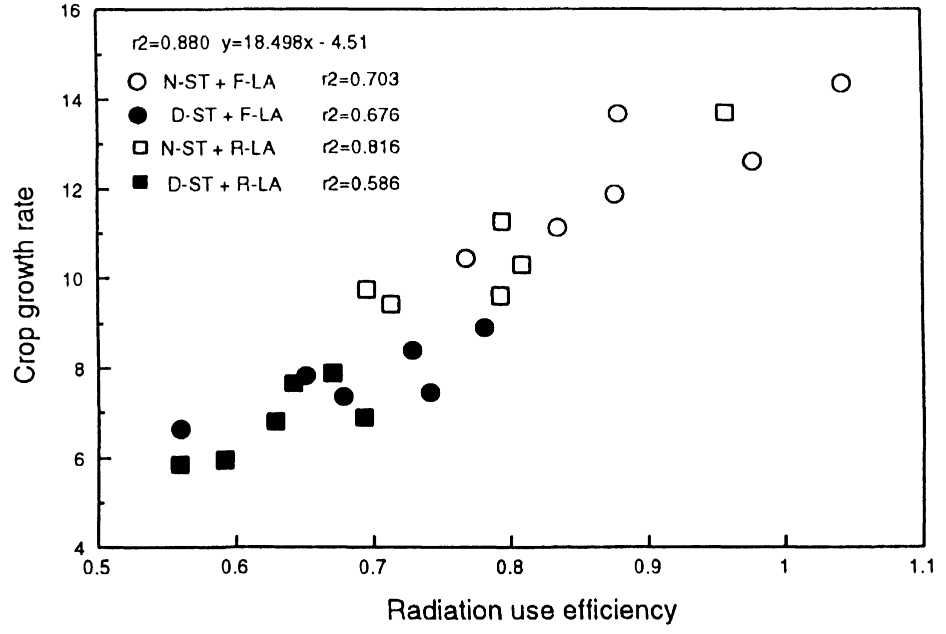


Figure 4.4.4: Relationship between radiation use efficiency and crop growth rate of extra-short-duration pigeonpea under different treatment.
N-ST (open symbol), D-ST (solid symbol), F-LA (circle symbol) and R-LA (square symbol).

in determining drought resistance in different genotypes. A decrease in RUE under stress and defoliation treatments in this study is possibly related to the fact that RUE is usually associated with mobilization of leaf nitrogen to the grain and also with losses of biomass due to leaf senescence (Muchow et al. 1993). This study, therefore, highlights the importance of RUE in the production of DM under drought situations, having greater effects than LAI or LAD.

The ESD pigeonpea had the highest TR and CD during the flowering stage (Figure 4.3.5) when maximum LAI was achieved and usually photosynthesis is also usually greatest at this stage due to maximum stomatal opening. The TR showed a positive correlation with LAI under N-ST but negative correlation under drought which indicates that conservation of water under drought was necessary for resistance to drought, although this relationship was not significant in both cases (Figure 4.4.5). When drought stress was imposed, CD reduced more than TR, especially during the early stress period, which indicated greater sensitivity of CD to drought than TR (Figure 4.3.5b). The main effect of reduced CD under stress is dehydration avoidance (Ludlow et al. 1983) because it reduces water loss and lowers the probability of dehydration. Nevertheless, reducing CD inevitably means lowered photosynthetic rate due to obstruction of the inflow of CO_2 into leaves and the loss of water vapor. There was a positive correlation between TR and CD which indicated the level of TR depended on the opening of stomata, but this relationship was highly significant under drought and non significant under well-watered condition (Figure 4.4.6). A major factor which could have contributed to a stronger relationship between RUE and DM production under drought was that TR and CD were distinctly correlated only in the drought treatment (Figure 4.4.6) . This was not so in the N-ST situation. This may have been mainly due to the boundary layer which is generally more effective in N-ST plots due to complete canopy closure, thus delinking transpiration from stomatal conductance. This suggests that plants in drought conditions were closely coupled with their external environment. All genotypes showed a significant decrease in their CD suggesting that this could be one of the mechanism to conserve moisture to avoid severe stress.

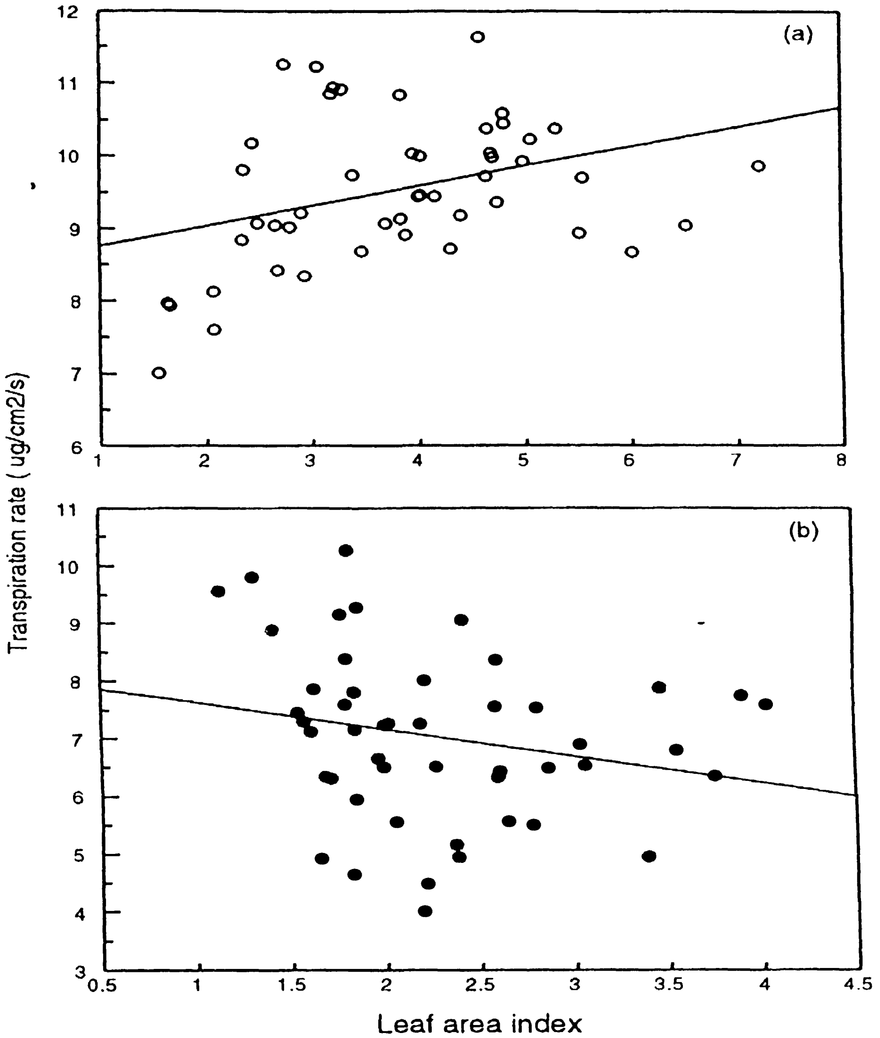


Figure 4.4.5: Relationship between leaf area index and transpiration rate of extra-short-duration pigeonpea under no-stress (a) and drought stress (b) conditions at the end of flowering stage (82 DAS).

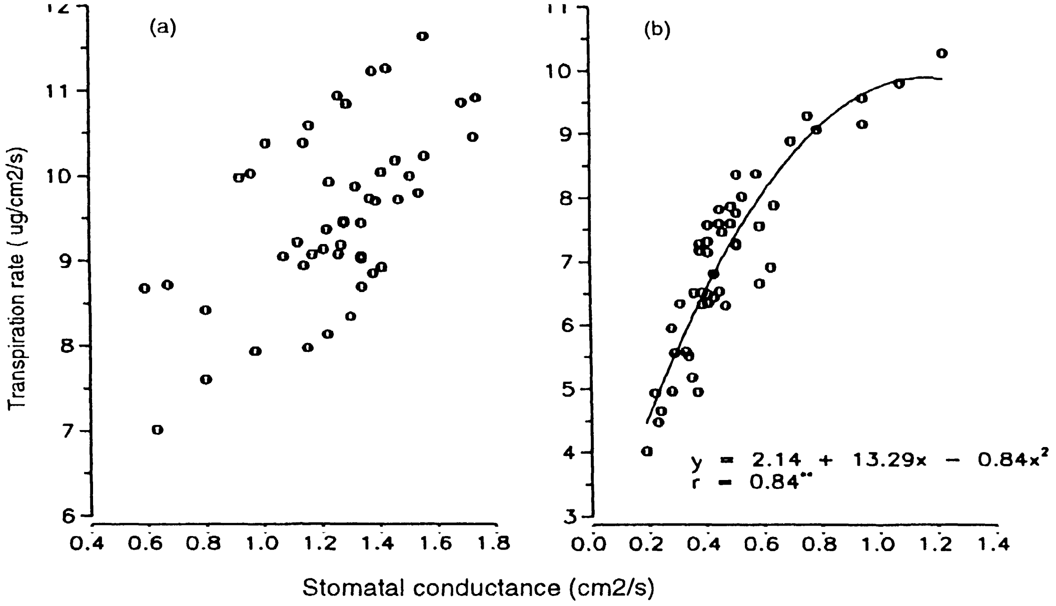


Figure 4.4.6: Relationship between stomatal conductance and transpiration rate of extra-short-duration pigeonpea at the end of stress at flowering stage (82 DAS). No-stress (a), drought stress (b).

From the foregoing, it is clear that the relative contribution of LA, LI and RUE to plant growth may vary with moisture availability. Various crop growth indices were evaluated to examine the integrated effect of these. Relative growth rate (RGR) decreased gradually with time from 40 DAS (Figure 4.4.7). The trend was similar in both irrigated and stress treatments. Similarly, the net assimilation rate (NAR) also showed the same trend as RGR except that there was an increase from 70-80 DAS, which coincided with the pod-filling stage. Drought significantly affected NAR at this growth stage which may have had some effect on yield determination. The most clear cut response to drought was seen in crop growth rate (CGR), which it was invariably less than the N-ST treatment (Figure 4.4.7). However, in both situations there were two distinct peaks in CGR. One was at 60 DAS coinciding with the flowering stage and another is at 80 DAS coinciding with the pod-filling stage. The increase in CGR at 60 DAS could be explained on the basis of increasing LAI around this time. The second peak could be due to a remobilization of carbohydrates from roots as there was substantial loss of LA at this stage. Drought stress affected CGR at both these stages but its affect was more drastic at the second stage when grain filling was in progress. A reduction in CGR under stress at the flowering stage could associate with a reduction in photosynthesis which appeared to be restricted by lower TR and CD. This may have a major effect in determining yield under drought as it would affect seed filling. This is supported by drought having a major effect on 100 seed mass (Figure 4.4.8c). This was also reflected in HI (Figure 4.4.8d). Decline in yield under drought stress was due to both 100 seed mass and number of pods m^2 (Figure 4.4.8b). Genotype ICPL 88039, which yielded significantly better than the other genotypes in both stress treatments had better HI and 100 seed mass suggesting that mobilization of assimilates from roots may have been better in this genotype.

Under drought stress, non-structural carbohydrate levels (starch and sugar levels) increased in stems at various stages during stress imposed as compared to the N-ST treatment

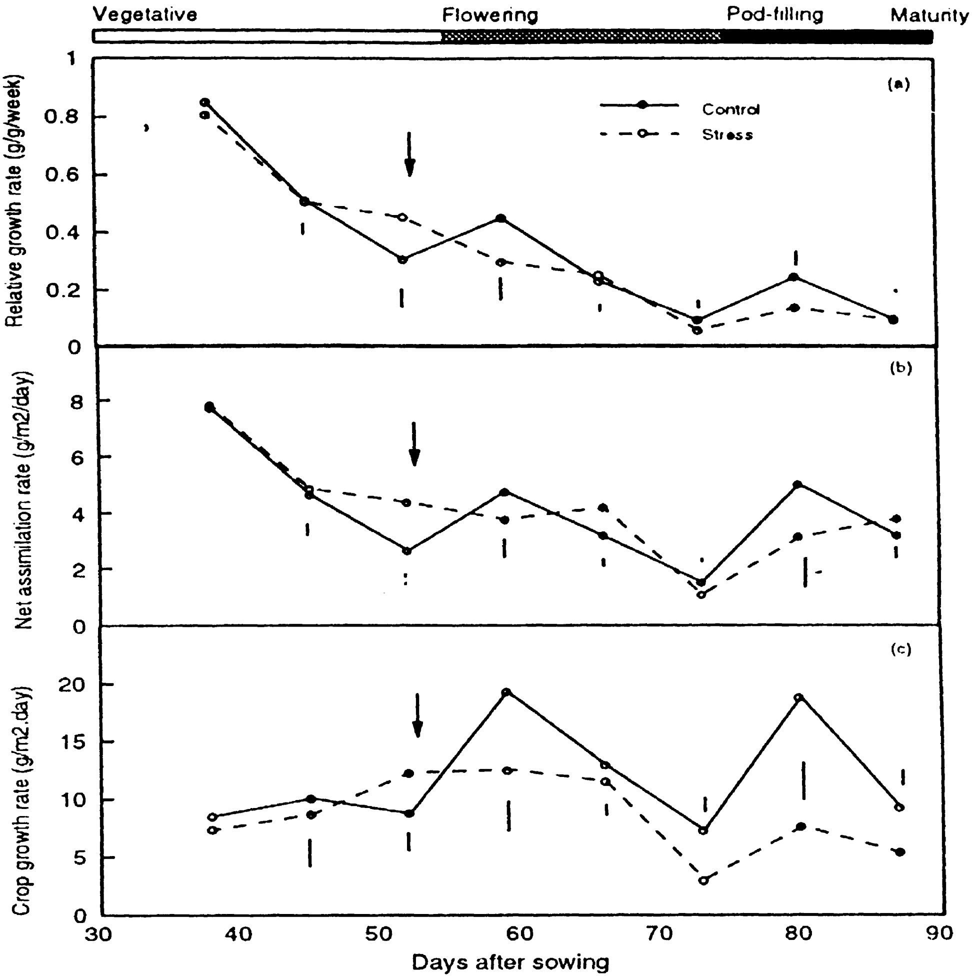


Figure 4.4.7: Effect of drought stress on mean relative growth rate (a), net assimilation rate (b) and crop growth rate (c) of extra-short-duration Pigeonpea, season 1993. (arrows indicate time of stress imposition). Vertical bar is SE( ) for comparing between stress treatments.

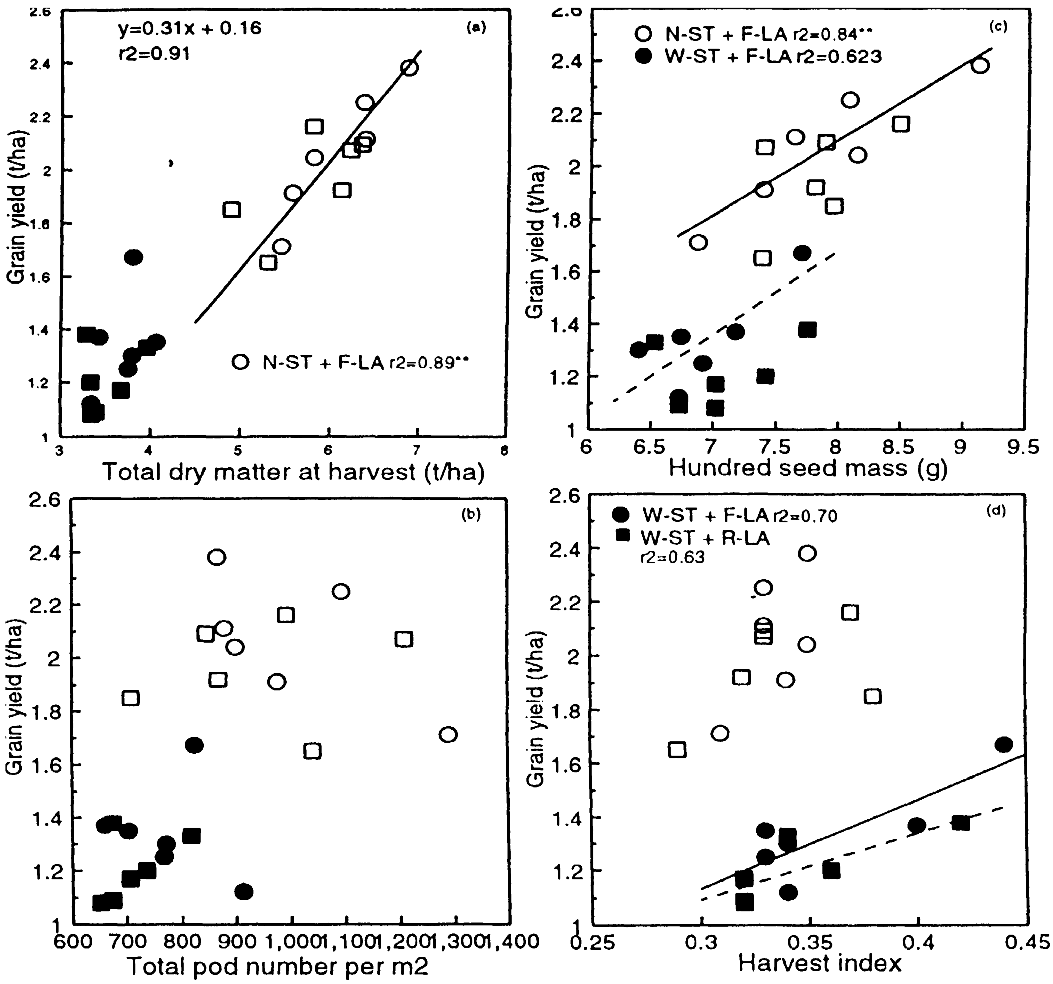


Figure 4.4.8: Relationship between grain yield with total dry matter at harvest (a), with total pods number per m2 (b), with 100 seed mass (c) and with harvest index (d) of ESD pigeonpea under N-ST (opend symbol) and D-ST (solid symbol), and under F-LA (circle symbol) and R-LA (square symbol).

(Figure 4.3.8.1). This trend was consistent in all genotypes although degree of accumulation varied among genotypes. In the present study, decline in 100 seed mass occurred inspite of higher levels of carbohydrates in stems. It appears that translocation of carbohydrates to the developing pods and seeds is inhibited under drought situations. This may be a major limitation to realizing the yield potential from the established sinks in the susceptible genotypes in droughted environments. Genotypes which are more efficient in remobilization and translocation of carbohydrates and nutrients to the developing pods are likely to be more productive under drought conditions. A poor correlation between DM and yield observed under drought conditions in this study is in contrast to the experiment discussed in Chapter III (Figure 4.4.8a), indicating that DM accumulation alone may not be a key factor for determining yield under drought. The present study indicates that selection for improved remobilization and translocation efficiency may be useful, especially under terminal drought situations.

As for the results reported in Chapter III, ESD pigeonpea responded to drought by reducing LWP, OP and leaf RWC but increasing osmotic adjustment and thus, TP to maintain extraction of water in the dry soil. Biomass production, grain yield and HI in crop plants were correlated with the ability to maintain a higher LWP and leaf TP under drought (Ackerson 1983; Bennett et al. 1986). In this study, a positive correlation between grain yield and LWP at the end of stress was observed (Figure 4.4.9a). Higher grain yield in the N-ST treatment was related to higher LWP and very low yield in the D-ST treatment was associated with decreasing LWP under drought, because reduced of LWP inhibits photosynthesis (Kirkhan 1990). The same relationship between grain yield and OP was also exhibited (Figure 4.4.9b). Plants growing in drought stress maintained lower LWP and OP than those with no-stress. However, within each genotype water status parameters such as LWP, OP, TP and leaf RWC were little affect by artificial manipulation of LA (Figure 4.3.7; Appendix 4.3). Moreover, genotypic differences observed within each stress treatment were not related to yield. This indicates a limited usefulness of these parameters in selecting for drought resistance among ESD pigeonpea genotypes. The results, however, confirm

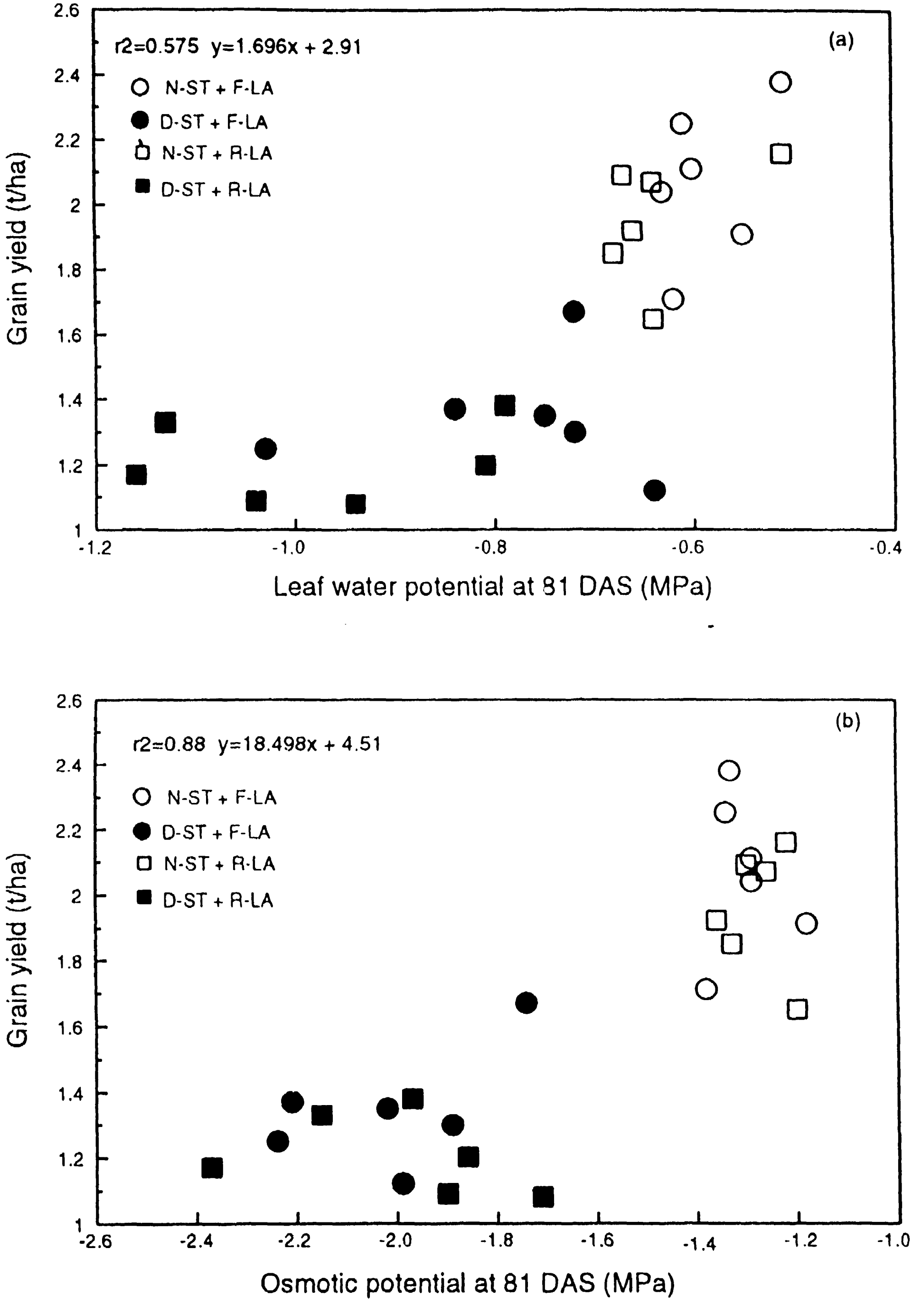


Figure 4.4.9: Relationship between grain yield with leaf water potential (a) and with osmotic potential (b) of extra-short-duration pigeonpea at 82 DAS under different treatments.
N-ST (open symbol), D-ST (solid symbol), F-LA (circle symbol) and R-LA (square symbol).

a high degree of osmotic adjustment as earlier reported in pigeonpea (Flower & Ludlow 1986). Again, due to a lack of significant relationship between yield and osmotic adjustment, its usefulness in selecting for drought resistance could not be adequately assessed in the present studies.

CHAPTER V

EFFECT OF EXCESS SOIL MOISTURE ON PLANT GROWTH AND GRAIN YIELD OF EXTRA-SHORT-DURATION PIGEONPEA

5.1 INTRODUCTION

Waterlogging has been recognized as a major constraint to stability of pigeonpea production during the rainy season in India (Reddy & Virmani 1981). Waterlogging is specially harmful for SD and ESD pigeonpea types because their durations are short and thus they have less time to recover after a waterlogging event. Many grain legumes are sensitive to waterlogging and excessive soil moisture can cause a severe depression or even complete failure of crops (Michin & Summerfield 1976; Wien *et al.* 1979; Sallam & Scott 1987; Turner *et al.* 1983). Excess soil moisture could inhibit various physiological processes which contribute crop productivity but the response of the crops depends upon genotypes, environmental conditions, stages of crop development and the duration of the waterlogging period (Jackson 1979; Orchard & Jessop 1984). The effects of waterlogging is more acute when plants experience waterlogging stress at the early stages of development (Michin *et al.* 1978). The greater the duration of waterlogging, the more damaging the effect (Orchard & Jessop 1984), though this may differ for different species or environments. With respect to the effect of waterlogging at different development stages of crop growth, many investigations have been limited to plants waterlogged only during the seedling stage of growth (Orchard & Jessop 1984). Although waterlogging is apparently an important stress, little work has been done on this in relation to SD and ESD pigeonpea.

Improvement programs for waterlogging resistance have received little attention probably because the underlying mechanisms for resistance have not yet been fully elucidated. For improving waterlogging resistance in pigeonpea, efforts to identify genotypes with improved tolerance to waterlogging are being made at ICRISAT Center and elsewhere (Chauhan 1987; Dubey & Asthana 1987). Screening for waterlogging tolerance in pigeonpea has been in progress since 1978 (Chauhan 1987) and has revealed genotypic differences in this regard (Johansen *et al.* 1990). Some promising results in screening for resistant genotypes in MD pigeonpea have been obtained (Legumes Program 1990; 1991). Nevertheless, improvement in the cultural practices is at least equally important for overcoming this constraint. Some of these, such as planting pigeonpea on ridges (Chowdhary & Bhatia 1971; Okada *et al.* 1991) or topdressing with nitrogen in order to allow waterlogged plants to recover quickly (Matsunaga *et al.* 1992), have been realized.

Although ESD pigeonpea has a good adaptive potential to rainfed semi-arid environments (Chauhan *et al.* 1993; Nam *et al.* 1993) it's growth and yield are considered to be depressed by the presence of excessive soil moisture during different stages of it's growth cycle. Furthermore, ESD pigeonpea showed dramatic responses to time of sowing which is not readily explicable in terms of changes in temperature, photoperiod and accompanying changes in solar radiation, as has been reported in MD genotypes (Troedson *et al.* 1990). It appeared that this effect of sowing date is mainly due to changes in soil moisture conditions caused by rains received before sowing (Chauhan *et al.* 1993). For example, rains prior to sowing could charge the soil profile to the extent that late-sown seedlings were exposed to anaerobic conditions from an early growth stage. Under this condition, it was suggested that soil aeration was the main factor limiting pigeonpea growth in fields where water was retained after rains (Okada *et al.* 1991). The detrimental effects of waterlogging to ESD pigeonpea, however, have not yet been adequately quantified.

The main objective of this study was to investigate and quantify the effects of waterlogging at different crop growth stages of several ESD pigeonpea genotypes. This included the effect of high soil moisture levels at the time of sowing and during the crop growth cycle of ESD pigeonpea. Such information would be useful in improving cultural practices for ESD pigeonpea, to understand the causes of variability in grain yield of ESD with sowing date and rainfall pattern and identification of plant traits that could alleviate waterlogging affects.

5.2. MATERIALS AND METHODS

5.2.1. Experiment design and layout

Two experiments were conducted at ICRISAT Center during the rainy season of 1993 as below:

Experiment 4: Effect of timing of application of waterlogging to extra-short-duration pigeonpea genotypes on Alfisol.

Experiment 4 was carried out in medium-deep Alfisol at the same site as Experiment 3 during the rainy season of 1993. A split-plot design with 4 replications was used. Two timings of waterlogging imposed at pre-flowering and flowering stages were compared with a no-waterlogged treatment, in main plots.

1) Pre-flowering stage waterlogging (PF-WL)
2) Flowering stage waterlogging (F-WL)
3) No-waterlogging (N-WL)

Each main plot was 3.0 m wide (10 crop rows spaced at 30 cm) and 20.0 m long. Two border rows between each main plot were used to separate different treatments and prevent water leakage between main plots.

The four ESD pigeonpea genotypes used for comparison in sub-plots were:

1) ICPL 84023 (DT)
2) ICPL 89021 (DT)
3) ICPL 88039 (IDT)
4) ICPL 89002 (IDT)

Sub-plot size was 3.0 x 5.0 m with 10 rows spaced at 30 cm. Sowing was done in furrows opened in both sides of 60 cm ridges and plant spacing was 30 x 10 cm between and within rows, respectively. Sowing was done on 14 June 1993.

Experiment 5: Effect of excess soil moisture during crop growth cycle in relation to sowing date on growth and yield of extra-short-duration pigeonpea, genotype ICPL 84023.

Experiment 5 was conducted in the rainy season of 1993 in a Vertisol (Typic Pellustert).

The available water holding capacity of the soil is approximately 200 mm.

A split-plot design with 3 replications was used. The soil chemical properties as described in Table 5.2.1.

Table 5.2.1: Soil chemical properties from 0-15 cm soil layer of experimental fields (Vertisol, field BP 13A).

pH	Electrical conductivity (dS m-1)	Organic[b] Carbon (%)	Available[b] Olsen P (mg kg^{-1} soil)	Available[b] N (mg kg^{-1} soil)	Total N[b] (mg kg^{-1} soil)
8.35	0.20	0.44	0.60	8.20	515

a: Analysis methods of soil chemical properties followed are as cited in Chapter III.

Three sowing dates were assigned to main plots as follows:

1) 15 June 1993 (1st sowing)
2) 13 July 1993 (2nd sowing)
3) 09 August 1993 (3rd sowing)

Two different soil moisture treatments comprising wet soil profile (excess moisture), which was charged by rain and irrigation water before sowing and during the crop growth cycle, and dry soil profile, which was created by using polyethylene sheets to cover the soil profile prior to sowing and after germination of the crop in order to prevent infiltration of rain or irrigation water in to the soil profile were compared in sub-plots. For simplicity, the treatments are referred to as wet and dry:

1) Wet (without covering of soil profile)
2) Dry (soil profile covered by polyethylene sheet before sowing and after crop germination in order to reduce the effect of waterlogging).

Sub-plot size was 4.8 x 5 m comprising 8 crop rows. Sowing was done in furrows opened in the top of 60 cm ridges. Plant spacing was 60 cm between rows and 5 cm within rows.

5.2.2. Agronomic practices

All agronomic practices were conducted as described in Chapters III and IV.

5.2.3. Soil moisture control and excess treatments

In Experiment 4, waterlogging treatments at different timings were created by continuously giving irrigation water through a drip irrigation system. Small bunds were formed at the end of furrows of each sub-plot to retain standing water in furrows during the waterlogging treatment period so that soil became saturated (Plate 5.2.3.1). Other treatments were kept under rainfed conditions.

In experiment 5, dry soil profile plots were covered by polyethylene sheets at the beginning of the growing season until sowing time. Bunds and drains around dry treatment plots were formed to keep out rain and irrigation water. Wet plot treatments were kept continuously charged by rain or irrigation water from before sowing time and during crop growth. For imposing different soil moisture treatments prior sowing time, irrigation water was applied 2-3 times by sprinkler to create excess moisture in the wet treatment. The polyethylene sheeting excluded rains or irrigations in the dry treatment and thus, the soil profile of this treatment remained in a dry condition. Polyethylene sheeting from the dry treatments was removed at the time of sowing. After sowing, all fields were lightly irrigated to ensure sufficient soil moisture for good crop establishment. The dry treatment was covered again by polyethylene sheets in furrows just after emergency to reduce the infiltration water into the soil profile. Small sand bags and metal stakes were used to firmly secure the polyethylene sheet on the ground (Plate 5.2.3.2). During the crop growth cycle, all of the experimental area was irrigated frequently if there was a large gap between rainfall events so that soil moisture in wet treatments would remain excessive while dry

Plate 5.2.3.2: Covering of soil profile by polyethylene sheeting to reduce infiltration of rain and irrigation water in the dry profile treatment, 1993 season.

treatment plots which were covered would have a distinctly lower soil moisture. Total water applied at each irrigation during the crop growth cycle at all sowing dates was recorded and rainfall data was recorded at the meteorology station located about 100 m away from the experiment site.

5.2.4. Observations and measurements

5.2.4.1. Soil moisture

In Experiment 4, soil moisture at 0-15 cm and 15-30 cm soil profile layers of all plots was measured gravimetrically at weekly intervals during the waterlogging treatment periods. In experiment 5, soil moisture during crop growth in dry and wet treatment was monitored at every 15 cm soil layer in the 0-90 cm soil profile by neutron probe at weekly intervals (as described in Chapters III and IV).

Soil moisture storage and runoff in Experiment 5 were calculated using the water balance model "WATBAL" of Keig and McAlpine (1974).

5.2.4.2. Soil aeration

Soil air was sampled at 25 cm depth using glass sampling tubes as described by Okada *et al.* (1991). The oxygen concentration of soil air was measured with an oxygen analyzer (Toray Enginering Co. Ltd., Model C700F, Japan), which uses a solid electrolyte as a detector.

5.2.4.3. Plant growth

Five plants were sampled for growth analysis at vegetative and flowering stages. Plant height, leaf area, TDM and growth analysis parameters were calculated by the same method described in Chapter IV.

5.2.4.4. **Chlorophyll content**

Leaf samples were cut into pieces and approximately 1 g of fresh tissue sample placed in a mortar and thoroughly crushed with 10 ml acetone 80% to allow the tissue to be thoroughly homogenized. Homogenized tissue was then transferred to a centrifuge tube. Ten ml of 80% acetone was then added to the mortar and the procedure repeated to ensure transfer of all of the sample into the tube. The sample was twice centrifuged and the supernatant decanted into a 50 ml volumetric flask and made up to volume with 80% acetone. Five ml of this solution was transferred to a 25 ml volumetric flask and made up volume with 80% acetone. The absorbance was measured at 652 nm and the result calculated as follows:

$$C = \frac{D \times 1000}{34.5} \times \frac{25}{1000} \times \frac{50}{5} \times \frac{1}{W_t}$$

where,

C = chlorophyll concentration (mg g^{-1})

34.5 = the specific absorption coefficient

D = observed absorbance

W_t = fresh weight of sample

5.2.4.5. **Nodulation and acetylene reduction assay**

Five plants were randomly selected in both N-WL and waterlogging treatments at 51 DAS when the PF-WL treatment was relieved. Plants were carefully uprooted and all the roots and nodules placed into 800 ml glass bottle. The bottles were covered with a lid and sealed with 'steel-grip' tape to make it air tight. Eighty ml of air was evacuated from the bottle and then 80 ml acetylene was injected into the bottle to given an acetylene concentration in the bottle of 10%. After approximately 30 min incubation, a 5 ml gas sample was collected in evacuated tubes and stored for subsequent gas-chromatography analysis (Perkin-Elmer, Gas Chromatograph, F33) of acetylene and ethylene. Calculation of acetylene reduction assay (ARA) was as follows:

$$\mu M\ C_2H_2\ h^{-1} = \left(\frac{S.C_2H_4}{S\ C_2H_2} \times Bl.C_2H_2 - Bl.C_2H_4\right) \times \frac{VCF \times BV \times 0.06 \times Vpm}{22.4 \times Std.C_2H_4 \times T}$$

Where, $\mu M\ C_2H_2\ h^{-1}$ = Micro moles of ethylene produced per hour

$S.C_2H_4$ = Sample ethylene chart unit x attenuation

$S\ C_2H_2$ = Sample acetylene chart unit x attenuation

$Bl.C_2H_2$ = Blank acetylene chart unit x attenuation

$Bl.C_2H_4$ = Blank ethylene chart unit x attenuation

VCF = Vacutainer correction factor (total volume of Vacutainer/amount of gas sample injected)

BV = Bottle volume

Vpm = Volume of standard ethylene (per million)

$Std.C_2H_4$ = Standard ethylene (chart unit x attenuation)

T = Time of incubation (min)

22.4 = Gas constant

After the ARAs were completed, nodules were counted and roots and nodules oven-dried to constant weight. Other parameters such as root dry weight plant^{-1}, number of nodules plant^{-1} and nodule dry weight plant^{-1} were calculated. Data were separately analysed for each genotype.

5.2.4.6. Grain yield and yield components

Total DM at harvest and grain yield were determined by harvesting all plants in the net plots as has been described in other experiments in previous chapters. Ten plant sub-samples were randomly collected for calculation of yield components.

5.2.5 Statistical analysis

Statistical procedures were done as the same as described in Chapter III.

5.3 RESULTS

5.3.1 Effect of timing of waterlogging

5.3.1.1 Soil moisture and soil oxygen concentration

Soil moisture under N-WL changed depending on the pattern of rainfall during the growing season as it was kept under rainfed conditions (Figure 5.3.1.1a). The highest soil moisture was approximately 12% during peak of rainfall in the later part of July (37-44 DAS). Soil moisture significantly increased up to 14-18% when waterlogging was imposed at 30 DAS for PF-WL and 54 DAS for F-WL and soil moisture at 0-15 cm depth was always higher than at 15-30 cm depth. At these moisture levels, the soil was thus in saturated condition during the period of imposed waterlogging.

Soil oxygen concentration in N-WL was around 20% but decreased to less than 18% (Figure 5.3.1.1b) when soil moisture increased due to peak of rainfall (44 DAS). Oxygen in soil air was significantly reduced just after waterlogging was imposed. In the main rooting zone of ESD pigeonpea to 20 cm depth, oxygen concentration dropped sharply to less than 12% (66% of the N-WL) during PF-WL but was relatively higher at 16% (80% of the N-WL) during waterlogging at flowering stage.

5.3.1.2 Crop growth

Crop growth characters of 4 genotypes in waterlogged condition at different treatments are presented in Figure 5.3.1.2. Waterlogging caused reduction of plant height but the differences were not significant between waterlogged and N-WL plants at the end of pre-flowering stage (Appendix 5.1). At the end of the flowering stage, the differences in plant height of PF-WL plants and the N-WL became highly significantly although waterlogging had been relieved but differences between waterlogging treatment during the flowering stage and N-WL was not

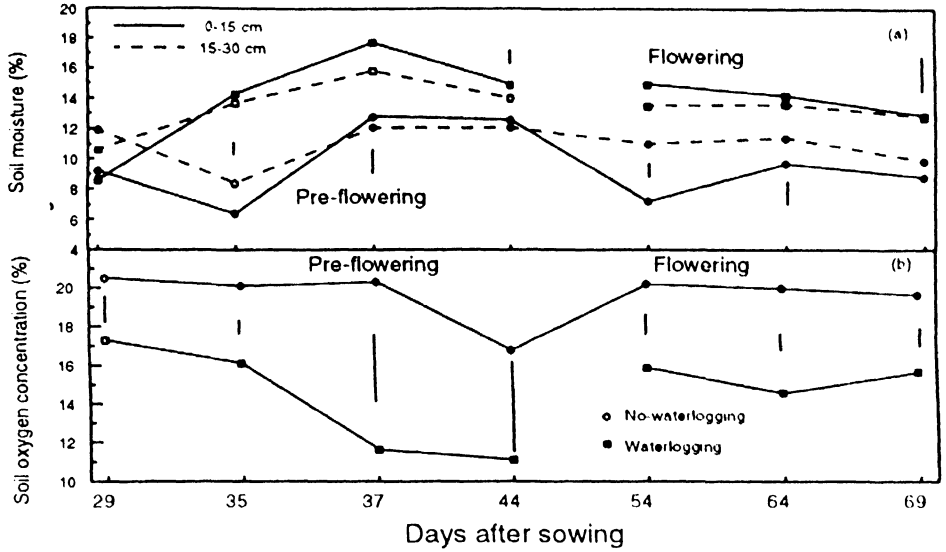


Figure 5.3.1.1: Soil moisture pattern (a) and soil oxygen concentration (b) during waterlogging treatment at pre-flowering stage (open square) and flowering stage (solid square) in comparison with no-waterlogging (open circle) of extra-short-duration pigeonpea in Alfisol, rainy season 1993.
Vertical bar is SE(±) for comparing between waterlogging treatments.

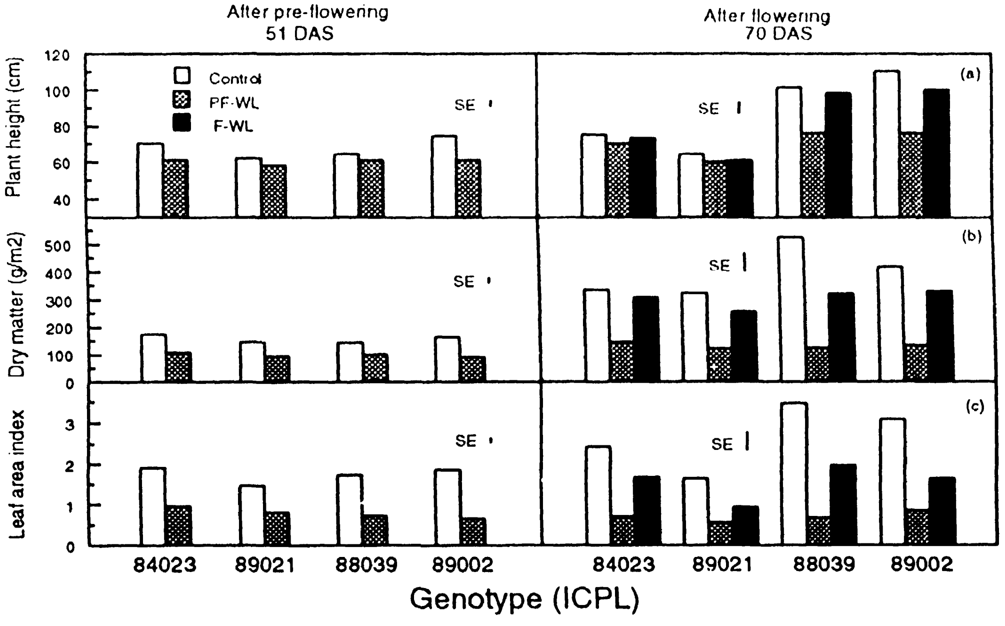


Figure 5.3.1.2: Plant height (a), dry matter accumulation (b) and LAI (c) of four extra-short-duration pigeonpea genotypes after waterlogging at pre-flowering stage (46 DAS) and after waterlogging at flowering stage (69 DAS), season 1993.
Vertical bar is SE(±) for comparing between waterlogging treatments.

significant (Figure 5.3.1.2a).

Waterlogging significantly reduced shoot dry weight of all genotypes at both timings of waterlogging (Figure 5.3.1.2b). Biomass production reduced to 30-45% and 10-40% compared with N-WL when genotypes experienced waterlogging at pre-flowering and flowering stages, respectively. The percentage of shoot dry mass reduction compared with N-WL was higher in ICPL 89002 and lower in ICPL 88039 in the PF-WL treatment and was higher in ICPL 88039 and lower in ICPL 84023 in the F-WL treatment. The recoverability was negligible in all ESD pigeonpea genotypes as DM accumulation showed little increase after PF-WL was released (Figure 5.3.1.2b).

Waterlogging had relatively more detrimental affect on canopy development for all genotypes under flooded treatments. The PF-WL reduced LAI by 45-65% and F-WL by 30-45% compared with N-WL. Compared with other genotypes, ICPL 89002 showed the highest sensitive to reduced LAI under both timings of waterlogging.

The timings of waterlogging and genotype interaction was not significant at the end of pre-flowering but was highly significant for all crop growth observations after the F-WL (Appendix 5.1).

5.3.1.3 **Chlorophyll content**

Under waterlogging at both timings, chlorophyll content of all genotypes was significantly reduced compared to control. The effect was more conspicuous in the F-WL treatment (Table 5.3.1.3). The highest reduction in chlorophyll was 45- 60% which was observed in ICPL 89002 under PF-WL and F-WL. The two DT genotypes ICPL 84023 and ICPL 89021 were relatively less affected than the two IDT genotypes. The interaction between timing of waterlogging and genotype was not significant with PF-WL but significant with F-WL.

Table 5.3.1.3: Effect of different timings of waterlogging on chlorophyll content (mg/g) of extra-short-duration pigeonpea genotypes at the end of the waterlogging treatment, rainy season 1993.

		Waterlogged after pre-flowering		Waterlogged after flowering	
Genotype		N-WL	WL	N-WL	WL
ICPL 84023		2.73	1.70	2.82	2.42
ICPL 89021		2.68	1.67	2.79	1.86
ICPL 88039		2.55	1.58	3.63	2.01
ICPL 89002		2.53	1.35	3.38	1.34
SE (±)	WL	0.053^{**}		0.219^{*}	
	G	0.056^{*}		0.122^{NS}	
	WL x G	0.086^{NS}		0.287^{*}	
		(0.079)		(0.215)	

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : Not significant.

SE values in parenthesis are used for comparing means at the same level of waterlogging.

5.3.1.4 Nodulation

The effect of PF-WL was not significant on the nodulations observed after waterlogging had been relieved, although at this stage number of nodules plant^{-1} was higher in the waterlogging treatments in both genotypes and nitrogenase activity was lower under waterlogging in both genotypes (Table 5.3.1.4). The root dry weight was similar in both treatments.

5.3.1.5 Total dry matter at maturity and grain yield

Total DM at maturity was reduced by waterlogging treatment, especially in IDT genotypes (Figure 5.3.1.5). Waterlogging reduced TDM by 15-45% and 5-40% compared with the N-WL when it was imposed at pre-flowering and flowering stages, respectively although the difference was not significant (Appendix 5.2) because of a high variation of plant stand in some plots due to phytophthora disease. The differences between genotypes and the interaction between timing of waterlogging and genotypes were significant ($P<0.01$ and 0.05, respectively). Under N-WL condition, the two IDT genotypes, ICPL 88039 and ICPL 89002 produced higher TDM at harvest than the two DT genotypes, ICPL 84023 and ICPL 89021. At maturity, genotype ICPL 84023 showed smallest reduction under both waterlogging treatments while both IDT genotypes suffered most, especially under PF-WL.

Both PF-WL and F-WL treatments reduced grain yield of ESD pigeonpea by 37-40% as compared with N-WL and the differences were significant (Figure 5.3.1.5). Yield losses varied considerably due to genotypes and waterlogging x genotype interaction ($p<0.01$). Genotype ICPL 88039 and ICPL 89021 were more sensitive than the others to waterlogging during the vegetative stage (yield loss up to 40%) while ICPL 89002 and ICPL 84023 showed more sensitivity during the flowering stage (yield loss up to 50% and 35%, respectively).

Table 5.3.1.4: Nodulation of two extra-short-duration pigeonpea genotypes after waterlogging at the pre-flowering stage was released, rainy season 1993.

	Genotype ICPL 84023				Genotype ICPL 88039			
Observations	N-WL	WL	SE	CV(%)	N-WL	WL	SE	CV(%)
No of nodule plant^{-1}	15	27	11.7^{NS}	86	15	25	6.5^{NS}	64
Nodule Dwt. (mg plant^{-1})	53	60	25.8^{NS}	82	56	58	13.5^{NS}	57
Root Dwt. (g plant^{-1})	0.79	0.78	0.093^{NS}	10	0.80	0.74	0.088^{NS}	8
Nitrogenase activity (μmole C_2H_4 g^{-1}h^{-1})	163	106	33.0^{NS}	43	172	97	55.0^{NS}	55

^{NS}: Non significant difference

5.3.1.6 **Yield components and harvest index**

Number of pods m^{-2} was significantly reduced by about 5-20% or 20-45% under PF-WL or F-WL, respectively compared with the N-WL treatment (Figure 5.3.1.6a). Reduction of pod number was higher under the F-WL treatment and the most susceptible genotypes were ICPLs 84023, 89021 and 89002. Genotype ICPL 88039 was relatively less affected than the others, especially under PF-WL.

Seed number pod^{-1} and 100 seed mass were relatively less affected by waterlogging, except for genotypes ICPL 89002 and ICPL 89021 which showed greater reduction in number of seed pod^{-1} and 100 seed mass for the F-WL treatment (Figures 5.3.1.6b; c). Differences were significant among the genotypes with ICPL 88039 having more seed number pod^{-1} and higher 100 seed mass compared to other genotypes under both timings of waterlogging and N-WL.

Harvest index showed considerable variation between waterlogging and N-WL although differences were not significant (Figure 5.3.1.6d and Appendix 5.2). Waterlogging reduced HI from 5-20% and 10-40%, depending on genotype at PF-WL and F-WL treatments, respectively. Genotype ICPL 84023 was most sensitive in terms of reduced HI under waterlogging, especially when imposed at the flowering stage.

5.3.2 Effect of excess soil moisture in relation to sowing date

5.3.2.1 **Total water supplied and soil moisture pattern during crop growth**

Excessive soil moisture status was created by increasing water supplied to the crop through supplemental irrigation whenever there was a gap of rainfall during the crop growth cycle at all sowing dates. The total amount of water supplied to different sowings was thus, 808.3 mm, 993.0 mm and 901.1 mm, to which the rainfall water contributed 60%, 54% and 43% in 1st, 2nd and 3rd sowing, respectively (Figure 5.3.2.1.1a). During the initial four weeks of crop growth

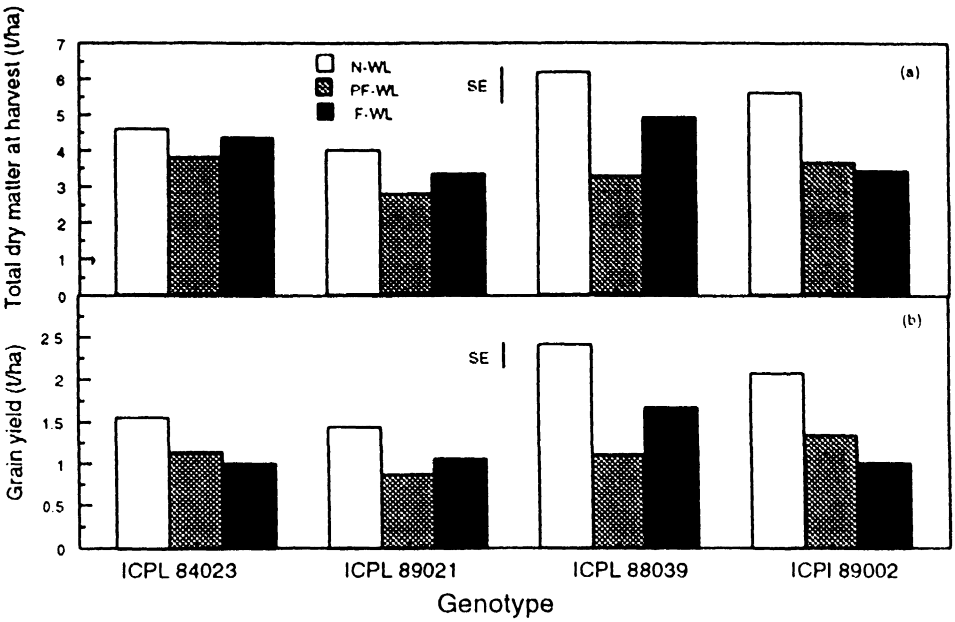


Figure 5.3.1.5: Total dry matter at harvest and grain yield of four extra-short-duration pigeonpea genotypes subjected to waterlogging at different crop growth stages, rainy season 1993.
Vertical bar is SE(±) for comparing between waterlogging treatments.

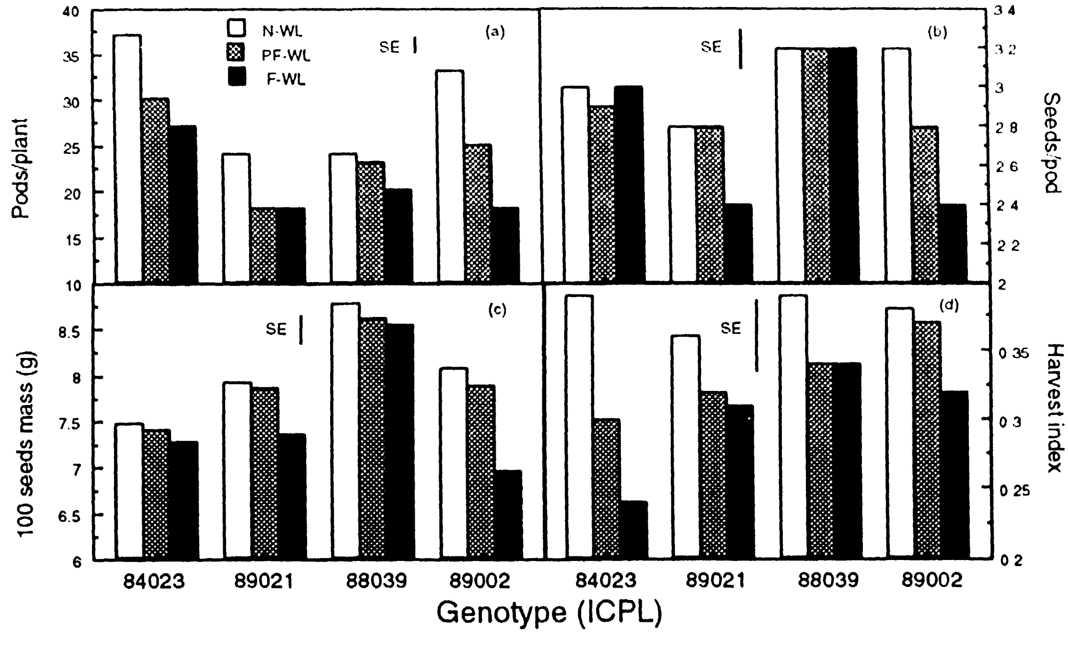


Figure 5.3.1.6: Yield components of four extra-short-duration pigeonpea genotypes subjected to waterlogging at different crop growth stages, rainy season 1993.
Vertical bar is SE(±) for comparing between waterlogging treatments.

when ESD pigeonpea is usually sensitive to excess soil moisture, total water received by the crop was 210.7 mm, 254.4 mm and 301.6 mm, to which rainfall water contributed 58%, 77% and 44% in 1st, 2nd and 3rd sowing, respectively (Figure 5.3.2.1.1b). Total rainfall water received in the 2nd sowing was highest during the crop growth cycle as well as during the initial four weeks (Figure 5.3.2.1.1). The 3rd sowing received the lowest amount of rainfall due to less rainfall at the end of season but received the highest amount of total irrigation water supplied.

As the 1st sowing received less water than 2nd and 3rd sowing, soil water content in 0-90 cm soil profile under wet treatment ranged from 36 to 39 mm, which was significantly less than for the two later sowings (Figure 5.3.2.1.2a). The soil water content of the 2nd and 3rd sowings ranged from 38 to 41 mm. In general, soil moisture was relatively higher during the crop growth cycle of the 2nd sowing and during early crop growth of the 3rd sowing (Figures 5.3.2.1.2b; c).

the soil profile covered by polyethylene sheeting effectively reduced soil moisture content by preventing the seepage of rain and irrigation water into the soil profile. The differences were maximum during the crop growth cycle of the 1st sowing and lowest during that of the 2nd sowing (Figure 5.3.2.1.2). All the wet profile treatments had more soil moisture than dry profile at all three sowing dates (Figure 5.3.2.1.2).

5.3.2.2 Crop growth

Plant height, DM accumulation and LAI at 31 and 51 DAS were significantly different between sowing dates and between soil moisture treatments (Figure 5.3.2.2.1). However, differences in crop growth at 31 DAS were smaller among the three sowing dates because DM accumulation and LAI did not show significant differences but plant height in the 3rd sowing was relatively more than in the two early sowings (Figure 5.3.2.2.1a). In contrast, crop growth at 51 DAS showed large differences between the three sowing dates. In the 1st sowing, plant height, DM accumulation as well as LAI attained the highest values. With late sowings (2nd and 3rd

(vertical bar is 2 SE for comparing between stress treatments)

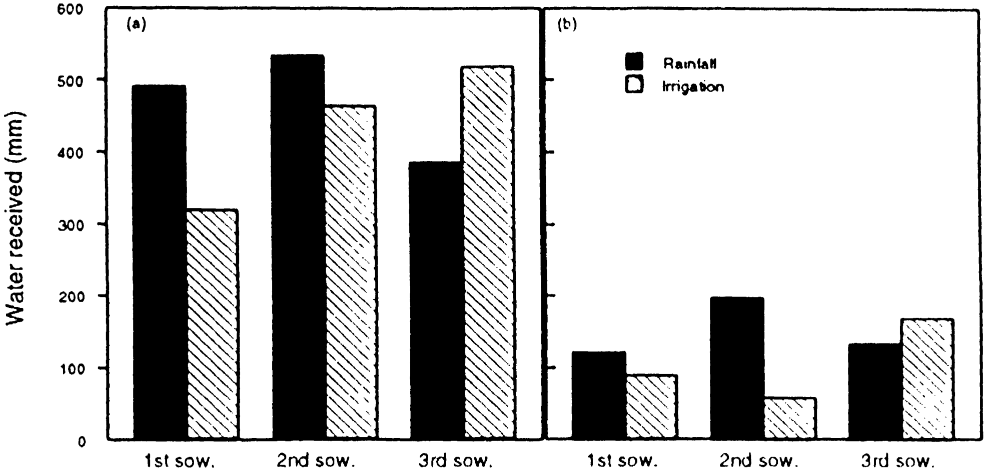


Figure 5.3.2.1.1: Total water received by rainfall and irrigation (mm) during crop growth cycle (a), and during initial four weeks of crop growth (b) at different sowing dates of extra-short-duration pigeonpea, ICPL 84023, rainy season 1993.

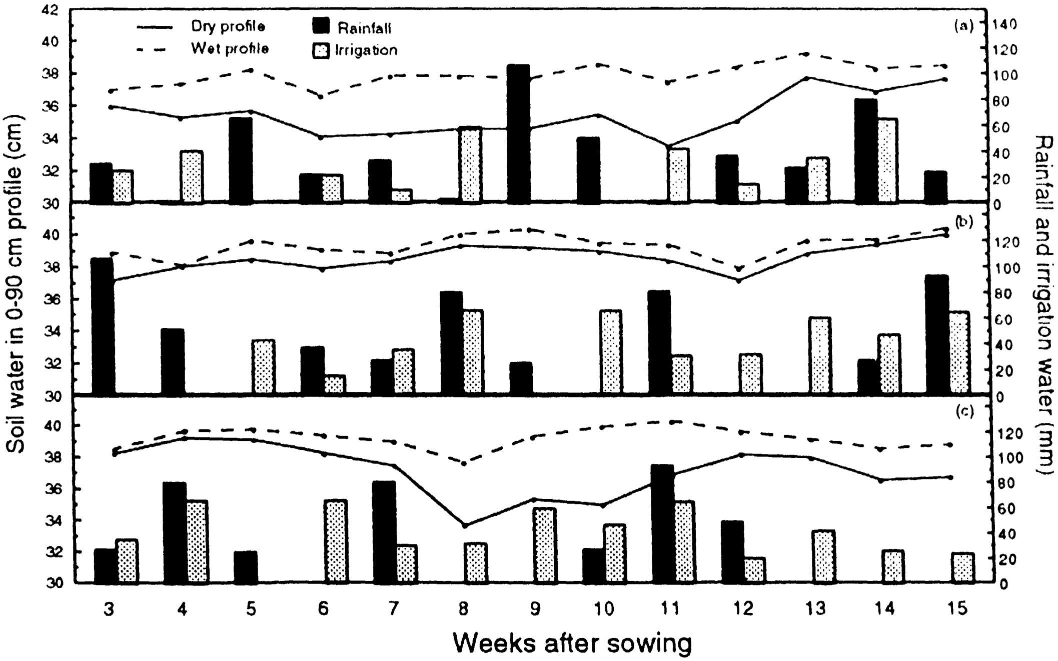


Figure 5.3.2.1.2: Distribution of rainfall and irrigation water and soil moisture pattern in wet (solid line) and dry (dashed line) treatments during crop growth cycle at different sowings: First sowing (a), second sowing (b), and third sowing (c).

sowings) plant height was reduced by about 25-30%, DM accumulation by about 50% and LAI by about 60% compared with the 1st sowing (Figure 5.3.2.2.1b).

The wet treatment restricted crop growth at all sowing dates. Plant height was not significantly reduced in the wet treatment at the 1st sowing but was significantly reduced by 20% in the 2nd and 3rd sowing compared with the dry treatments. Dry matter accumulation and LAI development were seemingly the most sensitive components affected by excess soil moisture in the wet profile. Under the wet condition, DM accumulation at 31 DAS was lowered by 10% in the first, 35% in the second and 45% in the third sowings compared with dry treatment whereas, LAI at 31 DAS was lowered by 20% in the first, 40% in the second and 45% in the third sowing compared with the dry treatment. The differences between dry and wet treatment became more significant at flowering time (51 DAS) in which DM was reduced by 15%, 45% and 65% and LAI was reduced by 20%, 25% and 60% compared with the dry treatment in 1st, 2nd and 3rd sowing, respectively.

Growth analysis data showed that CGR during vegetative stage (31 to 51 DAS) was very sensitive to late sowings as well as soil moisture levels (Figure 5.3.2.2.2a). The CGR was significantly greater in the early sowing and was significantly reduced under excess soil moisture of the wet treatments. The reductions of CGR under wet treatments were from 20%, 35% and 70% lower compared with dry treatments in 1st, 2nd and 3rd sowing, respectively. Net assimilation rate during this period was also reduced due to delayed sowing but the differences between soil moisture treatments were only significant in the 3rd sowing, in which the reduction of NAR was up to 30% compared with the dry treatment.

5.3.2.3 Total dry matter at maturity and grain yield

Total DM at maturity was significantly different ($P<0.01$) between sowing dates and soil moisture treatments (Appendix 5.3) showing a negative effect of delayed sowing and excess soil moisture

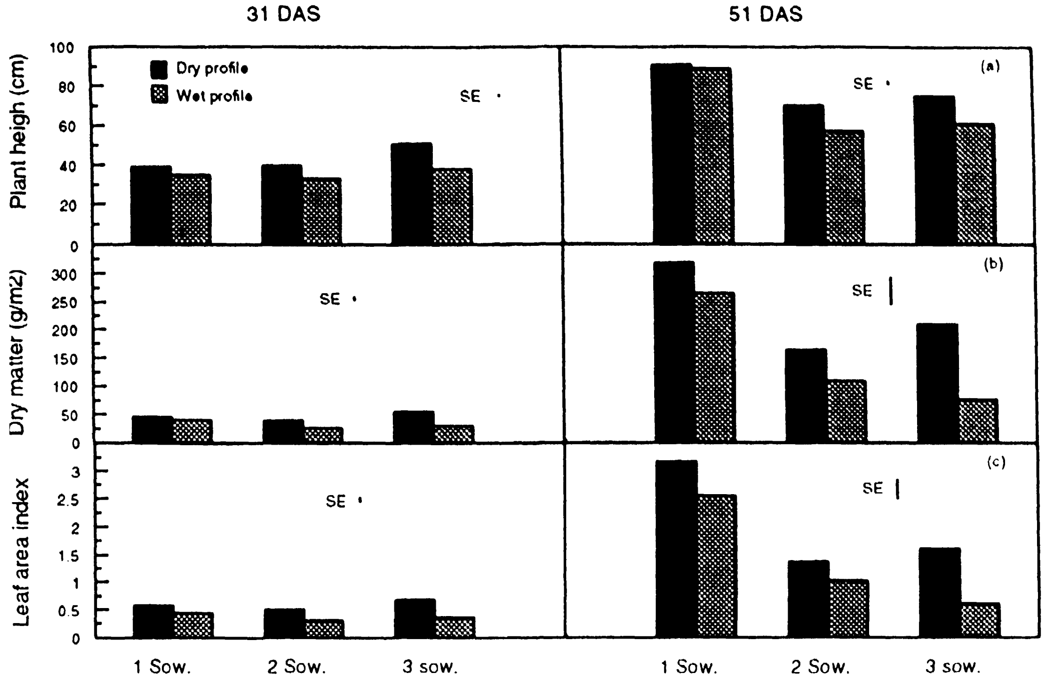


Figure 5.3.2.2.1: Plant heigh (a), dry matter accumulation (b) and leaf area index (c) of extra-short-duration pigeonpea (genotype ICPL 84023) at three sowing dates, rainy season 1993.

Vertical bar is SE(±) for comparing between waterlogging treatments.

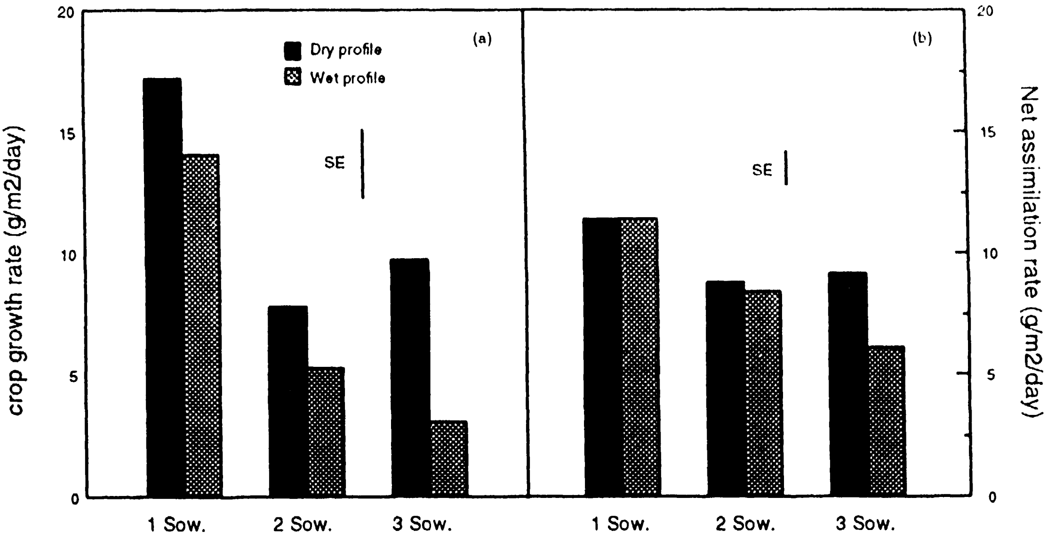


Figure 5.3.2.2.2: Crop growth rate and net assimilation rate during vegetative growth stage (31-51 DAS) of extra-short-duration pigeonpea (ICPL 84023) under wet and dry treatments at three sowing dates, rainy season 1993.

Vertical bar is SE(±) for comparing between waterlogging treatments.

condition (Figure 5.3.2.3.1a). Late sowings (2nd and 3rd sowings) reduced TDM at maturity by 16% and 30% compared with the 1st sowing. Excess soil moisture in wet treatments reduced TDM at maturity of ESD pigeonpea by 15% in the first, 25% in the second and 40% in the third sowings compared with the dry treatment in each sowing date.

The response of grain yield was the same trend with TDM at harvest. The highest grain yield was obtained in the earliest sowing. Yield observed in the 2nd sowing was 75% and in the 3rd sowing was 60% of the 1st sowing (Figure 5.3.2.3b). The reduction of grain yield under excess soil moisture was approximately 20% in 1st and 2nd sowings but was about 40% at the last sowing compared with dry treatment at each sowing date. There was no interaction between sowing dates and soil moisture treatments for both TDM at harvest and grain yield (Appendix 5.3).

5.3.2.4 **Yield components and harvest index**

The number of pod m^{-2} was reduced by late sowing, especially under excess soil moisture conditions (Figure 5.3.2.4a). The reduction of pod number caused by excess soil moisture was 40% in the 1st, 20% in the 2nd and 40% in the 3rd sowing compared with dry treatment at each sowing date.

Seed number pod^{-1} was relatively unchanged with sowing date but it was reduced under excess soil moisture conditions, especially in the latest sowing in which the extent of reduction increased up to about 20% compared with the control (Figure 5.3.2.4b).

Hundred seed mass showed a greater declined in the later sowing, especially in the 2nd sowing (Figure 5.3.2.4c). Excess soil moisture caused a reduction in hundred seed mass in the 1st and 2nd sowings but increased it in the last sowing and thus, the overall main effect was not significant. The interactions between sowing date and soil moisture treatments were not significant for any of the yield components in this experiment.

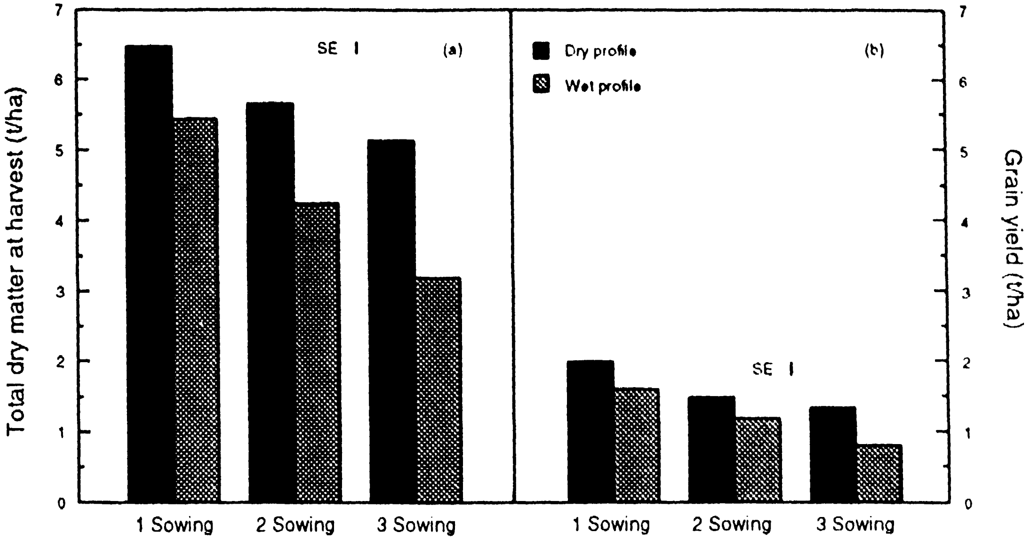


Figure 5.3.2.3: Total dry matter at harvest (a) and grain yield (b) of extra-short-duration pigeonpea (genotype ICPL 84023) under wet and dry treatments at three sowing dates, rainy season 1993.
Vertical bar is SE(±) for comparing between waterlogging treatments.

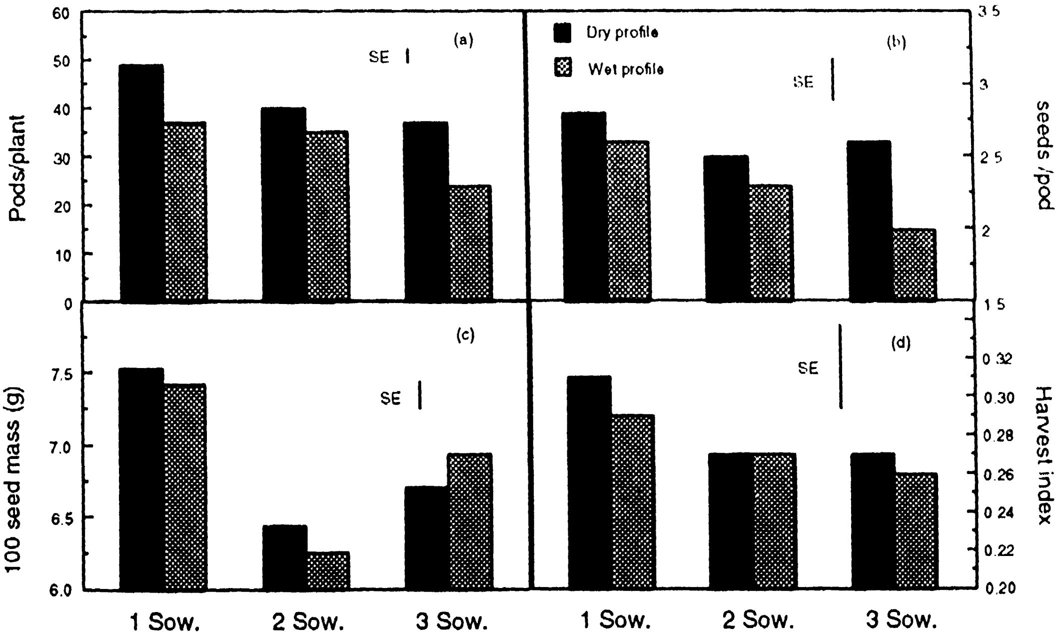


Figure 5.3.2.4: Yield components of extra-short-duration pigeonpea (ICPL 84023) under wet and dry treatments at three sowing dates, rainy season 1993.
Vertical bar is SE(±) for comparing between waterlogging treatments.

Differences in HI of ESD pigeonpea between waterlogging treatments, among genotypes and waterlogging x genotype interaction were not significant.

5.4 DISCUSSION

It is well recognized that waterlogging of soil causes considerable reduction of growth and yield of various crops with the legumes generally being more susceptible than the cereals (Krizeck 1982). In this study, excessive moisture treatments was created for ESD pigeonpea by flooding soil at two crop growth stages (Experiment 4) and by increasing supplemental irrigation (Experiment 5) whenever there was a gap of rainfall during crop growth cycle (figure 5.3.2.1.1a). Total water supplied during crop growth (rainfall plus irrigation) was approximately level of 800-1000 mm which was excessive for ESD pigeonpea. Thus, in both cases the crops experienced waterlogging by excessive soil moisture application.

During waterlogging, soil air space was displaced by water which caused significant decline in the oxygen concentration in soil (Figure 5.3.1.1b). This anaerobic condition was more serious during PF-WL as this period coincided with heavy rains during the last weeks of July (Figure 5.3.1.1). As a result of soil moisture storage building up quickly up to maximum level after the soil profile had been charged by rainfall and irrigation (Figure 5.4.1), poor soil aeration caused by lower oxygen concentration in saturated soil was also observed, which generally happens after heavy rains in both Alfisol and Vertisol (Okada *et al.* 1991). Soil oxygen concentrations of flooded soil for both growth stages in this study were higher than those observed by Okada *et al.* (1991) and Arihara *et al.* (1991a) in Vertisol. The reason was probably because the pigeonpea crop in this experiment was planted on both sides of the ridges with standing water only being in furrows. On the other hand, the saturation water conductivity of an Alfisol is usually higher than that of a Vertisol (Lal 1986) which causes higher aeration levels of Alfisol than Vertisol under excessive soil moisture conditions. The reduction of oxygen concentration in waterlogged soil recorded in this study indicated a major change in the soil environment caused by waterlogging.

Typical effect of waterlogging on plant growth include reduced plant height, DM yield and leaf area with visible symptoms of chlorosis and senescence (Krizek 1982; Scott *et al.* 1989). It was observed that growth of ESD pigeonpea was significantly reduced by waterlogging imposed at both crop growth stages (Appendix 5.1; Figure 5.3.1.2) and by excessive soil moisture under wet treatment regardless of dates of sowings (Figure 5.3.2.2.1). The reduction of LAI and consequently DM accumulation of all genotypes was higher under waterlogging during the pre-flowering stage than during the flowering stage and was higher in wet treatments in late sowings than at early sowing. During waterlogging periods, the lower leaves in main stem of waterlogged plants senesced and abscised whereas those on the N-WL plants remained green and persisted (Plate 5.4.1). All leaves of plants in wet treatments became obviously pale green in color and, individually, had smaller size than those in the dry treatments.

The physiological processes which caused lower growth rate of all ESD pigeonpea genotypes after waterlogging was imposed, especially during the vegetative stage and at later sowings could not been fully explained in this study due to limitation of observations. However, one possibility is that photosynthesis had been reduced because of leaf chlorosis and senescence which may have disrupted assimilate supply to the roots and nodules, and inhibited nodule activity in comparison with the N-WL or dry treatments. The development of chlorotic leaf symptoms caused by reduced of chlorophyll content in leaves of waterlogged plants was also characteristic of nitrogen deficiency which was always accompanied by slower DM accumulation. Chlorophyll content data showed the reduction was more pronounced by PF-WL compared with F-WL. Chlorophyll concentration was lower in the relatively waterlogging sensitive genotypes such as ICPL 88039 at PF-WL or ICPLs 89021 and 89002 at F-WL compared with the other relative waterlogging resistant genotypes. This finding is similar to those of Talbot *et al.* (1987) in some *Salix* species and Ashraf & Mehmood (1990) in *Brassica* species.

The adverse effects of waterlogging on plant growth may result directly from restricted root growth caused by anaerobic conditions in soil and indirectly from the interaction of plant and soil microorganisms (Michin & Summerfield 1976; Glinski & Stepniewski 1985; Nawata & Shigenaga 1988). Observations from experiment 4, however, showed non-significant differences in nodulation of ESD pigeonpea under the waterlogging and N-WL treatment. The reason for no significant difference may be because sampling was done at 51 DAS when the PF-WL has been relieved, by which time symbiotic nitrogen fixation of N-WL plants was not at its peak but that of waterlogged plants could recover under favorable conditions of dry soil. Hong et al (1977) observed rapid recovery of nitrogenase activity in cowpea nodules just after drainage of waterlogging. The high coefficient of variation (CV %) of these variables observed also contributed to the non-significant differences. Nevertheless, the symptoms of chlorosis and the stunted growth development of all genotypes during waterlogging at both stages indicated evidence of restriction of nitrogen fixation and nitrogen accumulation of waterlogged ESD pigeonpea genotypes. Root dry was not significantly different between waterlogged and N-WL treatments because waterlogged plants produced new adventitious roots near the soil surface although more roots at lower depth were damaged under excess moisture conditions. In addition, profusion of aerenchyma tissue which developed in the roots of waterlogged plants have been observed in ESD pigeonpea (Plate 5.4.2). Aerenchyma tissue has an important role in waterlogged plants because it can increase root porosity under waterlogging conditions (Kawase & Whitmoyer 1980).

Grain yield losses of ESD pigeonpea were equally large under both timings of waterlogging but differed in different genotypes. Genotype ICPL 89002 had highest yield under PF-WL among the four genotypes while ICPL 88039 yielded better than others under F-WL treatment. In this study, the grain yield of ESD pigeonpea also declined dramatically at late sowings, and also reduction could be explained by the effect of excessive of soil moisture caused by soil moisture storage which was raised to saturated levels by rainfall and irrigation (Figure 5.4.1). Higher grain yield in early sowing was related with better crop growth due to lower excess

Plate 5.4.1: Yellowing and leaf senescence caused by waterlogging at the pre-flowering stage in extra-short-duration pigeonpea, 1993 season.

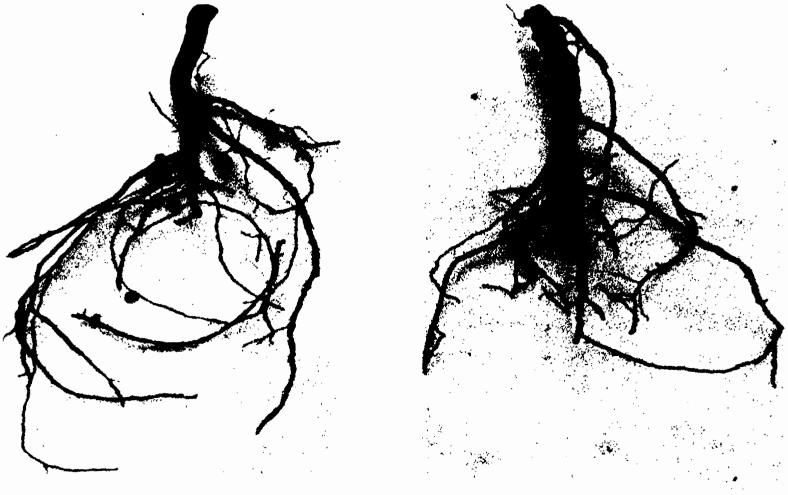


Plate 5.4.2: Waterlogging affected root (right) and normal root (left) of extra-short-duration pigeonpea, 1993 season.

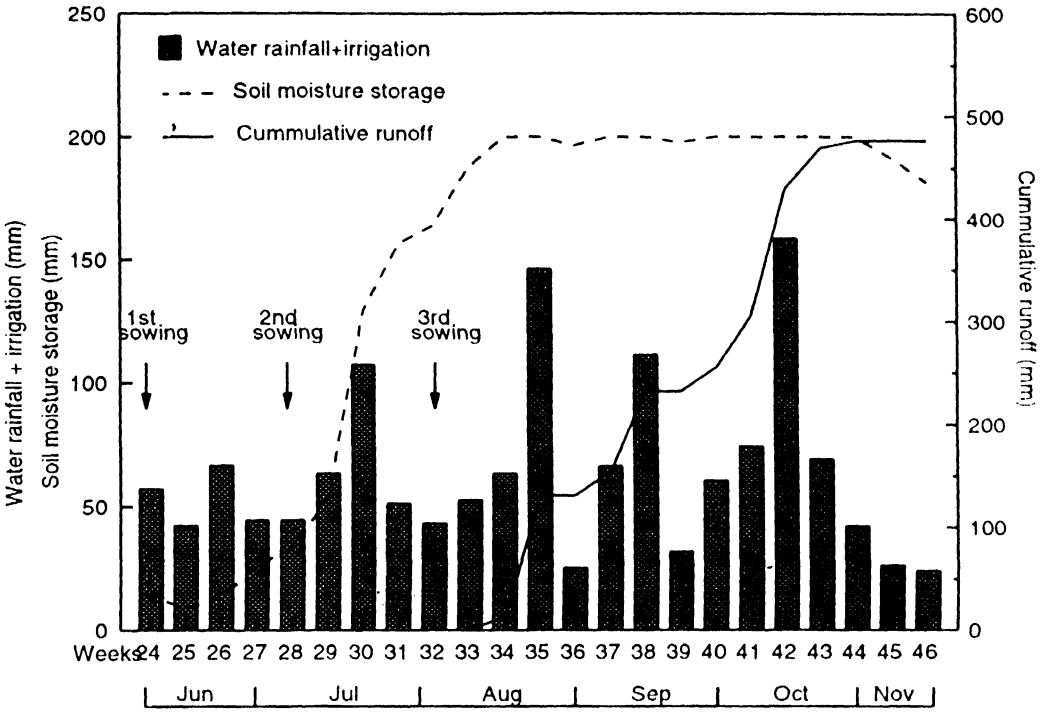


Figure 5.4.1: Distribution of total water supplied by rain and irrigation (bar), simulated soil moisture storage (dash line) and cummulative runoff (solid line) in Vertisol during crop growth season of ESD pigeonpea, season 1993.

water level at early crop growth than late sowings (2nd and 3rd sowings). The dry profile treatments gave significantly higher grain yield than wet treatments at all sowing dates and these differences tended to be higher at late sowings, which indicated the detrimental effect of excessive soil moisture condition.

In both experiments, there was very strong positive correlation between TDM at harvest with final grain yield (Figure 5.4.2). This indicated that yield losses caused by excessive soil moisture in ESD pigeonpea were primarily caused by a reduction in their TDM. More than 90% variation in grain yield of ESD pigeonpea was explained by variation of DM production under waterlogged as well as excess soil moisture.

Generally, waterlogging during the vegetative stage affected final DM production more than at the flowering stage due to less recovery ability after waterlogging was relieved, except for genotype ICPL 89002 which was equally sensitive to waterlogging at both the stages. The most detrimental effect of waterlogging during the pre-flowering stage on ESD pigeonpea was seen to restrict plant growth by reducing DM accumulation not only during waterlogging period but also after it had been relieved (Figure 3.5.1.2). The highest reduction of TDM and yield of 45% of the N-WL was observed in the relatively susceptible genotype ICPL 88039 while that of the relatively resistance genotype ICPL 84023 was reduced by only 15% of the N-WL treatment. The recovery ability of growth after waterlogging damage, which is considered very important in many crops (Nawata *et al.* 1989; DelRosario & fajardo 1991), was very slow in all ESD pigeonpea genotypes tested. The reason for the lack of recovery of ESD pigeonpea genotypes in this experiment may due to the long-term effect of waterlogging (20 days) which affected root function and nitrogen fixation in subsequent stages. Moreover, loss of plant density caused by phytophthora disease during and after a waterlogging event also caused reduction in TDM. Waterlogging during the flowering stage mostly affected TDM by increasing abscision of leaves induced by chlorosis and senescence, loss of plant stand by disease and ultimately reduced DM

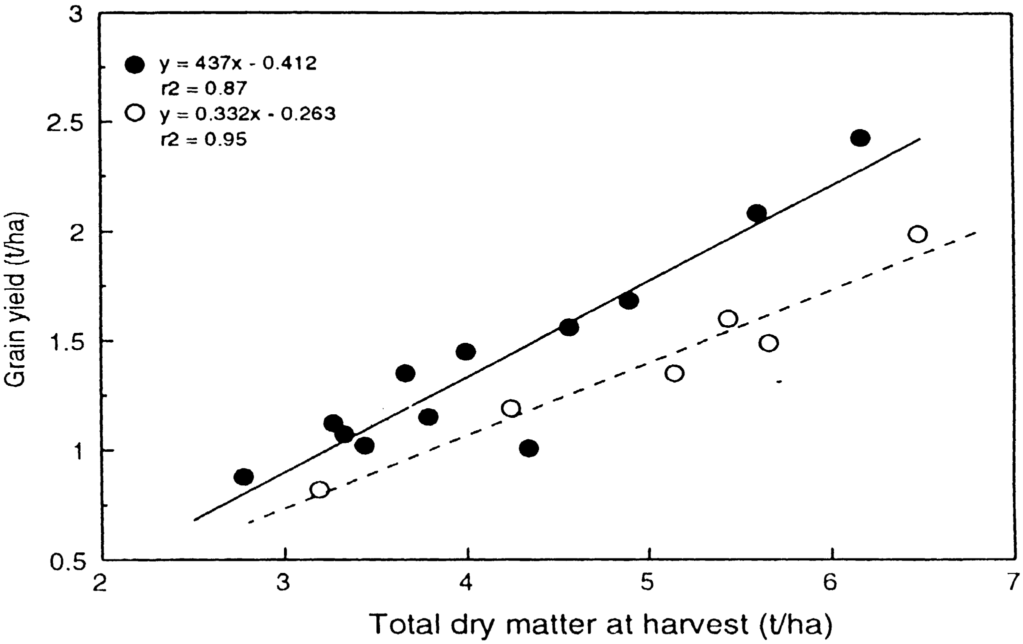


Figure 5.4.2: Relationship between grain yield and total dry matter at harvest of four extra-short-duration pigeonpea genotypes under different timings of waterlogging and no-waterlogging (solid line), and between dry and wet soil profile treatments at three sowing dates (dashed line), season 1993.

partitioning into yield components. Greater reduction of TDM due to late sowings and under wet treatments again showed clear evidence of the sensitivity of ESD pigeonpea to excessive soil moisture.

Among yield components, number of pods m^{-2} was the most sensitive yield component under waterlogging conditions because it had a greater effect on flower production and abortion. Number of pods was significantly more in dry conditions at all sowing dates (Figure 5.3.2.4a) and in relatively waterlogging resistant genotypes (Figure 5.3.1.4a) suggesting that higher ability to set pods under excessive moisture conditions may be important in improving waterlogging resistance of ESD pigeonpea. This could possibly need to be enhanced though genetic improvement. Waterlogging during the pre-flowering stage caused a significant reduction in pod numbers and HI whereas waterlogging during the flowering stage significantly reduced all yield components. Wet conditions mostly affected the number of pods and number of seeds pod^{-1} of ESD pigeonpea.

From the results of this study, ESD pigeonpea showed relatively higher susceptibility to waterlogging/excessive moisture and no evidence of acclimation, as seen in soybean which can withstand saturated soil conditions (Nathanson *et al.* 1984; Hunter *et al.* 1980; Hodgson *et al.* 1989). Although the number of genotypes used for comparison in this study was small, significant differences among them were apparent in relation to the stages of waterlogging. The interaction between waterlogging and genotype for the grain yield response of ESD pigeonpea suggested that scope exists for selecting genotypes resistant to waterlogging.

Improving agronomic managements to alleviate the effect of waterlogging by application of nitrogen fertilizer after the release of waterlogging can partially offset the inhibition by nitrogen deficiency and may increase the recovery ability of the waterlogged ESD pigeonpea. Although there are very few reports on this regard, nitrogen fertilizer application for waterlogged wheat (Trought & Drew 1980) or cotton (Hodgson & Macleod 1987) showed more benefit. Nitrogen also ameliorated the adverse effect of short-term waterlogging in MD pigeonpea (Matsunaga *et al.* 1991). The lower grain yield of ICPL 84023 in the dry treatments at late sowings caused by their higher soil moisture which were mainly due to the polyethylene covering soil profile did not effectively prevent water seepage. Moreover, no attempt has been made to discuss the causes of reduction in yield in the late sowing. It may be that waterlogging is only partly responsible, as even under dry treatment, for the reduction in yield was seen. There may be other unknown factors responsible for this. The significant higher grain yield in the dry treatments of all sowing dates indicated the necessity of reducing soil moisture levels by increasing internal soil drainage through agronomic practices (i.e., drainage or interculture, etc.) to alleviate the anaerobic status of soil for increasing yield of ESD pigeonpea.

CHAPTER VI.

GENERAL DISCUSSION AND CONCLUSIONS

Extra-short-duration pigeonpea genotypes have a reasonably high yield potential. The average grain yield observed under non-limiting soil moisture conditions over 3 years of this study was more than 2 t/ha which is comparable with short-duration pigeonpea genotypes or other grain legumes growing in similar environments (Chauhan *et al.* 1987; Nam *et al.* 1993).

The soil moisture availability period determines the effective length of a cropping season, which is usually short in the semi-arid environments (Singh & Subba Reddy 1988). Extra-short-duration pigeonpea genotypes can be useful in different cropping systems in semi-arid environments due to their short-duration and high yield potential. However, fitting ESD pigeonpea into various cropping systems in semi-arid regions will be difficult because of its limited adaptation to fluctuations in soil moisture availability during the growing period. These fluctuations are caused by low total amount of rainfall and its poor distribution which can cause both water deficits and waterlogging at different times of the growing season (Bunting & Kassam 1988). The results of this study suggest that relative high sensitivity of ESD pigeonpea to both soil moisture deficiency and excess situations during the crop growth cycle adversely affect the realization of its yield potential.

Improving resistance to drought and waterlogging of ESD pigeonpea (as for other crops) is feasible if the important traits which confer drought or waterlogging resistance can be identified and used as selection criteria in crop improvement (Blum 1983; Bidinger *et al.* 1982). Understanding plant traits which can improve the performance of ESD pigeonpea under these constraints is also useful in improving agronomic practices to obtain higher grain yield.

The following conclusions can be drawn from the different experiments conducted to obtain information on these aspects:

A. Effect of timing of drought stress

1. Drought stress during the pre-flowering stage clearly retards biomass production of ESD pigeonpea and consequently lowers grain yield. Genotypes with lower initial growth and lower crop growth rate (as seen in ICPL 89021) were more sensitive to stress at this stage. This may because early growth vigor tends to enhance transpiration at the expense of direct soil evaporation before drought stress has occurred. Higher DM accumulation at the early crop growth stage of some genotypes such as ICPL 84023 and ICPL 88039 in 1991 or ICPLs 83015, 84023, 86001 and 88039 in 1992 seemingly conferred better resistance to drought at this stage.

2. The flowering stage was the most critical stage for drought stress in all ESD pigeonpea genotypes, causing 15-55% reduction in yield. The extent of reduction varied due to degree of stress imposed and the response of different genotypes. The main reason for highest sensitivity to drought at this stage was because this coincided with the highest rate of accumulation of DM and LAI. Genotypic differences in response to drought at this stage were highly significant indicating the feasibility to screen for resistance genotypes.

3. Different genotypes were differentially affected by drought stress during the pod-filling stage. The relatively longer duration genotype ICPL 89002 was the most susceptible to this stress. Genotypes with early flowering (ICPL 89021) and vigorous growth (ICPLs 83015, 84023, 88039) which allowed higher DM accumulation and maximum number of pods and seeds suffered minimum losses due to terminal stress.

4. Extra-short-duration pigeonpea was extremely sensitive to drought if stress extended over two crop growth stages (from pre-flowering to end of flowering or from flowering to end of pod-filling). This was because the magnitude of the water deficit became very high with the

protracted stress period. None of the genotypes tested was able showed higher resistance to such extended stresses. Although both extended droughts represented extreme situations, none of the genotypes showed total failure and were able to produce some yield. More genotypes may be tested to determine if there is variation in response to prolonged water stress.

5. Limited flexibility in time to flowering and reproductive growth duration was observed in all the genotypes. This may cause to be them to be poorly adapted to erratic rainfall environments.

B. Plant traits and mechanisms of drought resistance

1. Drought escape

Extra-short-duration pigeonpea matured within 90 days and showed obvious potential for matching crop growth duration to soil water availability in short-growing season areas. Higher yield achieved by ICPL 89021, which had the shortest duration among genotypes tested under pod-filling stress, clearly indicated the advantage of escaping drought.

2. Rooting penetration and water extraction

Extra-short-duration pigeonpea has a shallower root system than traditional longer-duration varieties and this appeared to be one of the major reasons for its susceptibility to drought. It failed to exploit moisture at in 60 cm below the soil surface in both drought and no-drought situations. This indicated that existing root length density of ESD pigeonpea was insufficient to extract water below 60 cm. Development of genotypes with greater rooting depth may lead to improvement in grain yield and stability of yield of ESD pigeonpea.

3. Leaf area retention

Under water stress conditions, canopy development of ESD pigeonpea was most affected by reduced leaf growth and hastened leaf senescence. This feature tended to enhance survival by conserving water but was detrimental to yield due to lowering of LI and transpiration. Maintenance of LAI after stress imposed at pre-flowering was an important trait which was found to contribute to higher yield under this type of stress (Chapter III) because it enhanced recovery ability by better radiation interception after stress was relieved. However, LAI maintenance and also LAD under drought at the flowering or pod-filling stages was not correlated with higher grain yield (Chapter III and Chapter IV). A high LAI under those type of stress may be harmful for yield formation by increasing competition between vegetative growth and sinks (lower pod number) or by increasing the water loss under stress. Greater sensitivity to drought at its reproductive stage of genotypes ICPL 83015 (one of the genotype with highest yield potential) may be associated with having highest LAI during flowering stress.

4. **Radiation use efficiency**

Radiation use efficiency (RUE), thought to be considered conservative in the literature, was found to be an important determinant of biomass production under drought. There was significant variation among genotypes. It accounted for a very high (up to 90%) variation in DM production under drought (Chapter IV). Thus the maintenance of higher RUE may be an important mechanism for drought resistance under drought during the reproductive stage for ESD pigeonpea than retention of high LAI or LAD during drought stress at the reproductive stage.

5. **Maintenance of higher leaf water potential**

Leaf water potential and leaf RWC are important indicators of the degree of desiccation under drought stress. Different genotypes differentially maintained LWP under mild drought stress (as seen during the early stress period), which indicated high drought avoidance (Chapter III and Chapter IV). Loss of lower leaves under severe drought stress suggested that LA adjustment was probably a mechanism for water conservation while maintenance upper leaves favored photosynthesis. This, however, could not be confirmed in the LA removal treatments where no improvement of leaf water status was observed. Thus the potential utility of leaf abscission under stress could not be clarified.

6. Osmotic adjustment

Droughted crop plants exhibited a high level of OA under drought which helped maintain leaf turgor. Different genotypes could lower OP for the maintenance higher levels of TP. High levels of OA exhibited by genotypes are considered as a mechanism of dehydration avoidance. In this study, however, the LA removal treatment did not affect OP and the differences in OA of ESD pigeonpea genotypes were also not significant.

7. Reduced stomatal conductance and transpiration rate

Under stress conditions, ESD pigeonpea had lower CD and TR. Reduced TR may be an important mechanism for water conservation and minimizing the chances of dehydration (Chapter IV). The TR was highly linked to CD under drought stress but not under no-stress. The CD of ESD pigeonpea showed high sensitivity to drought under both defoliation and control treatments.

6. Remobilization of assimilate

Although yield is largely determined by current assimilation during reproductive development in most of the crops (Tanner & Sinclair 1983; Bunting & Kassam 1988) a significant contribution to yield by assimilates stored in ESD pigeonpea under drought conditions was observed (Chapter IV). This appeared to be an important mechanism conferring drought resistance in ESD pigeonpea, especially under terminal drought stress. Screening and selection for ESD pigeonpea genotypes with greater remobilization efficiency can favor of translocation stored assimilates and produce higher yields under terminal drought stress.

C. Effect of waterlogging and excessive soil moisture

1. Extra-short-duration pigeonpea showed sensitivity to waterlogging at both the pre-flowering and flowering stages. Grain yield could be reduced by about 40% of its yield potential. Waterlogging at the pre-flowering stage mainly affected plant growth and DM production during both the waterlogged period as well as during recovery. Waterlogging during flowering caused loss of DM thought leaf senescence and restricted development of yield components.

2. Low soil oxygen concentration in the root zone of waterlogged soil affected root growth and root function of waterlogged pigeonpea. The symptoms of chlorosis, poor crop growth and early leaf senescence appeared to be mainly due to deficiency of nitrogen assimilation.

3. Genotypic differences in response to different timings of waterlogging were highly significant. Genotype ICPL 89002 showed relatively resistance to the pre-flowering stage waterlogging whereas ICPL 88039 was highly resistant to the flowering stage waterlogging.

4. During the rainy season, profiles of poorly-drained soils (such as Vertisol) are generally filled to saturation as the rainy season advances. Under this condition, crop growth and development are restricted, especially for late sown crops. In this study, excessive soil moisture condition was observed when soil profiles of late sowings were charged by rain and irrigation. Grain yields of ESD pigeonpea were significantly reduced in the late sowings, which was mainly caused by higher soil moisture in late sowings than early sowings. The symptoms of poor crop growth observed in late sown crops were similar with those of pigeonpea in the waterlogged treatments, which indicated that anaerobic condition of the soil under excessive soil moisture ha similar effect as waterlogging condition.

5. Covering the soil with polyethylene sheeting significantly reduced soil moisture levels in this treatment compared with a wet soil profile treatment (no-cover) and thus improved crop

growth and yield of ESD pigeonpea, especially at late sowings. This result indicates the important role of soil aeration and the necessity to improve internal drainage of water if waterlogging/excessive soil moisture condition occur.

CHAPTER VII

SUMMARY

Soil water regimes in the semi-arid regions of the tropics and sub-tropics are dependent on the amount and distribution of rainfall and the soil characteristics, which determines the length of the cropping season. Drought is a major constraint to crop production in this region due to period of limited soil moisture availability. Moreover, excessive soil moisture can also be a constraint due to heavy rain and inadequate soil drainage. Extra-short-duration pigeonpea (*Cajanus cajan* L.) can mature within 90 days and is suitable for planting in water-limited areas of the semi-arid tropics where both water deficit and waterlogging can occur at different crop growth stages. The present investigation was under taken with the following objectives:

1. Assessment of the effect of different timing and duration of drought stress on growth and yield of different ESD pigeonpea genotypes.

2. Understanding of the physiological traits associated with drought resistance in ESD pigeonpea.

3. Assessment of the effect of timing of waterlogging and the effect of different levels of excess soil moisture on growth and yield of ESD pigeonpea.

This investigation was conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Andhra Pradesh, India, during the growing seasons of 1991,1992 and 1993.

An automatic rainout shelter and drip irrigation system were used to conduct the experiments in 1991 whereas a manual rainout shelter was used in 1992 to study the effect of timing of drought stress on ESD pigeonpea genotypes, which permitted reliable imposition of drought stress. These experiments were laid out in a split-plot design with drought stress timings in main plot (6 treatments in 1991 and 4 treatments in 1992) and different ESD pigeonpea

genotypes in sub-plot (4 genotypes in 1991 and 8 genotypes in 1992).

To further understand the effect of drought stress at the reproductive stage in relation to leaf canopy development, physiological traits and yield of ESD pigeonpea, an additional experiment using the automatic rainout shelter was conducted in split-split-plot design during the 1993 season. Drought stress imposed from the beginning of flowering to maturity was compared with no-stress in main plots. Defoliation treatments, comprising 50% leaf area (LA) removal before stress was compared with full LA development, were in sub-plots and 6 ESD pigeonpea genotypes were in sub-sub-plots.

To assess the effect of timing of waterlogging and of different excess soil moisture levels in relation to sowing dates of ESD pigeonpea, two experiments were conducted in split-plot design during the 1993 season. One was on Alfisol with pre-flowering waterlogging, waterlogging at flowering and no-waterlogging treatments in main plots and 4 ESD pigeonpea genotypes in sub-plots. Another was on Vertisol with three sowing dates as main plot treatments and two soil moisture levels (wet and dry profiles) in sub-plots.

It was observed that ESD pigeonpea genotypes could produce high yields of up to more than 2 t ha^{-1} under non-limiting soil moisture conditions but they were relatively sensitive to drought, especially when drought stress was imposed during the flowering stage when grain yield was reduced by 40-55% compared with the well-watered treatment. Drought stress during the pre-flowering and pod-filling stages was less damaging with yield reductions of 15-20%, dependent on the degree of stress as well as the response of each genotype. The reduction of grain yield under extended stress over two crop growth stages (pre-flowering + flowering or flowering + pod-filling) was the most severe and yield of all genotypes was severely reduced. There was considerable variation in grain yield among genotypes under different timings of drought stress. Genotypes ICPLs 83015, 84023, 86001 and 88039 were identified as relatively resistance to pre-flowering drought stress. Under the flowering stress, genotype ICPL 88039 showed promise as it had least reduction in yield. Genotype ICPL 89021 gave high yield under pod-filling stress as it could escape the stress while genotypes ICPL 88032 and ICPL 89002 were most sensitive to pod-filling stress. There were no substantial differences between genotypes when exposed to stress over two crop growth stages.

The ESD pigeonpea genotypes showed symptoms of severe drought stress even when there was considerable soil moisture below 60 cm in the soil profile, which indicated that they had shallow root systems and could not extract water from deeper soil layers. Higher grain yield in some genotypes relatively resistant to drought was found to be associated with physiological responses such as: (a) Shorter duration which allowed escape of drought stress during the pod-filling stage (as seen in ICPL 890210), (b) a high degree of LA retention under pre-flowering drought stress which could increase recovery ability after the stress was relieved (as seen in ICPLs 83015,84023 and 88039), (c) maintenance of higher radiation use efficiency (RUE) under drought stress at the reproductive stage which was found to be an important trait for increasing dry matter production and thus grain yield, (d) maintenance of higher leaf water potential and osmotic adjustment, (e) reduction of stomatal conductance, and thus transpiration rate, to reduce water loss and minimize dehydration, (f) increased remobilization of assimilates to contribute to a higher grain yield.

Waterlogging/excessive soil moisture was quantified as detrimental to grain yield of ESD pigeonpea. Yield losses of up to 40% were recorded. Leaf chlorosis and early senescence, and thus poor crop growth, were major effects of waterlogging. Low soil oxygen concentration in the root zone caused by excess soil moisture appeared to be the main cause of reduced root growth and function and of restricted nitrogen assimilation. There were considerable genotypic differences in response to timing of waterlogging. Genotype ICPL 89002 was relatively tolerant to waterlogging at the pre-flowering stage while ICPL 88039 was relatively tolerant at the flowering stage.

It was clearly shown that the soil profile charged to a saturated condition by rain and irrigation in late sowings restricted crop growth and yield of late sown ESD pigeonpea. Under this situation, covering the soil profile to reduce the level of excess soil moisture significantly increased dry matter production and grain yield of late sown ESD pigeonpea.

The results of the study clearly demonstrated that ESD pigeonpea genotypes were relatively sensitive to both soil moisture deficits and excess. Much of the variation in their yield under these conditions resulted from variation in crop growth and DM production, number of pods m^{-2} and 100 seed mass. The extent of these changes depended on the timing, duration, intensity of water deficition, excess and also on the response of different genotypes. Although the number of genotypes used in this study is small, the significant differences in response to both drought and waterlogging among genotypes demonstrated the potential of selecting genotypes relatively resistant to these constraints. The physiological traits conferring drought resistant in ESD pigeonpea could be used as criteria for breeding improvement of this crop. Alleviation of waterlogging in ESD pigeonpea can be achieved by both selecting resistant genotypes as well as by applying agronomic practices for reducing excess moisture and improving soil aeration.

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APPENDIX

Appendix 3.1: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on leaf area index of extra-short-duration pigeonpea at the end of different timings of stress, rainy seasons 1991 and 1992.

	Source of variation		
Timing of stress	S	G	S x G
	Season 1991		
Pre-flowering	0.110^{*}	0.115^{NS}	0.205^{NS}
Flowering	0.091^{**}	0.078^{NS}	0.188^{*} (0.190)
Pod-filling	0.081^{**}	0.073^{**}	0.175^{NS}
	Season 1992		
Pre-flowering	0.099^{**}	0.174^{*}	0.299^{NS}
Flowering	0.277^{NS}	0.209^{**}	0.392^{NS}
Pod-filling	0.096^{*}	0.190^{**}	0.269^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

SE value in parenthesis is used for comparing means in the same level of stress

Appendix 3.2: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on light interception of extra-short-duration pigeonpea at the end of flowering and pod-filling drought stresses, rainy seasons 1991 and 1992.

	Source of variation		
Timing of stress	S	G	S x G
	Season 1991		
Pre-flowering	2.21^{**}	0.85^{**}	2.85^{NS}
Flowering	3.38^{**}	1.00^{*}	3.99^{NS}
	Season 1992		
Pre-flowering	0.93^{**}	2.22^{NS}	3.08^{NS}
Flowering	0.088^{*}	1.72^{*}	2.44^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

Appendix 3.3: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on total dry matter accumulation of extra-short-duration pigeonpea at the end of different timings of stress. Rainy seasons 1991 and 1992.

	Source of variation		
Timing of stress	S	G	S x G
		Season 1991	
Pre-flowering	13.0^{NS}	11.9^{NS}	22.1^{NS}
Flowering	21.7^{**}	10.5^{NS}	$31.1\ (25.8)^{*}$
Pod-filling	26.6^{**}	21.3^{NS}	52.4^{NS}
		Season 1992	
Pre-flowering	9.5^{**}	15.7^{NS}	21.7^{NS}
Flowering	56.7^{NS}	41.1^{NS}	78.5^{NS}
Pod-filling	20.3^{NS}	62.5^{NS}	85.1^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.
SE value in parenthesis is used for comparing means in the same level of stress.

Appendix 3.4: F values and levels of significance of drought stress (S), genotype (G) and interaction effect (S x G) on total abscised dry matter and its constituents of extra-short-duration pigeonpea at the end of different timings of stress, rainy seasons 1991 and 1992.

	Source of variation					
	Season 1991			Season 1992		
Timing of stress	S	G	S x G	S	G	S x G
			After flowering stress			
Leaf	0.117^{**}	0.067^{**}	0.165^{*}	0.046^{*}	0.107^{*}	0.149^{NS}
Flower	0.120^{**}	0.077^{**}	0.179^{NS}	0.053^{NS}	0.147^{**}	0.202^{NS}
Pod	0.013^{NS}	0.015^{NS}	0.029^{NS}	0.025^{NS}	0.028^{**}	0.045^{NS}
Total DM	0.152^{**}	0.114^{**}	0.249^{NS}	0.057^{*}	0.169^{**}	0.231^{NS}
			After pod-filling stress			
Leaf	0.098^{**}	0.050^{**}	0.145^{NS}	0.094^{NS}	0.116^{**}	0.180^{NS}
Flower	0.047^{**}	0.032^{*}	0.083^{NS}	0.004^{NS}	0.022^{**}	0.029^{NS}
Pod	0.014^{NS}	0.006^{NS}	0.019^{NS}	0.031^{NS}	0.057^{NS}	0.081^{NS}
Total DM	0.109^{**}	0.057^{NS}	0.162^{NS}	0.120^{NS}	0.153^{**}	0.235^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.

Appendix 3.5: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on leaf water potential at the end of different timings of stress on extra-short-duration pigeonpea, rainy seasons 1991 and 1992.

	Source of variation		
Timing of stress	S	G	S x G
	Season 1991		
Pre-flowering	0.067^{NS}	0.062^{NS}	0.114^{NS}
Flowering	0.189^{**}	0.053^{*}	0.210^{**}
Pod-filling	0.097^{**}	0.054^{NS}	0.149^{NS}
	Season 1992		
Pre-flowering	0.106^{NS}	0.089^{NS}	0.158^{NS}
Flowering	0.154^{NS}	0.139^{*}	0.240^{NS}
Pod-filling	0.050^{NS}	0.086^{*}	0.125^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.
SE value in parenthesis is used for comparing the means in the same levels of stress.

Appendix 3.6: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on leaf osmotic potential at the end of different timings of stress on extra-short-duration pigeonpea, rainy seasons 1991 and 1992.

	Source of variation		
Timing of stress	S	G	S x G
	Season 1991		
Pre-flowering	0.099^{NS}	0.090^{*}	0.167^{NS}
Flowering	0.239^{**}	0.066^{NS}	0.265^{**}
Pod-filling	0.153^{**}	0.070^{NS}	0.213^{NS}
	Season 1992		
Pre-flowering	0.322^{NS}	0.043^{NS}	0.327^{*}
Flowering	0.054^{**}	0.137^{NS}	0.189^{NS}
Pod-filling	0.069^{*}	0.076^{NS}	0.122^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.
SE values in parenthesis are used for comparing the means in the same levels of stress.

Appendix 3.7: F values and levels of significant of drought stress (S), genotype (G) and interaction effects on leaf turgor potential at the end of different timings of stress on extra-short-duration pigeonpea, rainy seasons 1991 and 1992.

Timing of stress	Source of variation S	 G	 S x G
		Season 1991	
Pre-flowering	0.140^{NS}	0.100^{**}	0.205^{NS}
Flowering	0.101^{**}	0.035^{NS}	0.118^{NS}
Pod-filling	0.108^{NS}	0.048^{*}	0.149^{NS}
		Season 1992	
Pre-flowering	0.408^{NS}	0.094^{NS}	0.427^{NS}
Flowering	0.029^{*}	0.100^{NS}	0.135^{NS}
Pod-filling	0.119^{NS}	0.142^{NS}	0.222^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

Appendix 3.8: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on leaf relative water content at the end of different timings of stress on extra-short-duration pigeonpea, rainy seasons 1991 and 1992.

Timing of stress	Source of variation S	 G	 S x G
		Season 1991	
Pre-flowering	1.92^{NS}	1.24^{NS}	2.68^{*}
Flowering	1.32^{**}	0.85^{*}	1.97^{**}
Pod-filling	1.14^{**}	0.75^{NS}	2.03^{**}
		Season 1992	
Pre-flowering	2.66^{NS}	1.00^{NS}	2.97^{NS}
Flowering	1.14^{*}	1.64^{**}	2.45^{NS}
Pod-filling	1.05^{*}	2.47^{NS}	3.43^{NS}

*, **: Significant at levels of 0.05 and 0.01 probability, respectively.

NS : No significant.

Appendix 3.9: F values and levels of significance of drought stress (S), genotype (G) and interaction effects on yield components of extra-short-duration pigeonpea, rainy seasons 1991 and 1992.

Timing of stress	Source of variation S	G	S x G
	Season 1991		
Pods m^{-2}	81.0**	42.2*	120.8 (103.4)*
Seeds pod^{-1}	0.09*	0.07^{NS}	0.17^{NS}
100 seed mass	0.20*	0.10**	0.29 (0.26)*
Harvest index	0.022**	0.009**	0.028 (0.021)**
	Season 1992		
Pods m^{-2}	49.5*	48.8**	103.9^{NS}
Seeds pod^{-1}	0.04*	0.09*	0.17^{NS}
100 seed mass	0.06**	0.16**	0.30^{NS}
Harvest index	0.009*	0.012**	0.024 (0.023)*

*, **: Significant at levels of 0.05 and 0.01 probability, respectively

NS : No significant.

SE values in parenthesis are used for comparing means in the same level of stress

Appendix 4.1: F values and significant levels of drought stress (S), leaf area removal treatment (T), genotype (G) and interaction effects on total dry matter at harvest, grain yield and yield components of extra-short-duration pigeonpea, rainy season 1993.

Yield components	Source of variation						
	S	T	G	SxT	SxG	TxG	SxTxG
TDM at harvest	0.072^{**}	0.052^{**}	0.144^{**}	0.089^{NS}	0.200^{NS}	0.194^{NS}	0.278^{NS}
				(0.074)	(0.204)		(0.274)
Grain yield	0.021^{**}	0.017^{**}	0.051^{**}	0.027^{NS}	0.069^{NS}	0.068^{NS}	0.096^{NS}
				(0.024)	(0.072)		(0.096)
Pods m^{-2}	28.7^{*}	39.2^{NS}	52.9^{*}	48.6^{NS}	74.1^{NS}	78.7^{NS}	108.1^{NS}
				(55.4)	(74.8)		(111.3)
Seeds pod^{-1}	0.06^{NS}	0.06^{NS}	0.12^{**}	0.09^{NS}	0.16^{NS}	0.16^{NS}	0.23^{NS}
				(0.08)	(0.16)		(0.23)
100 seed mass	0.100^{**}	0.072^{NS}	0.099^{**}	0.123^{NS}	0.162^{NS}	0.146^{NS}	0.218^{NS}
				(0.101)	(0.139)		(0.207)
Harvest index	0.005^{NS}	0.005^{NS}	0.007^{**}	0.007^{NS}	0.010^{**}	0.010^{NS}	0.015^{NS}
				(0.008)	(0.010)		(0.015)

*, **: Significant difference at 0.05 and 0.01 probability levels, respectively

NS : Non significant difference.

Values in parenthesis are used for comparing means in the same level of stress

Appendix 4.2: F values and significant levels of drought stress (S), leaf area removal treatment (T), genotype (G) and interaction effects on total dry matter accumulation and leaf area index of extra-short-duration pigeonpea at different stages of drought stress imposed, rainy season 1993.

Sources of variation	Day after sowing		
	59	73	87
	Total dry matter accumulation		
Stress (S)	11.3^{NS}	27.0^{NS}	19.4**
Treatment (T)	11.0**	17.7^{NS}	22.3^{NS}
Genotype (G)	19.4*	24.3*	29.5*
S x T	15.8 (15.6)^{NS}	32.3 (25.1)^{NS}	29.5 (31.5)^{NS}
S x G	27.5 (27.5)^{NS}	41.4 (34.4)^{NS}	42.7 (41.7)^{NS}
T x G	27.4^{NS}	36.0^{NS}	44.1^{NS}
S x T x G	38.8 (38.7)^{NS}	54.9 (51.0)^{NS}	61.4 (62.4)^{NS}
	Leaf area index		
Stress (S)	0.100**	0.244*	0.194*
Treatment (T)	0.144**	0.147**	0.120*
Genotype (G)	0.214**	0.164**	0.143**
S x T	0.175 (0.203)^{NS}	0.285 (0.208)^{NS}	0.228 (0.170)^{NS}
S x G	0.294 (0.303)^{NS}	0.323 (0.232)^{NS}	0.268 (0.203)^{NS}
T x G	0.312^{NS}	0.258^{NS}	0.221^{NS}
S x T x G	0.429 (0.441)^{NS}	0.413 (0.365)^{NS}	0.347 (0.312)^{NS}

*, **: Significant difference at 0.05 and 0.01 probability levels, respectively

NS : No-significant difference.

Values in parenthesis are used for comparing means in the same level of stress

Appendix 4.3: F values and significant levels of drought stress (S), leaf area removal treatment (T), genotype (G) and interaction effects on leaf water relation observations of extra-short-duration pigeonpea at different stages of drought stress imposed, rainy season 1993.

Sources of variation	Day after sowing		
	57	71	85
	Leaf water potential		
Stress (S)	0.025^{NS}	0.048^{NS}	0.009**
Treatment (T)	0.026^{NS}	0.010*	0.050^{NS}
Genotype (G)	0.028^{NS}	0.037*	0.055^{NS}
S x T	0.036 (0.036)^{NS}	0.049 (0.014)^{NS}	0.051 (0.071)^{NS}
S x G	0.044 (0.040)^{NS}	0.068 (0.052)^{NS}	0.071 (0.078)^{NS}
T x G	0.044^{NS}	0.049^{NS}	0.087^{NS}
S x T x G	0.063 (0.063)^{NS}	0.084 (0.069)^{NS}	0.113 (0.123)^{NS}
	Osmotic potential		
Stress (S)	0.047*	0.070*	0.066**
Treatment (T)	0.016^{NS}	0.028^{NS}	0.042^{NS}
Genotype (G)	0.032*	0.045^{NS}	0.068^{NS}
S x T	0.050 (0.022)^{NS}	0.076 (0.039)^{NS}	0.079 (0.060)^{NS}
S x G	0.063 (0.045)^{NS}	0.092 (0.064)^{NS}	0.110 (0.097)^{NS}
T x G	0.044^{NS}	0.065^{NS}	0.098^{NS}
S x T x G	0.077 (0.063)^{NS}	0.112 (0.092)^{NS}	0.147 (0.138)^{NS}
	Turgor potential		
Stress (S)	0.070*	0.025**	0.058*
Treatment (T)	0.032^{NS}	0.026*	0.043*
Genotype (G)	0.047^{NS}	0.050^{NS}	0.054^{NS}
S x T	0.077 (0.046)^{NS}	0.036 (0.037)^{NS}	0.073 (0.061)^{NS}
S x G	0.093 (0.067)^{NS}	0.069 (0.071)^{NS}	0.091 (0.076)^{NS}
T x G	0.069^{NS}	0.070^{NS}	0.082^{NS}
S x T x G	0.116 (0.098)^{NS}	0.098 (0.099)^{NS}	0.122 (0.116)^{NS}
	Leaf relative water content		
Stress (S)	1.04^{NS}	2.02^{NS}	1.77*
Treatment (T)	0.50^{NS}	0.84^{NS}	0.68^{NS}
Genotype (G)	1.14^{NS}	1.50^{NS}	1.47^{NS}
S x T	1.16 (0.70)^{NS}	2.19 (1.19)*	1.89 (0.96)^{NS}
S x G	1.81 (1.62)^{NS}	2.80 (2.12)^{NS}	2.58 (2.07)^{NS}
T x G	1.56^{NS}	2.11**	2.01^{NS}
S x T x G	2.39 (2.20)^{NS}	3.50 (2.98)^{NS}	3.27 (2.84)^{NS}

*, **: Significant difference at 0.05 and 0.01 probability levels, respectively

NS : No-significant difference.

Values in parenthesis are used for comparing means in the same level of stress

Appendix 4.4: F values and significant levels of drought stress (S), leaf area removal treatment (T), genotype (G) and interaction effects on non structural carbohydrate in the stem of extra-short-duration pigeonpea at different stages of drought stress imposed, rainy season 1993.

Sources of variation	Day after sowing		
	59	66	73
		Total soluble sugar content	
Stress (S)	0.863^{NS}	0.030^{**}	0.949^{NS}
Treatment (T)	0.794^{NS}	0.090^{*}	0.430^{NS}
Genotype (G)	0.825^{*}	0.735^{**}	0.642^{*}
S x T	$1.173\ (1.230)^{NS}$	$0.095\ (0.128)^{**}$	$1.042\ (0.609)^{NS}$
S x G	$1.371\ (1.167)^{NS}$	$0.950\ (1.040)^{NS}$	$1.261\ (0.909)^{NS}$
T x G	1.328^{NS}	0.953^{NS}	0.934^{NS}
S x T x G	$1.909\ (1.879)^{NS}$	$1.346\ (1.348)^{NS}$	$1.569\ (1.321)^{**}$
		Starch content	
Stress (S)	0.116^{NS}	0.009^{**}	0.216^{NS}
Treatment (T)	0.160^{NS}	0.250^{NS}	0.287^{NS}
Genotype (G)	0.266^{NS}	0.254^{NS}	0.235^{**}
S x T	$0.198\ (0.227)^{NS}$	$0.250\ (0.354)^{NS}$	$0.359\ (0.406)^{NS}$
S x G	$0.362\ (0.376)^{NS}$	$0.328\ (0.359)^{NS}$	$0.372\ (0.332)^{**}$
T x G	0.379^{NS}	0.412^{NS}	0.418^{NS}
S x T x G	$0.524\ (0.536)^{NS}$	$0.527\ (0.583)^{NS}$	$0.560\ (0.590)^{NS}$

*, **: Significant difference at 0.05 and 0.01 probability levels, respectively

NS : No-significant difference.

Values in parenthesis are used for comparing means in the same level of stress

Appendix 5.1: F values and levels of significant of water logging (WL), genotype (G) and interaction (WL x G) effect on growth of extra-short-duration pigeonpea at before and the end of different timings of water logging, rainy season 1993.

	Source of variation		
Plant growth	WL	G	WL x G
	Before waterlogged treatment		
- Plant height	1.0^{NS}	1.7^{*}	$2.3\ (2.4)^{NS}$
- TDM	4.0^{ns}	5.2^{NS}	$7.6\ (7.4)^{NS}$
- LAI	0.040^{NS}	0.064^{NS}	$0.088\ (0.091)^{NS}$
	After pre-flowering waterlogged		
- Plant height	1.8^{NS}	1.7^{*}	$2.7\ (2.3)^{NS}$
- TDM	11.3^{*}	10.3^{NS}	$16.9\ (14.5)^{NS}$
- LAI	0.057^{**}	0.119^{NS}	$0.156\ (0.168)^{NS}$
	After flowering waterlogged		
- Plant height	3.6^{*}	2.2^{**}	$4.9\ (3.8)^{**}$
- TDM	34.6^{**}	17.4^{**}	$43.3\ (30.2)^{*}$
- LAI	0.219^{**}	0.121^{**}	$0.284\ (0.209)^{*}$

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.
SE values in parenthesis are used for comparing means in the same level of waterlogged.

Appendix 5.2: F values and levels of significance of water logging (WL) treatment, genotype (G) and interaction (WL x G) effect on total dry matter at harvest, grain yield and yield components of extra-short-duration pigeonpea under different timings of water logging, rainy season 1993.

	Source of variation		
Components	WL	G	WL x G
TDM at harvest	0.513^{NS}	0.196^{**}	$0.591\ (0.339)^{*}$
Grain yield	0.152^{*}	0.055^{**}	$0.173\ (0.095)^{**}$
Pods plant^{-1}	0.9^{**}	1.4^{**}	$2.3\ (2.4)^{NS}$
Seeds pod^{-1}	0.10^{NS}	0.11^{*}	$0.19\ (0.19)^{NS}$
100 seed mass	0.151^{NS}	0.135^{**}	$0.252\ (0.233)^{NS}$
Harvest index	0.026^{NS}	0.016^{NS}	$0.035\ (0.028)^{NS}$

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.
SE values in parenthesis are used for comparing means in the same level of waterlogged.

Appendix 5.3: F values and levels of significant of sowing date (S), dry profile treatment (T) and interaction (S x T) effect on total dry matter at harvest, grain yield and yield components of extra-short-duration pigeonpea ICPL 84023 on Vertisol, rainy season 1993.

	Source of variation		
Components	S	T	S x T
TDM at harvest	0.089^{**}	0.178^{**}	$0.253\ (0.308)^{NS}$
Grain yield	0.093^{*}	0.025^{**}	$0.098\ (0.043)^{NS}$
Pods m^{-2}	24.7^{*}	56.0^{*}	$72.9\ (97.0)^{NS}$
Seeds pod^{-1}	0.15^{NS}	0.07^{*}	$0.17\ (0.13)^{NS}$
100 seed mass	0.111^{**}	0.133^{NS}	$0.197\ (0.230)^{NS}$
Harvest index	0.022^{NS}	0.010^{NS}	$0.025\ (0.018)^{NS}$

*, **: Significant at levels of 0.05 and 0.01 probability, respectively
NS : No significant.
SE values in parenthesis are used for comparing means in the same level of waterlogged.