Institute of Plant Nutrition

Morphological and Physiological Responses of Sorghum (Sorghum bicolor L. Moench) to Different Patterns of Drought

Thesis

in partial fulfilment of

the requirements for the

academic degree of

Master of Science

of the

Faculty of Agriculture

Rheinische Friedrich-Wilhelms-Universität zu Bonn

Submitted on 21.03.2005

by

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Acknowledgements

Dedication

To my wonderful wife Philomina Kutame Abdulai and my lovely children Hilda Wunniche Alhassan, Grace Wunyubu Alhassan and Walter Nassara Alhassan

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Abstract

Drought is a major stress affecting rainfed sorghum production systems. An experiment was setup in a greenhouse to evaluate the morphological and physiological responses of sorghum to different drought patterns. Two-week old seedlings of "ICSV 111 IN" were transplanted into 9 L pots filled with loamy sand (11.3 kg) or silt loam (10.8 kg) and grown for one month. Pots were subjected either to constant drought (70% of field capacity (CD)) or to progressive drought (slow drying-out close to permanent wilting point (PD)).

Growths, biomass accumulation, assimilate partitioning, xylem ABA content, gas exchange, and plant water relations were determined. Drought effects were more pronounced on loamy sand than on silt loam. Soil moisture content, rather than soil water potential triggered drought responses. Constant drought and Progressive drought conditions reduced growth and biomass accumulation, as well as all the gas exchange components, in both loamy sand and silt loam. Assimilate partitioning did not change under constant drought conditions, but was shifted in favor of roots under progressive drought conditions. Xylem ABA content increased (more pronounced on loamy sand than silt loam) under progressive drought conditions, but was not affected by constant drought conditions. The genotype adjusted and adapted to constant drought conditions but employed survival mechanisms under progressive drought conditions.

List of Abbreviations

ABA-	Abscisic acid
CD-	Constant drought
CK-	Cytokinins
DNA-	Deoxyribonucleic acid
ELISA-	Enzyme-linked Immuno-sorbent Assay
FAO-	Food and Agriculture Organization
FC-	Field capacity
GA-	Giberrellic acid
GS1-	Growth stage one
GS2-	Growth stage two
GS3-	Growth stage three
ICRISAT-	International Crops Research Institute for the Semi-arid Tropics
L1-	Youngest fully exserted leaf
L2-	Third youngest fully exserted leaf
LOP-	Leaf osmotic potential
LWP-	Leaf water potential
MPa-	Mega-Pascal
PAR-	Photosynthetically active radiation
PC-	Partitioning co-efficient
PD-	Progressive drought
QTL-	Quantitative trait loci
RGR-	Relative growth rate
RMR-	Root-mass ratio
RWP-	Root water potential
SARI-	Savanna Agricultural Research Institute
SPAC-	Soil-Plant-Atmosphere-continuum
SWP-	Soil water potential
TGL-	Total green leaf
WUE-	Water use efficiency

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1 Introduction

1.1 Background

Sorghum (*Sorghum bicolor* L. Moench), currently the 5th most important grain crop, is the primary food source for people in many developing countries (Doggett, 1988) and a major source of fodder in many countries in the developed world. It is endemic to Sub-Saharan Africa, and has been cultivated for centuries as a staple in much of arid and semi-arid Africa and Asia where water availability is the major limiting factor to crop production.

The maximum recorded yield for sorghum is 21 t ha^{-1}, but the average yield worldwide is only 1.28 t ha^{-1} (Wittwer. 1980; FAO. 2001). Even in the USA average yields are only 3.2 t ha^{-1} (FAO, 2001). Based on these numbers, sorghum, in a typical production environment, averages between 5 and 15% of its recorded maximum yield potential. While biotic stresses reduce yield potential in specific environments, most of the reduction in sorghum yield is attributed to abiotic stress, primarily drought (Kramer and Boyer. 1995).

Drought is a multidimensional stress affecting plants at various levels of their organization (Blum, 1996), and is generally accepted as the most widespread abiotic stress experienced by crop plants (Quarrie *et al*., 1999), as well as a major limiting factor to crop production in most areas of the world, especially the tropics. Even intermittent water deficit at critical stages of cereal crops may reduce yield (Ludlow and Muchow 1990), and in high rainfall (>800mm) areas, short periods of drought can decrease yield considerably.

Plants adapt to stresses using different mechanisms involving changes in morphological and developmental pattern as well as physiological and bio-chemical processes (Bohnert *et al*., 1995). Mechanisms such as escape (which allows a plant to grow and complete its life cycle before soil moisture becomes limiting), avoidance (which enables plants to maintain positive tissue water relations even under limited soil moisture conditions), and tolerance (which stabilize and protect cellular integrity under conditions of tissue desiccation) (Ludlow and Muchow, 1990), and morphological and physiological traits such as prolific root system (Jordan and Miller, 1980), high osmotic

adjustment (Ludlow *et al*, 1990), and an ability to delay reproductive development (Hsiao *et al*., 1976) have been proposed as enabling sorghum to achieve economic yields in drought-prone environments.

Soil-water status (water content, water potential, soil hydraulic conductivity and soil water availability) influences the extents of both drought and its associated plant responses. These soil-water characteristics, which vary widely and non-linearly with water content, are also greatly influenced by soil texture, and to some extent, soil structure (Kern, 1995). Soil texture, which influences infiltration and drainage, is very important in drought studies because it determines the water-holding characteristics of most agricultural soils (Bauer and Black, 1992).

To survive drought stress, a plant must either extract more water from the soil, and/or effectively control the amount of water it loses through transpiration. The efficiency of soil water uptake by the root system as well as control of stomatal aperture, are key factors in determining the rate of transpiration. The root characteristics like, rooting depth, thickness of roots and root length density, that determine water uptake during drought (Cruz et al., 1992), may be influenced by assimilate partitioning pattern. It has long been apparent that the major plant growth regulating hormone ABA strongly promotes stomatal closure (Jones and Mansfield 1970).

Sorghum is characterized by an ability to tolerate and survive under conditions of continuous or intermittent drought (Hulse *et al*, 1980), but genotypic differences exist between cultivars with regard to photosynthetic activity and in photosynthate partitioning under drought stress (Sung and Krieg, 1978; Krieg *et al*., 1978). The cultivar used in this study, "ICSV 111 IN" has been adopted, to a large extent, by farmers in Northern Ghana, but it is not known exactly, which of soil water availability and soil water potential drives its adaptation to drought. Little is also known about both the extent to which the cultivar employs ABA-related regulation of transpiration and how it modifies partitioning of assimilates under drought stress.

Elucidating the variations and modifications of morphological and physiological traits, photosynthetic activity and photosynthate partitioning, under different drought patterns is significant in the development of strategies for coping with drought.

2 Hypothesis and Objectives

2.1 Hypothesis

The availability of soil water to plants depends primarily on the quantity of water stored in the soil (capillary water) and its relationship to soil water potential. This availability is determined mainly by the matric potential (energy with which the capillary water is held by surface forces) in any given soil. The matric potential can become particularly large in soils with fine pores.

A high root mass ratio (RMR) is typical of any plant grown under dry conditions. Soil drying during drought stress results in shrinking of both soil and roots. The shrinkage reduces the contact between roots and the soil water films as well as conductance into the root. In dry environments, the contact between roots and soil is the greatest resistance to water flux from the soil to leaves. Plants increase root conductance primarily by increasing allocation to production of new roots (Lambers *et al*., 1998).

It is hypothesized that drought response in sorghum is influenced by matric potential rather than absolute water content. Another hypothesis is that during drought stress, the export of assimilates to the roots is enhanced as long as photosynthesis is affected less than leaf expansion.

2.2 Objectives

The overall objective of the proposed study was to assess variations in morphological and physiological traits of a sorghum genotype under different patterns of drought stress. This was done by trying to find answers to the following questions:

1) Is it the available water or the matric potential that influences drought responses in sorghum?

2) Do sorghum plants partition more biomass to the roots than the shoot during drought stress?

3 Literature Review

3.1 Drought and drought resistance

Drought denotes a period without appreciable precipitation, during which the water content of the soil is reduced to such an extent that plants suffer from lack of water (Larcher, 1995). It is therefore defined by Yoshida (1981) as an imbalance between water uptake and water lost through transpiration. On a large scale, drought results from the combination of low precipitation and high evapotranspiration (Thornthwaite, 1948), caused by dryness of the air and high levels of radiation (Larcher, 1995). Nevertheless, plants may experience transient drought stress during noon hours of hot days even with adequate rainfall or irrigation (McKersie & Lesshem, 1994b). If plants are to survive this imbalance they must have a range of both morphological and biochemical mechanisms that enable them to grow and reproduce despite water limitations (Turner, 1997).

Drought events can be classified according to their cause; meteorological drought occurs when precipitation is significantly below expectations for the year and location; agricultural drought is when water supplies used directly for agriculture are scarce resulting in a consistently high soil moisture deficit over the growing season. The threshold for agricultural drought may be influenced by shifting to another crop because different crops have different water requirements (Ashley, 1993).

Responses to drought vary considerably between different plant types, species, and cultivars (Nguyen *et al.*, 1997), and drought resistant plants do not necessarily require lower amounts of water. Timing of rainfall is critical because drought sensitivity during a certain developmental stage may have fatal consequences and is not necessarily caused by the absence of required "drought resistance" genes (McKersie & Lesshem, 1994b). When the term "drought resistance" is applied to crop plants it means not only the ability to survive, but also to grow and yield satisfactorily under conditions where rainfall is insufficient. By using the term drought resistance no distinction is made between the plants' possible strategy of drought tolerance, avoidance, escape and its capacity to recover from such a situation (Ashley, 1993).

O'Toole & Chang (1979) have defined drought resistance as an umbrella term that covers those four plant response strategies in relation to drought. Ludlow and Muchow (1990), however, have indicated that there are two main drought survival strategies: (1) escape, where plants such as desert ephemerals and short season annuals germinate, grow rapidly and complete the whole life cycle before the soil water is exhausted in arid environments with low and variable rainfall and (2) drought resistance, where the longer season annuals and perennials survive water stress by either avoiding dehydration or tolerating dehydration.

Drought avoidance is the ability of plants to prevent reduction of tissue water potential during water deficit by increasing water uptake through the roots and by increasing stomatal resistance (O'Toole & Chang, 1979). Drought avoiding mechanisms can be divided into water conserving mechanisms and water collecting mechanisms (Yambao *et al*., 1992). Water conserving mechanisms decrease water loss and reduce leaf growth, increase stomatal and cuticular resistance, and accelerate leaf senescence (Jones, 1980), whereas water-collecting mechanisms are extended root growth and decreased resistance for water uptake through the roots.

Drought tolerance is the ability of cells and tissue to withstand reduced water potentials during water deficit. Drought tolerant plants can actually cope with the stress factor, and tolerate desiccation to a greater extent, and therefore survive longer when water is deficient (Hsiao, 1982). Osmotic adjustment is an important drought tolerance trait (Nguyen *et al*., 1997). Drought recovery, when plants have the ability to resume growth and finish their life cycle after a period of water deficit (O'Toole & Chang, 1979), is another form of drought tolerance.

In most plants response to water deficit is a combination of these survival strategies and this makes drought resistance complex. Water deficit causes a whole series of both physiological and physical events to take place and this makes the determination of the function of an observed response a difficult task (Bray, 1997).

3.2 Water transport in the soil-plant-atmosphere continuum

Water movement through the soil-plant-atmosphere continuum (SPAC) determines the degree or extent to which plants can survive drought. It is greatly determined by e. g. the roots' resistance to water permeability, stomatal resistance as

well as boundary layer resistance. Plants with higher chances of survival under conditions of moisture deficit are the ones having the ability to adjust to environmental conditions (moisture deficit) by modulating resistances to water flow through the SPAC, and also the ability to increase the efficiency with which the available water is used. Water movement in the SPAC is mostly bulk flow and, to a lesser extent, by diffusion (Stirzaker & Passioura, 1996).

3.3   Aspects of soil-plant water transport

Water movement through the soil to the roots of a transpiring plant is caused by potential gradients in hydrostatic pressure and osmotic potential. Water uptake by the roots depends on both interactions with the soil and roots' ability to maintain hydraulic continuity with the soil (Passioura, 1988). As the plant absorbs water from the soil, the soil near the root surface is depleted. This establishes a pressure gradient with respect to neighboring regions from which water starts to move through inter-connected water-filled pore spaces down the gradients in hydrostatic pressure (Lambers *et al*., 1998).

Water movement across the soil-root-interface is more complicated and may be affected by a mucilaginous layer containing pores so small as to greatly hinder the flow of water. Additionally, if the root is growing in a pore or, if the root or the soil has shrunk because of sudden drying, there might be a poor hydraulic continuity between root and soil (Stirzaker & Passioura, 1996). Water enters the root most readily in the apical part of the root that includes the root hair zone, where root hairs contribute a large share of the root surface. Intimate contact between the root surface and the soil is essential for effective water uptake by the root. This contact provides the interface for water uptake and is maximized by the growth of the root and of root hairs into the soil (McCully & Canny, 1988).

3.3.1 Water transport through the plant

When it enters the root, water flows through the cortex either apoplastic or symplastic. The apoplastic pathway is a continuous system of cell walls and intercellular air space and water moves exclusively through the cell wall without crossing any membranes (Stirzaker & Passioura, 1996). The cellular pathway can be divided into two different pathways (although the two pathways have not yet been separated experimentally), the trans-cellular pathway and the symplastic pathway. The trans-

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cellular pathway is dominated by water channels (aquaporins), through which water crosses a membrane at least twice for each cell in its path. The symplastic path is mediated by the plasmodesmata (Steudle, 2001). Before leaving the cortex for the vascular bundle water must enter the symplast at least temporarily because of the Casparian bands (Stirzaker & Passioura, 1996). Trans-membrane water movements are primarily determined by hydrostatic and osmotic pressure gradients.

In the vascular bundle water enters the xylem that constitutes the longest pathway of water transport in most plants. The xylem is a simple low resistance pathway with a specialized anatomy that enables water transport in large quantities with great efficiency. From the xylem, water is drawn into the cells of the leaf and along the cell walls. From the cell walls water evaporates into intercellular air spaces and moves then by diffusion to the stomatal cavity and further through the stomatal opening and the boundary layer before it is finally lost to the atmosphere. The force driving water transport from the soil through the plant and out to the atmosphere is a negative gradient in hydrostatic pressure or vapour pressure generated mainly by transpiration (Losch & Schulze, 1994).

3.3.2 Resistances and their effects/influence on water transport

The plant can be described as a system with water input through roots and water output through the stomatal pores. In the past there has been a strong emphasis on the output function (Steudle, 2001), but resistance to water flow can nevertheless increase in all parts of the plant. The vapour pathway in mesophyll air spaces, stomatal pores, and boundary layer outside the leaves usually represent the highest hydraulic resistance in the SPAC, and most of the water potential difference between soil and atmosphere will occur here (Yang & Tyree, 1994).

The hydraulic resistance of roots is known to be variable, but because of the difficulties in examining root hydraulic resistance in the natural environment of roots it has not been possible so far to obtain an adequate understanding of the extent to which roots contribute to whole plant hydraulic resistance. However, root hydraulic resistance may be influenced by several factors including the rate of fall of mean soil water content with time, diffusivity of soil water and the radius of the putative cylinder of soil surrounding the root (Clarkson *et al.*, 2000; Steudle, 2000).

The water status of the shoot can be improved either by increasing stomatal resistance and/or decreasing root hydraulic resistance. However, it is not clear whether or not these adjustments are purely physical adjustments or involves some active regulation (Steudle, 2000). Xylem hydraulic resistance is small but it may be important under conditions of stress (Tyree & Sperry, 1988).

3.4 Roots and root systems

Root distribution and root system structure, which are both affected by soil moisture, play an important role in the plant's ability to survive drought situations. Plants having the ability to increase root growth into regions with more available soil water have better chances of survival under drought situations (Mambani and Lal, 1983), since increased root growth re-establishes the soil-root contact and facilitates water uptake (Yambao *et al*, 1992).

Plants having the ability to develop deep and thick roots are better adapted to growth in drought prone areas than thin rooted plants with a shallow root system (Chang *et al*., 1986). Thick (fibrous) roots reach deeper soil layers and have less axial resistance to water flow because of a larger meta-xylem, and thereby facilitate and increase water uptake (Passioura, 1982). Irrespective of root axial resistance, a few long roots can theoretically sustain the transpirational demand and maintain adequately high leaf water potential in the shoot (Yambao *et al*., 1992), and thick roots have also been confirmed to have a better ability to penetrate compact soil. They persist longer, produce more and larger branch roots and thereby increase water uptake capacity (Ingram *et al*., 1994).

When drought develops, the root/shoot dry matter ratio may increase and in the roots both morphology and distribution changes. These changes may have a genetic basis and they are an integrated expression of various adaptive processes taking place in the roots in response to plant water deficit (Nguyen *et al*., 1997).

3.5 Water use efficiency

High WUE implies good returns on a given amount of water used (Nguyen *et al*., 1997). In environments where the amount of plant available water is limiting growth, water use efficiency (WUE = biomass production per unit water use) is an important

trait, but it is a difficult trait to select for in breeding because it varies with both species and environmental conditions (van den Boogaard *et al.*, 1997). WUE is not unambiguous and it is important to distinguish between WUE in its agronomic sense, ratio of crop productivity to crop water- use, and WUE in its physiological sense, ratio of carbon assimilation to transpiration (Farquhar *et al.*, 1989). The correlation between WUE and dry matter production has been found to be inconsistent in experiments conducted over different water regimes and years (Matus *et al*, 1996).

The actual WUE is affected by both climatic and genotypic factors. Climatic factors like vapour pressure deficit, wind, high temperatures and high irradiance may increase transpiration and, therefore, negatively affect WUE. Oppositely, factors like high photosynthetic capacity, optimal plant density and adjusted plant architecture may increase WUE because these factors may increase either the carbon assimilation or decrease water loss (Davies & Pereira, 1992).

WUE may increase as drought stress increases. Different cultivars of wheat have been compared and depending on cultivar WUE increased between 0% and 12%. The cultivar where the highest increase in WUE was found also had the highest WUE under fully watered conditions (van den Boogaard *et al.*, 1997). As a single trait WUE may be a misleading parameter and before selection for high WUE, other parameters like genotypic variation in deep soil moisture extraction should also be taken into account (Richards *et al.*, 1993; Hall *et al.*, 1994). High WUE is related to the biomass allocation pattern, such that WUE increases with increasing leaf area per unit plant weight. Besides, a higher WUE is associated with a lower photosynthetic nitrogen use efficiency cultivars having a higher WUE, however, may be most suited to be used in drought prone areas (van den Boogaard *et al.,* 1997).

3.6 Plant physiological responses to drought.

Globally, the availability of water is the factor that most strongly influences terrestrial plant production, and low water availability limits the productivity of many natural ecosystems, particularly in dry climates. In addition, losses in crop yield due to water stress (flooding and drought) exceed losses due to all other abiotic and environmental factors combined (Boyer 1985). It has long been known that in order to conserve the water, nutrients and carbohydrates required for survival, plants respond to

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stresses such as soil drying by reducing leaf expansion, closing stomata and may maintain root growth rates in order to continue to access water.

Traditional explanations for drought-induced regulation of gas exchange and leaf growth have emphasized the importance of a decline in shoot water status which commonly accompanies severe soil drying. It is now accepted, however, that many of the plant's responses to soil drying can occur in the absence of changes in shoot water status via chemical signals (Wilkinson & Davies 2002).

In a series of experiments, pressure had been applied to roots to counteract the increasing soil suction that occurs as soil dries. This generated shoot water relations, in drought-stressed plants that were comparable to those of well-watered plants. Despite this, there were still restrictions in rates of gas exchange and leaf growth of the treated plants compared to rates shown by well-watered plants (Gollan *et al.*, 1992).

Root-sourced chemical signaling was also demonstrated by Gowing *et al.*, (1990) who split the roots of young apple trees between two containers, allowing the soil in one container to dry, and applying normal irrigation to the other. This treatment restricted the rate of leaf growth, which could be restored to control rates by removing the roots in contact with the drying soil, i.e. by removing the source of the chemical signal. Blackman & Davies (1985) used the same technique to demonstrate that chemical signals sent from drying soil could close the stomata of wheat leaves.

Several groups have also used the root pressure vessel technique to restore the shoot water relations of a range of species growing in drying soil, and have demonstrated that stomata re-open (e.g. Saliendra *et al.*, 1995; Fuchs & Livingstone 1996; Comstock & Mencuccini 1998). These results indicate that drought-induced limitations in stomatal opening in these species are mostly hydraulic, suggesting that the relative importance of hydraulic versus chemical signaling may differ between species. It might be surprising if this were not the case, but care should be taken in using the root pressurization technique to differentiate between chemical and hydraulic signaling mechanisms because pressurization of plant parts is known to change the pH of different compartments of the shoot and root (Hartung, Radin & Hendrix 1988). It is possible that such a change in pH could significantly modify the signaling process,

hence raising the possibility of root pressurization minimizing both hydraulic and chemical limitation of stomatal behavior simultaneously (Wilkinson & Davies 2002).

Drought results in physiological responses such as accumulation of phytohormones (especially ABA), formation of radical scavenging compounds, stomatal closure and reduced transpiration rates, decrease in water potential of plant tissues, photosynthetic rate, and synthesis of new proteins (mostly dehydrin-like) and mRNAs (Pelah *et al*, 1997). Besides the above physiological responses, plants undergo also morphological changes. One of the largest is the drought-induced adaptation of plants and chloroplasts to high or low irradiance (Lichtenthaler *et al*., 1981)

3.7 The role of phytohormones

Phytohormones are a group of naturally occurring organic substances that influence physiological processes and have certain biochemical trends in common. They are mostly small molecules synthesized from ubiquitous precursors, sometimes via multi-stepped pathways, in a wide range of tissues or cells within tissues and are deactivated by either oxidation or conjugation. They may act either in the cell or tissue in which they are synthesized or may be transported through a distance to bring about specific physiological responses (Davies, 1995). Phytohormones are active in very small quantities, and some of them have both promoting and inhibitory influences. Hormones are not only stimulators, but are also chemical regulators that communicate information about both the developmental or physiological state of cells and tissues, and conditions in the surrounding environment both beneath and above the soil surface (Turner, 1997).

Cells are thought to recognize phytohormones using receptor proteins, but to date, only ethylene receptors have been identified (Kende & Zeevart, 1997; Rock, 2000). Receptor proteins contain binding sites for specific hormones. Binding of a hormone to its receptor might allow the receptor to interact either with other components in the cell or directly with regulatory sequences of DNA in order to activate or repress the transcription of specific genes (Davies, 1995). The concept of phytohormone action can be divided into changes in concentration, sensitivity and transport. Changes in hormone concentration can be brought about by changes in environmental conditions (Schurr & Gollan, 1990), or by changes in levels of substances that enhance or inhibit

the response to the hormone (Firn, 1986). At the same time sensitivity to the hormone might change as a result of a change in the number of receptors (receptivity), a change in receptor affinity (affinity), or a change in the subsequent chain of events (response capacity) (Firn, 1986). In addition, hormone movement or transport may be enhanced or inhibited by a change in sap flow, membrane permeability or pH in and along the pathway (Hartung & Davies, 1991).

Abscisic acid (ABA) is a phytohormone known to synergistically or antagonistically with other hormones coordinate and control plant growth and development in response to external factors, including water deficit. Within the context of drought stress, ABA is probably the most intensively investigated phytohormone, and is widely thought to influence plant growth and development (Beardsell & Cohen, 1975; Bunce, 1999). ABA appears to be the promoting agent in some physiological processes and the inhibitory agent in others, and its action, in most situations, is determined by a balance between its roles of an inhibitor and a promoter (Hoffmann-Benning & Kende, 1992).

ABA can inhibit both shoot and root growth. As a response to drought it may have less effect on root growth, and thereby cause root-shoot ratio to change. Cytokinins (CK) that are generally considered to be antagonists of ABA have opposing effects in the developmental processes including stomatal opening (Blackman & Davies, 1984). Giberellic acid (GA) promotes shoot growth but is not known to be involved in any of the other processes (Davies, 1995).

While ABA production is increased during drought, the production of CK that have been suggested to affect guard cell sensitivity to ABA is decreased (Schurr *et al*., 1992). Ethylene promotes the growth of root hairs and its production is stimulated by ABA. This might explain the lesser inhibition of root growth than shoot growth by ABA (Reid 1995). In addition to phytohormones salicylic acid, jasmonic acid, secondary messengers such as calcium ions (Ca+), and shifts in pH are considered to play important roles in the phytohormone-mediated control of plant growth and development (Atkinson *et al*., 1990).

3.8 ABA and physiological reaction to drought

ABA is ubiquitous in all flowering plants and is generally recognized as a stress hormone that regulates expression of many drought responses. When plants wilt, ABA levels typically rise as a result of an increase in the rate of synthesis (Taylor 1991). Increasing ABA concentration leads to many changes in development, physiology, and growth. Most importantly, ABA accumulation in higher plants in response to water deficit is thought to act as a signal for the initiation of processes involved in adaptation to drought and other environmental stresses (Hartung & Davies 1991; Bray 1993).

The main developmental and morphological effects of ABA are in altering the plant in such a way that less water is lost through transpiration and roots obtain more water as reviewed by Setter (1997). Briefly ABA alters the relative growth rates of various plant parts such as increase in root-shoot dry weight ratio, inhibition of leaf area development, enhancing root growth hence deep rooting (Sharp *et al*., 1994). Stomatal closure, the most important water-conserving response, involves a complex series of events triggered by ABA (Ward et al,. 1995). ABA is also involved in effecting cellular changes that confer an ability to maintain cell turgor and withstand the damaging forces associated with lowered water potential and desiccation. As examples, ABA stimulates osmotic adjustment, (Ober & Sharp 1994), induces the synthesis of protective proteins (the LEA and related proteins) (Bray 1993; Chandler & Robertson 1994).

3.9 Time as a factor in drought resistance

Many processes influence drought resistance in plants, and the initiation of the different traits may span over a wide range of time scales. In general, the most important processes match, in time scale, the influential environmental changes. In Table 1 some environmental phenomena and the physiological changes they cause in the plant are listed (Passioura, 1996).

Crop phenology is an important aspect regarding drought resistance because optimal yield depends on how the pattern of development of the crop matches the pattern of water supply. Drought resistant crops may have abilities to adjust their development in relation to temporal changes in water supply. This is most important in environments where rapid changes in both temperature and vapor pressure deficit occur as the growing season draws to a close (Passioura, 1996).

Literature Review

Table 1: Some phenomena occurring at different time scales in plants and their environment that may bear on drought tolerance or other aspects of water relations (After Passioura, 1996).

Time scale	In the plant	In the environment
Minutes or less	Stomatal movement,	Movement of shadows, rain or irrigation
Hours	Leaf movement, wilting, osmotic adjustment, response to ABA	Diurnal evaporative demand, soil surface run-off, rewetting of previously dried topsoil
One to two days	Cellular "hardening", seed-set, floral initiation, flowering	Weather (cool to hot, dry winds), water infiltration in topsoil
Several days to weeks	Canopy development, leaf senescence, root system development	Deep percolation of soil water
Weeks to months	Clocks controlling development (e.g. fertilization, time to flowering, grain filling	Seasonal evaporative demand, prevailing rainfall pattern

The response of the plant depends on the extent and rate of water loss. A slow rate may permit acclimation to the water deficit and limit the extent of injury, while a rapid rate of loss may preclude acclimation (Leone *et al.*, 1996). The same water deficit in a sensitive species and a resistant species may not trigger the same response (Kahn *et al.*, 1993).

Rapid evaporation from the soil surface may within hours lead to leaf surface drying and heating to potentially lethal temperatures (Howart & Ougham, 1993). On the other hand in slowly intensifying drought, plants modulate their leaf area and thereby adjust the loss of water from the canopy to the supply in the soil (Passioura, 1996). The modulation is presumably brought about either by changes in water status in the growing tissue or by phytohormonal regulation (Mullet & Whitsitt, 1996).

Short-term responses of plants to changes in water status include many physiological, biochemical, and molecular changes. Such changes are not necessarily adaptive in the sense that they contribute to productive processes that lessen the impact of drought on yield. Many of these changes are "housekeeping" activities that prepare the plant for entering a survival mode when the water supply runs out. How to decide which of these changes are important, and which may be treated as little more than "noise", is very difficult (Passioura, 1996).

Abscisic acid exerts both short-term and long-term control over plant development. The long-term effects are mediated by ABA-induced gene expression. ABA stimulates the synthesis of the LEA/RAB/DBN family of proteins during water stress. These proteins may protect membranes and other proteins from desiccation damage. For detailed description of pathways to abscisic acid-regulated gene expression see the review by Rock (2000).

Despite the complex multitude of physiological, molecular, genetic and biochemical data that implicate ABA in stress responses and developmental programs, the adaptive responses of plants to ABA and stresses, and the pathways that trigger them, are largely unknown (Rock, 2000).

3.10 Sorghum cultivar response to drought

Even though sorghum possesses excellent drought resistance compared to most other crops, drought stress is the primary factor that reduces sorghum production worldwide (Rosenow *et al.*, l997c). The crop is commonly grown in regions of the world where water is limiting and, therefore, the crop commonly experiences periods of extreme drought stress at some point within the growing season. Sorghum improvement programs have long realized that enhancing the drought tolerance of sorghum would improve and stabilize yield and increase the productivity of the crop.

Because genotypes respond differently to different types of drought stress, several general types of drought resistance mechanisms in sorghum must be considered. Early research in sorghum indicated that the most effective way to reduce loss due to water- stress was through the use of early maturing genotypes to avoid late

season water stress. (Blum,1979). While technically not a drought resistance mechanism, sorghum production and its growth as a crop in the Midwest US was based on the development of early maturing genotypes that avoided late season drought stress (Smith and Frederiksen, 2001). In many regions of the world, the use of specific maturity types to utilize seasonal rainfall is still a common practice and an important mechanism for controlling losses due to water stress

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While drought escape is a desirable method of controlling losses due to water stress, it is not a feasible method in many areas of the world because of inconsistent weather patterns or the fact that unacceptable yield potential may be lost to avoid drought stress (Dalton, 1967). In these situations, the plant must have the morphological or genetic capability to tolerate the water stress. A significant effort to identify these characteristics, their expression and their genetic control has been undertaken so that the drought tolerance of the crop is further improved (Blum, 1979; Howarth *et al*., 1997; Rosenow *et al*., 1997a-c).

Drought stress response in sorghum depends on the stage of growth in which the drought stress occurs. Pauli *et al*., (1964) divided sorghum growth into three stages. Growth stage 1 (GS1) is the vegetative stage that begins with germination and ends at panicle differentiation. Growth stage 2 (GS2) is the pre-flowering or reproductive phase of growth ranging from panicle differentiation until the cessation of anthesis. Growth stage 3 (GS3) is the post-flowering or grain fill phase that begins immediately after anthesis and continues until physiological maturity of the grain. This division of growth stages is particularly useful in classifying drought reaction, as in each stage the drought resistance reaction is controlled by different genetic mechanisms (Rosenow *et al.,* 1997a-c).

Drought stress tolerance in GS1 is an important trait especially in the harsher production environments and the interaction between genotype and environment begins at planting with the germination process. Sorghum germination is influenced by the amount of available soil water and the genotype of the seedling and the environment in which the seed was produced (Evans and Stickler. 1961; Howarth *et al*., 1997). There have been relatively few reports on variation within sorghum for seedling drought

tolerance. Differences in germination and emergence among genotypes were observed at different levels of soil water stress (Smith *et al.*, 1989; Gurmu and Naylor,1991). Wenzel (1991) reported that additive effects controlled variation for seedling drought tolerance and that the trait was highly heritable. However, the relative magnitude of this effect was minimal compared to the variation observed for soil temperature effects. Significant differences among hybrid genotypes for seedling survival have not been reported in the US (Rosenow *et al*, 1997a-c). For these reasons, research to improve germination and seedling emergence has focused on tolerance to temperature extremes.

In later stages of growth, two distinct types of water stress reaction have been identified and characterized. Both reactions are based on growth stage and have distinct and different phenotypic expressions (Rosenow and Clark, 1981; Rosenow *et al*, 1983;). The pre-flowering stress response occurs when the plant encounters significant drought stress during GS2 prior to anthesis.

Sorghum susceptible to pre-flowering drought stress will exhibit symptoms such as leaf rolling, leaf tip burn, delayed flowering, poor panicle exertion, panicle blasting, and reduced panicle size (Rosenow *et al.*, I997a-c). In a breeding nursery, pre-flowering susceptibility is evident when a characteristic "saddle effect" is observed where panicle development occurs only at the ends of a plot (presumably due to additional soil moisture available in the alleys between plots). Because pre-flowering stress occurs during panicle development, it affects yield potential by influencing panicle size and seed number.

Because of the importance of the trait and its impact on yield, sorghum improvement programs have identified and successfully used numerous source-of resistance to pre-flowering drought stress. These sources of resistance have been utilized by breeders to develop inbred lines, hybrids, and cultivars that have excellent pre-flowering drought stress tolerance. While the physiological basis of pre-flowering drought stress is not well known, the genetics of pre-flowering drought stress have been evaluated. Because the evaluation of pre-flowering drought stress is primarily subjective and is related to numerous phenotypic characteristics, there has been relatively little research to determine the inheritance of the trait (Rosenow *et al.*, 1997a -c).

Literature Review

More recently, the development of molecular marker technology has allowed sorghum breeders to dissect the inheritance of pre-flowering drought tolerance. Tuinstra *et al*. (1996) evaluated a recombinant inbred line population and found six distinct genomic regions that were specifically associated with pre-flowering drought tolerance. These loci accounted for approximately 40% of the total phenotypic variation for yield under drought stress and most of these regions were detectable across environments. Kehede *et al*. (2001) identified four QTLs that controlled pre-flowering drought tolerance in sorghum, but none of the QTLs identified were consistent across all environments. They also noted a strong relationship between QTL for pre-flowering drought resistance and days to flowering.

Post-flowering water stress results from drought stress that is encountered at GS3 during grain fill. Water stress encountered during GS3 can also result in significant reduction in yield, as the plant is unable to completely fill the grain. Sorghum susceptible to post-flowering drought stress will exhibit symptoms such as reduced kernel size, significant leaf and stem death and lodging (Rosenow *et al*., I997a-c). The increase in lodging is due to the plant remobilizing carbohydrate from the stem in an attempt to complete the grain fill process. Once the stem is weakened, charcoal rot (caused by *M. phaxcoliiui*) invades and further weakens the plant, resulting in significant lodging.

Sources of resistance to post-flowering drought stress are less common than those found for pre-flowering drought stress, but breeders have succeeded in identifying genetic resistance to post-flowering drought stress. Because sources of post-flowering drought resistance remain green while susceptible types do not, the resistance to post-flowering drought stress is known as stay-green drought tolerance (Rosenow *et al*., I983). Stay-green genotypes are less susceptible to lodging, more resistant to charcoal rot, and they retain greater green leaf area and higher levels of stem carbohydrates than non stay-green genotypes (Mahalakshmi and Bidinger. 2002).

While sources of post-flowering drought stress are more limited than those for pre-flowering drought stress, there has been substantially more research on the heritability and physiology of post-flowering drought resistance. The genetic control of non-senescence in sorghum has been described both dominant and recessive in terms of inheritance Duncan, (1984). Tenkouano *et al*., (1994) determined that non-senescence was regulated by dominant and recessive epistatic interactions between

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two loci controlling non-senescence. In a diallel analysis, Van Oosterum *et al*. (1996) also found that stay-green was moderately heritable with dominant gene action.

Tuinstra *et al*., (1997) identified 13 regions of the genome associated with at least one measure of post-flowering drought tolerance, but only two of these QTLs were stable across environments with major effects on stay-green and yield. Crasta *et al*., (1999) identified seven genomic regions associated with stay-green in line B35, but only three of these QTLs were stable across environments. These three QTLs also accounted for 42% of the total phenotypic variability for stay-green. Xu *et al*., (2000) also identified several genomic regions with major effects for stay-green. Tao *et al*. (2000) identified two genomic regions that were consistently associated with stay-green response in Australia.

These reports consistently indicate that at least two loci account for a significant amount of the variability associated with stay-green, but there is no way to know if the genomic regions were consistent across studies.

The phenotypic manifestation of pre- or post-flowering drought tolerance is the result of several phenotypic and physiological traits that have been identified and characterized by sorghum physiologists. Traits that have been associated with drought resistance include heat tolerance, osmotic adjustment (Basnayake *et al*., 1995), transpiration efficiency (Muchow *et al*., 1996), rooting depth and patterns (Jordan and Miller. 1980), and epicuticular wax (Maiti *et al*., 1984). The physiological basis of these and other traits associated with drought tolerance has been reviewed by Kreig (1993) and Ludlow (1993). While all of these traits have been associated with drought tolerance in sorghum, most have not been of any practical use in improvement programs because of the difficulty in evaluation and/or selection.

4 Materials and Method

4.1 Experimental Site and Climate

The experiment was conducted in a green house at the Institute of Plant Nutrition (IPE) of the Rheinische Friedrich- Wilhelms-Universität, Bonn in Germany.

Growth conditions were adjusted to day and night temperatures of 42 and 22 respectively and this was monitored by a sixth`s maximum and minimum thermometer hanged in the green house. The kinetics of temperature recorded during the period of the experiment is presented in Figure 1.

The photoperiod was 12 hours, and artificial illumination from 12 HQI or Na 400W lamps was used to supplement daylight. The lamps were programmed to automatically switch on whenever the sunlight was less than 30 klux for a period spanning 30 minutes, and to switch off whenever the sunlight was at least 30 Klux for a period spanning 30 minutes. The uppermost part of the canopy received 650-850 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR) depending on the plant height. Relative humidity during the measurement periods was 50-65%.
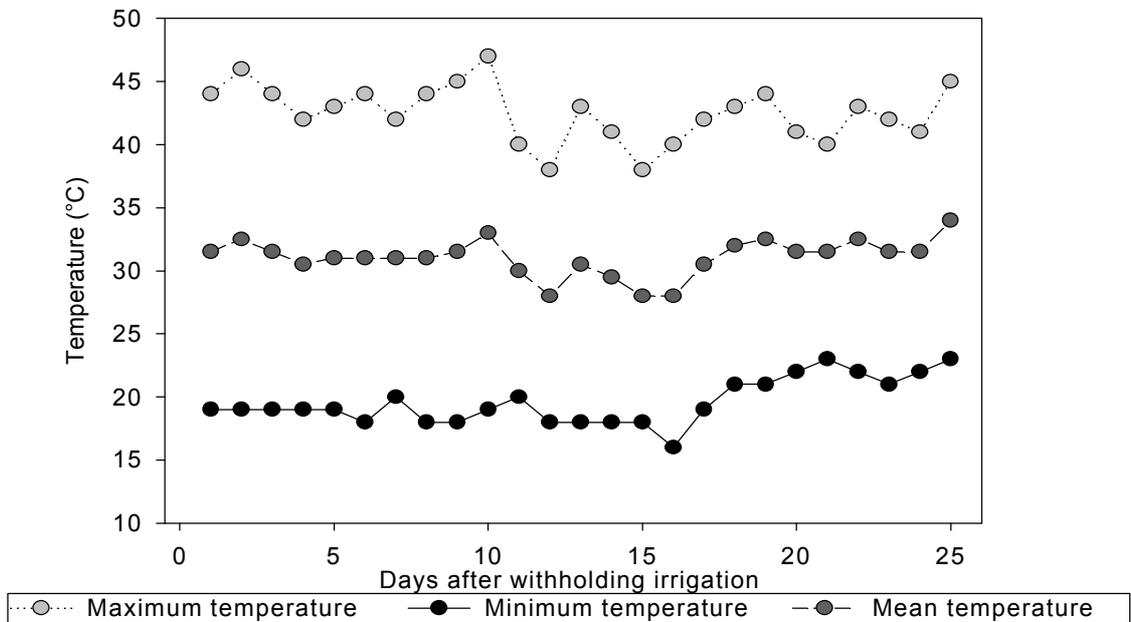
Figure 1: The kinetics of temperature for the duration of the experiment

4.2 Experimental Material and Setup

4.2.1 Treatments

A factorial of two soil types and three water regimes constituted the treatments. The soils were loamy sand and silt loam. The physico-chemical properties of the soils are presented in Table 2.

Table 2: Physico-chemical properties of the soils used for the study.

Parameter	Loamy sand	Silt loam
Organic carbon (%)	0.85	0.77
Clay (%)	5.7	13.9
Silt (%)	18.1	65.3

Each soil type was filled into fifty one pots (one-half the number of pots). The Loamy Sand pots had 11.5 ± 0.01 kg of soil, whiles the Silt Loam pots had 11.0 ± 0.01 kg of soil, since they had different bulk densities but had to occupy the same volume. The three water regimes were "Field capacity" for each of the soils (control), "70% of field capacity" for each of the soils, and "Dynamic drought" (progressing from field capacity to a little above wilting point) for each

4.2.2 Pots

One hundred and two (102) pots were used in the study. Pots were constructed from PVC tubes with 0.15m internal diameter, had capacities of 9 L, and were 0.5m high. Half of the number was filled with each of the two soil types used. For moisture distribution, rooting depth and root distribution studies, the tubes were subdivided into four equal compartments of 0.125m and held together with cello-tape. To ensure homogeneity in the distribution of irrigation water in the pots, funnel-topped silicon tubes

with perforations were inserted through the entire length of the pot (see plate 1). The bottom of each pot was covered with fly mesh fixed with cello-tape to prevent soil loss.

4.2.3 Plant Material

Seed of "ICSV 111 IN" (released as "Kapaala" in Ghana) was obtained from the Sorghum Breeder (Dr I.D.K. Atokple) of Savanna Agricultural Research Institute (SARI), Ghana. The variety is an early-maturing one, developed jointly by ICRISAT and national researchers, which has been adopted by many farmers in sorghum growing areas of West Africa. It is believed to escape rather than tolerate drought because of its earliness.

4.2.4 Experimental Design

Treatments were arranged in a Completely Randomized Design with three repetitions. Each repetition had 34 pots made up 17 pots of each of the soil types. Within each soil type, six (6), five (5), four (4), and two (2) were allotted to dynamic drought, 70% of field capacity, field capacity and estimation of evaporation respectively.

4.3 Cultural Practices

4.3.1 Plant Establishment and Maintenance

Seeds were sown in plastic nursery trays. The trays were filled with the soils used in the study (one for each soil type) before sowing the seed. The trays were watered immediately after sowing and placed in a water bath. Seedling emergence was observed two days after sowing. The seedlings were nursed for two weeks before transplanting. Seedlings with uniform vigor and height were selected, lifted with a ball of soil, and transplanted into the filled pots. Plastic plates with on which three weeping/drainage holes had been drilled were placed on wooden pellets and the pots placed on the plates.

4.3.2 Irrigation and Nutrient Supply

Pot capacity weights were 13.46 ± 0.01 kg and 13.76 ± 0.01 kg for loamy sand and silt loam respectively. (Pot capacity was determined by saturating the pots with water, covering the top with aluminium foil, and weighing daily until there was no further

weight loss). All pots were weighed daily and soil moisture losses due to evapotranspiration were replenished according to the water regimes. An equivalent of 90-45-45 kg ha-1 N-P-K was applied in two equal doses (2 weeks and 6 weeks after transplanting).

4.4 Observations, Estimations, and Measurements

4.4.1 Soil water content determination

The soil moisture content was determined using the lysimeter method. The field capacity was determined by saturating the soils in the pot, covering the tops with aluminium foil, and weighing daily until there was no weight loss within a 24-hour period. The pots were weighed daily and the amount of water lost replaced by irrigation according to the treatments. Relative available soil moisture (RASM) was calculated from actual soil water content ($?_{actual}$) and the soil water content at field capacity ($?_{f.c.}$) and at permanent wilting stage ($?_{p.w.}$) according to Jensen *et al*. (1998) as: RASM = ($?_{actua}$ - $?_{p.w}$)/($?_{f.c}$ - $?_{p.w}$).

4.4.2 Plant data

Data were collected on plant height, number of leaves and leaf area. The plant height was measured (in centimeters) from the base of the plant to the tip of the highest leaf using a ruler. This was done weekly from the onset of the drought treatments until the last sampling was done. Data on number of leaves were recorded only at sampling. This therefore indicates the number of green leaves rather than the total number of leaves produced. Leaf area data were collected using a leaf area meter model LI-3000A (LI-COR, Inc., Lincoln, Nebraska). These were the green leaf areas at the time of sampling only, but the dry or wilted leaves were added for determining the leaf dry matter. The shoots were separated into stems and leaves, and dried to a constant weight at 70°C. SPAD readings were taken on two leaves (the youngest fully developed and the third fully developed).using a "Minolta Chlorophyll meter" model SPAD 502 (Japan). The two leaves were cut, put into plastic bags after measuring their water potentials, and stored in a freezer at -20°C for further analysis later. After the analysis, the two leaves were dried, weighed and their weights added to that of their respective samples.

4.4.3 Gas exchange

Photosynthetic rate, transpiration rate, stomatal conductance and stomatal resistance were measured from the middle of the youngest fully developed and the third youngest leaves, between 12:00PM and 2:00PM, using a leaf chamber analyser model LCA-4 (Analytical Development Company Bio-Scientific Ltd., England) These measurements were made on intact leaves.

4.4.4 Water potentials

The soil water potentials were estimated according to Saxton *et al*. (1986), as a function of soil water content and soil textural properties. Root water potentials and leaf water potentials were determined using Scholander type pressure chambers of different sizes. The small one (industrial product) was used for determining leaf water potentials, while the big one (custom made copy of the industrial one) was used for determining root water potentials and for sampling xylem sap.

The entire pot was sealed into the pressure chamber and the stem was cut a few centimeters above the lid. Pressure was applied up to the balancing pressure, and the root water potential (in bars) was read from a manometer. In the case of leaf water potentials, the leaves were sealed in the chamber with some few centimeters of the mid rib protruding out. The same procedure as for the root water potentials determination was used.

4.4.5 Xylem sap collection

To sample xylem sap, tight fitting silicon tubes were fitted on top of the cut stem after the root water potential was determined and the first drop of exudates blotted away. The pressure was increased to root water potential plus a maximum of 20%, and the xylem sap collected with syringe pipettes into well labeled 1.5mL Eppendorf vials. Sampling was stopped when the vial was filled or after 15 minutes, depending on which came first, and the Eppendorf vial put immediately into insulated box filled with ice. The vials were at the end of the day's sampling, transferred to a freezer and stored at -20°C for later analysis.

4.4.6 Determination of moisture and root distribution

To determine the moisture distribution within the soil columns in the pots, the cello-tapes were removed and the pots separated into the four compartments. Each compartment was weighed and representative samples of the soil taken with pre-weighed scintillation vials with their tops cut. The vials containing the wet soil were weighed and oven dried at 70°C to constant weight. The dry weight was determined using a precision balance. The moisture content within each compartment was expressed in gg^{-1} dry soil basis.

The distribution of roots within the compartments was also determined and recorded as root dry matter (g). The compartments were placed over 2mm sieves and the soil washed out with running water. The roots were collected into well labeled envelopes, oven dried at 70°C to a constant weight, and weighed with a precision balance.

4.4.7 Osmotic potential of leaves and ABA content of xylem sap

To determine the leaf osmotic potential, the frozen leaves were immersed in liquid nitrogen and placed on blotting paper to thaw. The thawed leaves were put into a garlic press and the sap pressed into an Eppendorf vial. The sap was centrifuged at 10000 rpm for 5 minutes to produce a clear supernatant. 20µL of the clear sap was put into a cryoscopic osmometer model OSMOMAT 030-D (GONOTEC GmbH, Germany) for determining the osmotic potential in "Osmol/Kg. The readings were converted to MPa using the appropriate conversion factors. The ABA content of the xylem sap was determined using an indirect Enzyme Linked Immuno-sorbent Assay (ELISA) procedure according to Asch (2000).

Statistical analyses (ANOVA and mean separation) were carried out with the SPSS software (version 11.5, SPSS Inc., Chicago, USA) whiles all graphs were made with the Sigma plot 7.0 (Systat Software, Inc.) One standard error of means was used as error bars where needed.

Plate1

Plate 2

Plate 3

Plate 4

Plate 5

Plate 1:   Inserting an irrigation tube

Plate 2:   Determining Field Capacity

Plate 3:   Complete setup

Plate 4:   Pots for estimating evaporation

Plate 5:   Industrial Pressure bomb used for determining leaf water potentials

5 Results

5.1 Experimental set-up and moisture distribution

The aim of the study was to investigate morphological and physiological responses of sorghum plants sown in pots filled with loamy sand or silt loam, and subjected to three different moisture regimes: (1) progressive deficiency of moisture to levels slightly above permanent wilting point, (2) constant sub lethal deficiency and (3) optimal water supply. Unless otherwise stated, p-values for significantly different parameters are = 0.05.

Soil moisture status

The study was carried out under high evaporative demands with actual evapotranspiration values for the under field capacity conditions ranging from 8.3 mm to 30 mm/day. Figure 2 (a, b) shows the daily soil moisture contents as influenced by sorghum plants in loamy sand and silt loam under the three moisture regimes. Three days after withholding irrigation, pots dried down to the moisture contents required for the constant drought treatment in both soils.

At the onset of the progressive drought treatments (day 0), the soil water content, ranged from 13% to 19% and from 19% to 27% on loamy sand and silt loam respectively. Pots filled with silt loam had significantly higher moisture contents than those filled with loamy sand. Pots treated to progressive drought (PD) and field capacity (FC) had similar moisture contents. At this point in time, these contained significantly more moisture than the pots treated to constant drought (CD). Moisture content did not differ significantly among the combined effects of soil type and moisture regime at this point in time.

Figure 2 (c, d) shows the kinetics of relative available soil moisture (RASM) as a function of treatments over time. In the pots subjected to FC conditions for both soil types, relative available soil moisture (RASM) was maintained above 80% during the experiment. Under CD conditions, RASM was maintained above 50% on both soils throughout the experiment (Figure 2a, b). Fourteen days after starting the PD treatments, RASM decreased from 88% to 3% and 2.4% in the pots filled with loamy

sand and silt loam respectively (Figure 2c, d), and the pots were re-watered to field capacity level at this point in time.

The kinetics of soil water potential (SWP), as influenced by treatments over time is presented in Figure 2 (e, f). On loamy sand, SWP ranges were -0.01MPa to -0.02MPa, -0.04MPa to -0.17MPa, and -0.009MPa to -3.17MPa for FC, CD and PD conditions respectively. On silt loam, the respective ranges of SWP for FC, CD and PD conditions were -0.03MPa to -0.05MPa, -0.04MPa to -0.0.17MPa and -0.02MPa to -2.32MPa. For the first nine days of the drying cycle, SWP under PD conditions was lower in pots filled with silt loam than in those filled with loamy sand. This trend was reversed between the ninth and fourteenth day, and reverted back to the first trend after re-watering.

Soil drying rates under progressive drought

Soil moisture contents, (as percentages of the FC), were similar on both soils during the first two days, higher on loamy sand than on silt loam from the third to the sixth day, and higher on silt loam than loamy sand until re-watering on the fourteenth day (Figure 3a). The rate of decrease in soil moisture was very similar on both soils throughout the drying cycle, except on the sixth day when it was strikingly higher on the loamy sand (Figure 3b). Soil moisture content was significantly higher in the pots filled with silt loam than in the pots filled with loamy sand from the second day of the drying cycle until re-watering.
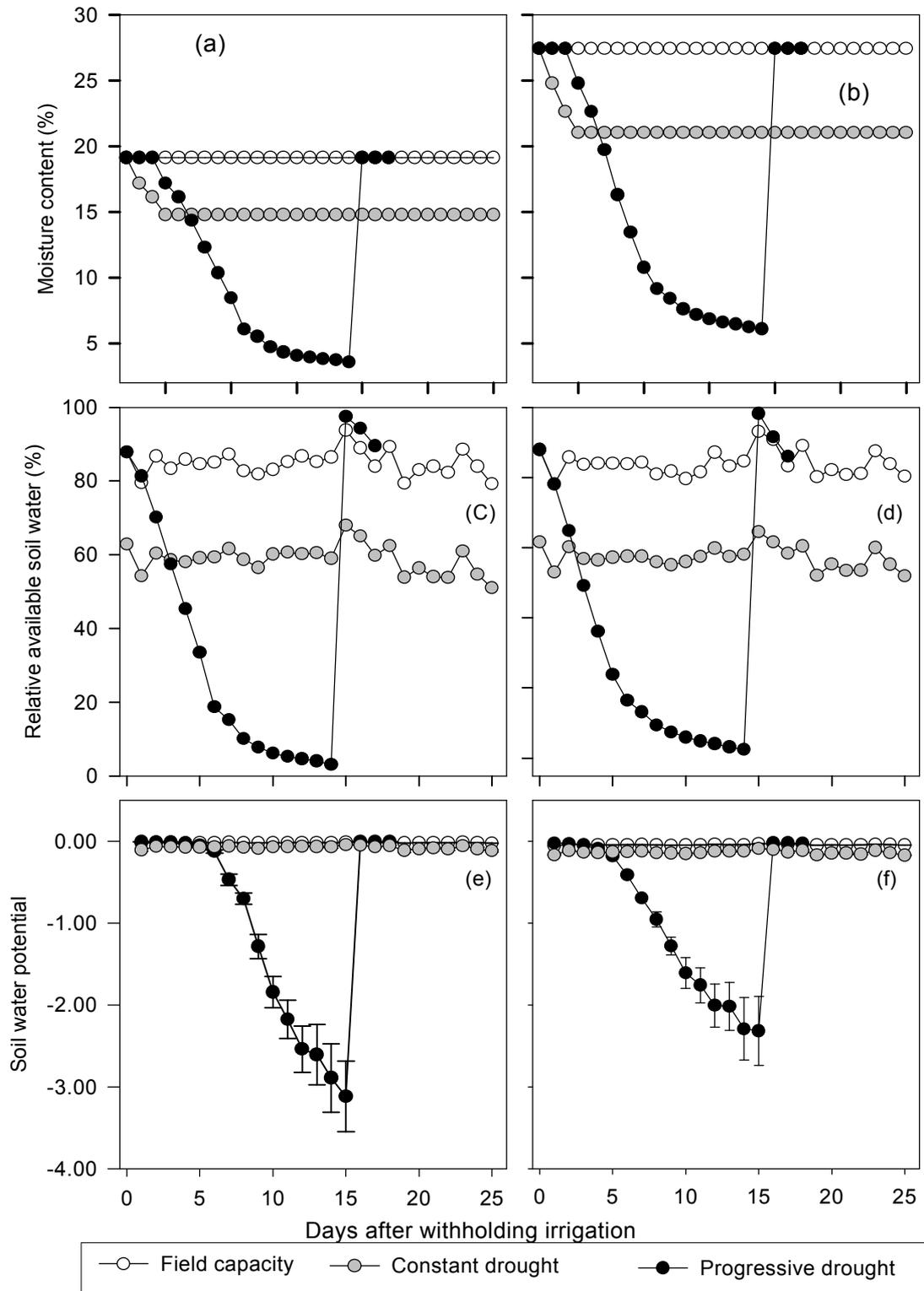
Figure 2. Kinetics of soil moisture content (a, b), relative available soil moisture (c, d) and soil water potential (e, f) as influenced by sorghum planted on loamy sand(a, c, e) and silt loam (b, d, f) and subjected to three different moisture regimes
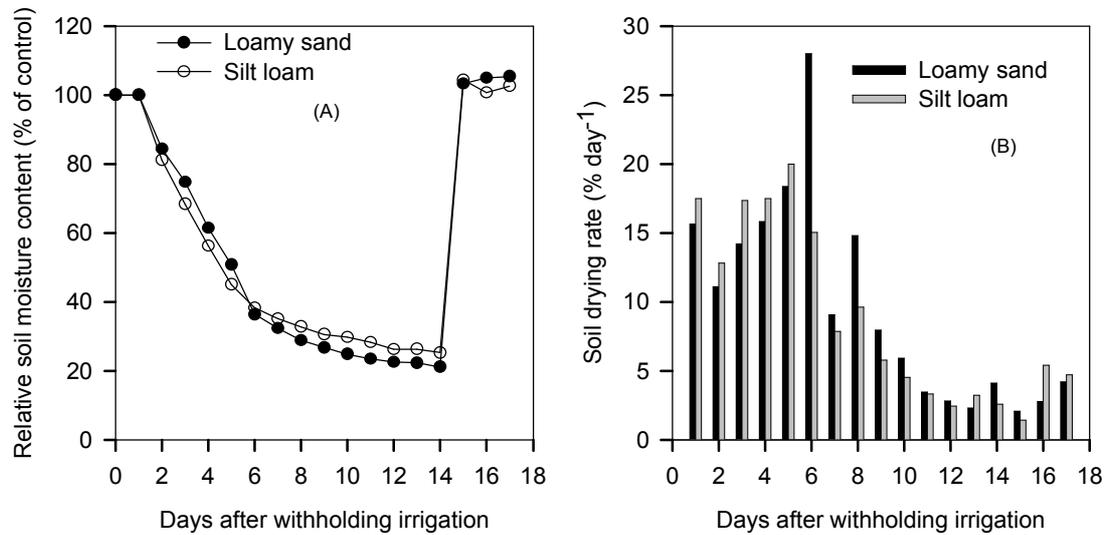
Figure 3. Time course of the relative soil moisture contents (A) and drying rates (% day-1) (B) of pots sown with sorghum and treated to progressive drought on loamy sand and silt loam

5.2 Vertical distribution of soil moisture in pots

Field capacity

The distributions of moisture (for the different sampling days) within the profiles of the pots filled with the two types of soil (loamy sand and silt loam) and subjected to three different moisture regimes (FC, CD and PD) are presented in Figure 4.

On loamy sand, moisture distribution patterns under FC conditions were similar for all the sampling days. Moisture content increased with depth, and the moisture contents of the top two compartments (0-000-0.250m) were similar. The moisture contents of the last two compartments (0.251-0.500m) were also similar, and more than the top two compartments Figure 4a. The moisture distribution patterns for FC conditions were also similar (nearly uniform) on all the sampling days in pots filled with silt loam Figure 4b.

Constant drought

Figure 4 (c, d) shows the moisture contents, within the different compartments of the pots subjected to constant drought (CD), for the sampling days. On loamy sand, moisture contents of the top two compartments were similar but lower than that of the last two compartments (which were also similar) at the onset of progressive drought treatments. For the rest of the sampling days, the moisture contents were more or less similar in all the compartments (Figure 4c).

The distribution of moisture in silt loam was nearly uniform for the constant drought treatment, apart from the tenth day after starting drought when moisture content appeared to decrease with depth of pot (Figure 4d)

Progressive drought

Figure 4 (e, f) shows the distribution patterns of moisture, in the pots subjected to progressive drought, during the sampling days. The moisture distribution in the pots filled with loamy sand was variable, but most of the days, more moisture was found in the lowest compartment than the others. The first and second compartments had more or less similar moisture contents, apart from the sixth day after starting progressive drought when the first had lower moisture content than the second one (Figure 4e).

For all the sampling days, moisture content was nearly similar in all the compartments for the pots filled with silt loam (Figure 4f).
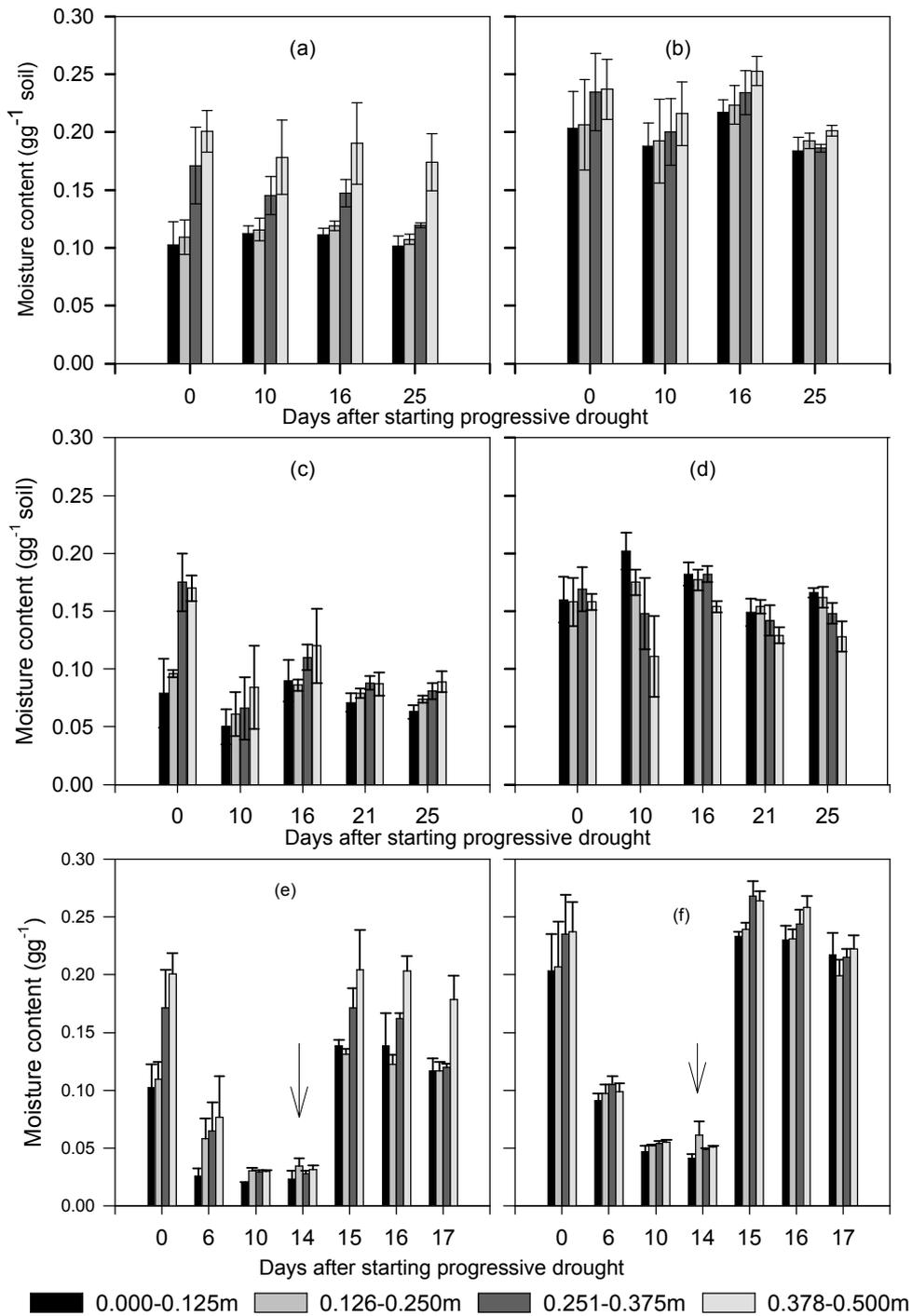
Figure 4. Vertical distribution (on sampling dates) of soil moisture within pots filled with loamy sand (a,c&e) and silt loam (b,d&f), sown to sorghum, and subjected to field capacity (a,b), constant drought (c,d) and progressive drought conditions (e,f) conditions. (Bars indicate S.E. of mean, n=3). Arrows indicate re-watering point for pots subjected to progressive drought conditions.

5.3 Plant Growth and Dry Matter Accumulation and Partitioning

5.3.1 Total dry matter

The kinetics of dry matter accumulation by sorghum, as affected by moisture regime on loamy sand and silt loam for the duration of the experiment, is presented in Figure 5(a, b).

Total dry matter accumulation at the onset of the drought treatments ranged from 25g (FC and PD on loamy sand) to 41g (FC and PD on silt loam). Total dry matter differed significantly among the soil types; with the plants on silt loam accumulating more dry matter than the plants on loamy sand. However, differences in total dry matter among moisture regimes or among the combined effects of soil types and moisture regimes were not significant at this point in time.

Ten days after imposing the drought treatments, total dry matter accumulated by the plants ranged from 32g to 62g. The difference in total dry matter as affected by soil type was significant; with the plants on silt loam accumulating more dry matter than the plants on loamy sand. At this same time, total dry matter was not affected differentially by either moisture regime or the combined effects of soil types and moisture regimes.

The total dry matter on the sixteenth day after starting drought (i.e. two days after re-watering the PD treated pots), was between 39g and 77g. Mean total dry matter for pots filled with silt loam was significantly greater than for the pots filled with loamy sand. Differences in total dry matter, as affected by moisture regimes, were also significant; with the mean total dry matter for pots subjected to FC being significantly greater than the means of the pots subjected to CD or PD, whiles the mean total dry matter for pots treated to CD was also significantly greater than that of pots subjected to PD. At this point in time, the differences in total dry matter as affected by the combined effects of soil types and moisture regimes were not significant. It was clear from the trend that the plants treated to CD adapted to the moisture levels.

5.3.2 Root dry matter

Root dry matter data are presented in Figure 5(c, d). The values of root dry matter per pot ranged from 7g to 15g at the onset of drought treatments. Root dry matter for pots filled with silt loam was significantly higher than for pots filled with loamy sand, but the differences in root dry matter, as affected by moisture regimes or by the combined effects of soil type and moisture regime, was not significant.

Ten days after the onset of drought, root dry matter per pot ranged from 11g to 24g. Pots filled with silt loam produced significantly higher root dry matter than pots filled with loamy sand, but neither moisture regime nor the combined effects of soil types and moisture regimes affected root dry matter differentially.

Two days after re-watering the pots treated to PD (after a fourteen-day drying cycle), root dry matter per pot ranged from 15g to 26g. Root dry matter on silt loam was significantly higher than that of loamy sand. Differences in root dry matter, as affected by moisture regimes, were also significant at this point in time. The pots subjected to FC had significantly higher root dry matter than those subjected to CD or PD (which had similar root dry matter). Differences in root dry matter, among the combined effects of soil types and moisture regimes, were not significant at this point in time.

5.3.3 Root-shoot ratio

The time courses of root-shoot ratio, as affected by the moisture regimes on loamy sand and silt loam, are presented in Figure 5(e, f). At the onset of progressive drought, root-shoot ratios ranged between 0.40 and 0.55; with neither soil type nor any other factor affecting this parameter differentially.

Ten days after imposing progressive drought treatments, root-shoot ratios ranged from 0.46 to 0.78. Differences in root-shoot ratio, as affected by soil type, were not significant, but the differences in root-shoot ratio as affected by moisture regimes were significant at this point in time. Plants subjected to FC and CD had similar mean root-shoot ratios that were significantly lower than that for plants subjected to PD. At this point in time, none of the combinations of soil types and moisture regimes influenced root-shoot ratio differentially.

Two days after re-watering the PD treated pots, root-shoot ratios ranged from 0.50 to 0.67; At this point in time, differences in root-shoot ratio among soil types, and among the different levels of the other factors studied, were not significant.

5.3.4 Plant height

The height of sorghum as affected by moisture regime on loamy sand and silt loam are presented in Table 3. At the onset of drought treatments (i e 43 days after transplanting) mean plant height ranged from 131cm to 144cm. Plant height differed significantly among the soil types ($p < 0.05$), with plants on silt loam being taller than those on loamy sand. Differences in plant height were significant ($p < 0.05$) among the moisture regimes. Plants from pots subjected to FC and PD (same at this stage) were significantly taller than those subjected to CD, but the differences in heights among the combined effects of soil type and moisture regime were not significant at this point in time.

Seven days after the onset of progressive drought treatments, mean plant heights were between 139cm and 153cm. Differences in plant heights were significant among the water regimes ($p = 0.05$), but non-significant among the soil types ($p = 0.05$) and the combined effects of soil type and moisture regime ($p = 0.05$). Plants subjected to FC and PD (with similar heights), were significantly taller ($p = 0.05$) than those subjected to CD at this point in time.

Fourteen days after the onset of progressive drought treatments, plant heights were between 146cm and 167cm. Differences in plant heights, among soil types, were not significant ($p = 0.05$), but were significant among moisture regimes ($p = 0,05$) and among the combined effects of soil type and moisture regime ($p = 0,05$). The plants subjected to FC were significantly taller than the others, while those subjected to CD were also significantly taller than the plants subjected to PD. The pattern was FC > CD > PD. Same patterns as above, were found for the heights of plants as affected by the combined effects of moisture regime and each of loamy sand and silt loam.
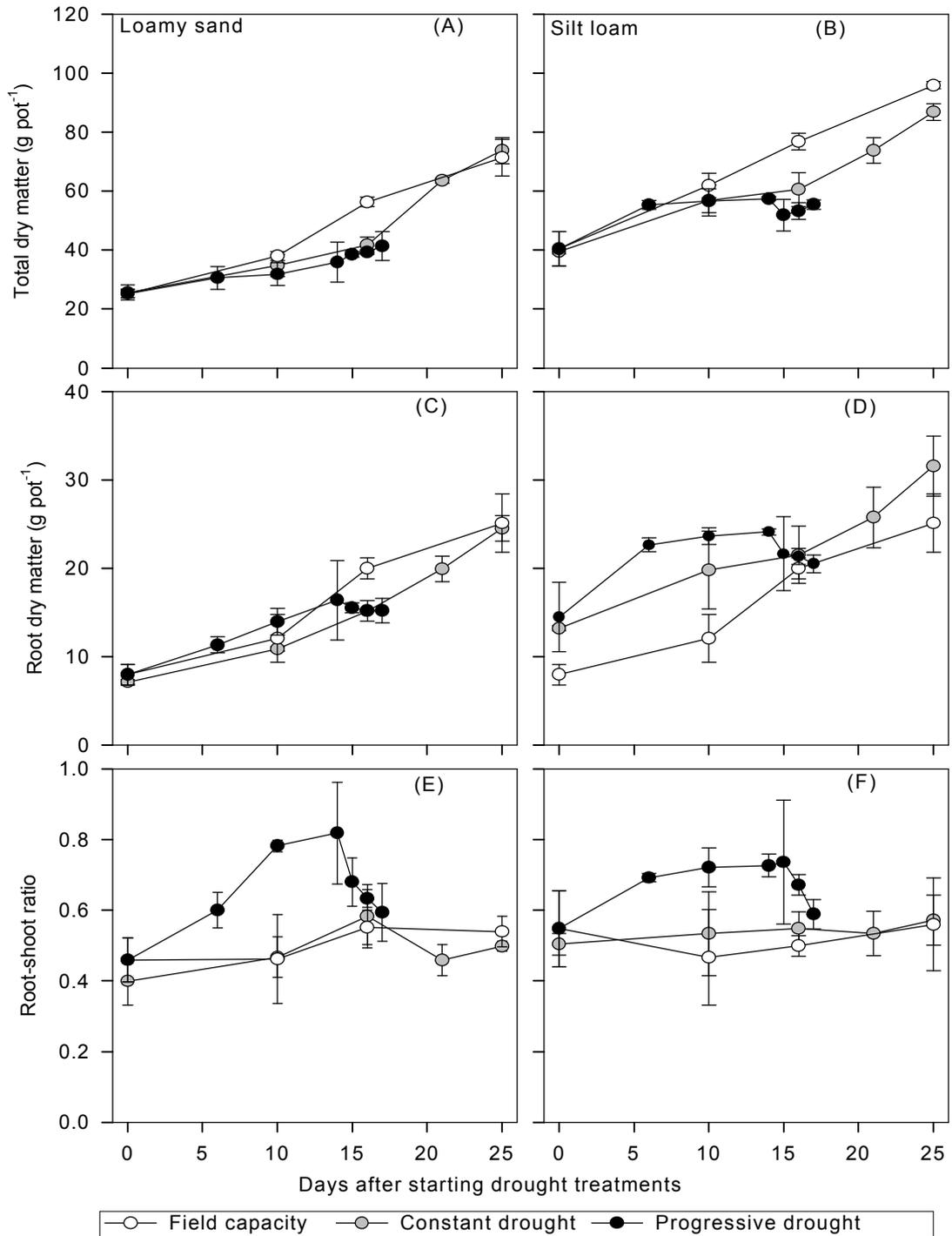
Figure 5. Time courses of total dry matter (a, b), root dry matter (c, d) and root-shoot ratio of sorghum subjected to three different moisture regimes in pots filled with loamy sand and silt loam. (Bars indicate S.E of means, n=3). Arrows indicate days for re-watering pots subjected to PD conditions.

Table 3: Plant height (cm) of a sorghum cultivar grown under field capacity (FC), 70% of field capacity (CD), and dynamic drought (PD) on loamy sand and silt loam. N=3.

Soil	Moisture	43 DAT		50 DAT		57 DAT	
		Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	136	4	153a	1	167	1
	CD	131	2	139c	2	146	2
	PD	136	4	152a	3	158	2
Silt loam							
	FC	144	3	151a	3	166	2
	CD	136	1	144b	1	152	1
	PD	144	3	152a	3	157	2

5.3.5 Leaf area

At the onset of progressive drought the area of the youngest fully extended leaf (L1) ranged from 293 cm^2 (FC and PD on loamy sand) to 405 cm^2 (CD on silt loam) Table 4, whiles that of the third youngest fully extended leaf (L2) ranged from 240 cm^2 (FC and PD on loamy sand) to 343 cm^2 (FC and PD on silt loam) Table 5.

Table 4: Kinetics of mean area (cm2) for the youngest fully extended leaf, during the sampling days, as affected by moisture regime in pots filled with loamy sand or silt loam

		Onset		10DAWI		16 DAWI	
Soil	Water	Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	293	31	315	26	287	21
	CD	310	20	289	28	261	7
	PD	293	21	329	82	325	11
Silt loam							
	FC	376	30	357	25	327	15
	CD	405	52	362	35	333	20
	PD	376	30	393	20	333	22

Results

The area of the total green leaf (TGL) per pot ranged from 2224 cm^2 (FC and PD on loamy sand) to 3183 cm^2 (FC and PD on silt loam) Table 6. Differences in area, as affected by soil type, were significant, for each of L1, L2, and TGL; with the areas from pots filled with silt loam being significantly greater than areas from pots filled with loamy sand for all the three parameters.

Table 5: Kinetics of mean area (cm^2) for the third youngest fully extended leaf, during the sampling days, as affected by moisture regime in pots filled with loamy sand or silt loam

		Onset		10DAWI		16 DAWI	
Soil	Water	Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	240	43	294	12	292	17
	CD	254	5	248	99	275	12
	PD	240	43	183	92	147	17
Silt loam							
	FC	343	6	409	32	397	30
	CD	287	25	400	43	392	25
	PD	343	6	295	97	128	2

At the time of starting the drought treatments, differences in area, as affected by moisture and also the combined effects of soil type and moisture regime, were not significant for each of L1, L2 and TGL.

The area of L1 was significantly greater than the area of L2 on both soil types. For moisture regime effects, the area of L1 and L2 were similar for pots subjected to FC or PD, but the area of L1 was significantly greater than L2 for pots subjected to CD.

Ten days after starting drought treatments, leaf areas ranged from 288 cm^2 to 395 cm^2 for L1, from 183 cm^2 to 408 cm^2 for L2 and from 1594 cm^2 to 3089 cm^2 for TGL. Though no significant differences were found in the area of L1 as affected by soil type, differences in areas of both L2 and TGL (as affected by soil type) were significant. The areas of L2 or TGL for pots filled with silt loam were significantly greater than areas for pots filled with loamy sand. Leaf areas of either L1 or L2 did not differ among the moisture regimes, but that of TGL (as affected by moisture regime) differed significantly

at this point in time. Differences in areas of L1 or L2, as affected by the combined effects of soil type and moisture regime, were not significant, but the area of TGL (as affected by the combined effects of soil type and moisture regime) differed significantly.

Sixteen days after imposing drought (two days after re-watering of PD pots), leaf areas ranged from 260 cm^2 (CD on loamy sand) to 332 cm^2 (FC on silt loam) for L1, 52 cm^2 (PD on loamy sand) to 397 cm^2 (FC on silt loam) for L2, and from 1608 cm^2 (PD on loamy sand) to 3563 cm^2 (FC on silt loam) for TGL. The differences in areas of L1, L2 and TGL, as affected by soil type, were significant; with the areas from pots filled with silt loam being greater than those of pots filled with loamy sand for all the three leaf parameters (L1, L2 and TGL).

Table 6: Kinetics of mean area (cm^2) for total green leaves, during the sampling days, as affected by moisture regime in pots filled with loamy sand or silt loam

		Onset		10DAWI		16 DAWI	
Soil	Water	Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	2224	392	2272	217	2367	8
	CD	2424	167	2481	51	2675	30
	PD	2224	392	1468	60	1496	79
Silt loam							
	FC	3183	211	3340	74	3563	54
	CD	3182	46	3274	80	3356	86
	PD	3183	211	1931	166	2146	81

5.4 Plant water household

5.4.1 Root water potential

The time course of root water potential (RWP) as affected by treatments, for the two different soils is presented in Figure 6. At the onset of the drought treatments, root water potentials ranging between -0.27 MPa (CD on silt loam) and -0.17 MPa (FC on loamy sand) were measured. At this point in time, RWP did not differ significantly

among the levels of any of the factors (soil type and moisture regime) and the combined effects of the factors.

Ten days after imposing the treatments, root water potentials ranged from -2.3 MPa (PD in silt loam) to -0.16 MPa (CD on loamy sand). RWP differed significantly among soil types; with plants grown in pots filled with loamy sand having significantly higher RWP than those grown in pots filled with silt loam. RWP also differed significantly among moisture regimes. Plants subjected to FC and CD (with similar RWP) had significantly higher RWP than those subjected to PD. At this point in time, RWP did not differ significantly among the combined effects of the factors (soil type and moisture regime). CD increased RWP from -0.31 MPa (FC) to -0.16 MPa in pots filled with loamy sand and from -0.40 MPa (FC) to -0.32 MPa in pots filled with silt loam. On the other hand, PD reduced RWP to -2.05 MPa and -2.30 MPa in pots filled with loamy sand and silt loam respectively.

Sixteen days after imposing moisture treatments (two days after re-watering PD pots), RWP ranged from -0.10 MPa (FC on loamy sand) to -0.45 MPa (PD on silt loam). RWP did not differ significantly among soil types, but differed significantly among the moisture regimes; with plants subjected to FC and CD (which had similar RWP) having significantly higher RWP than plants subjected to PD. RWP did not differ among the combined effects of the factors (soil type and moisture regime). CD and PD reduced RWP from -0.1 MPa (FC) to -0.2 MPa and -0.4 MPa respectively on loamy sand, and the corresponding reductions were from -0.19 MPa (FC) to -0.28 MPa and -0.45 MPa respectively on silt loam.

Figure 7 shows the time courses of leaf water potentials (LWP) measured in leaves of sorghum plants subjected to three moisture regimes on loamy sand and silt loam. At the onset of the treatments, water potentials ranged from -1.27 MPa (FC on loamy sand) to -1.18 MPa (FC on silt loam) for the youngest fully extended leaf (L1) and from -1.18 MPa (FC on silt loam) to -0.98 MPa (CD on silt loam) for the third youngest fully extended leaves (L2). LWP of each of the two leaves (L1 and L2) did not differ significantly among the levels of the factors (soil type and moisture regime) and also the combined effects of the factors.
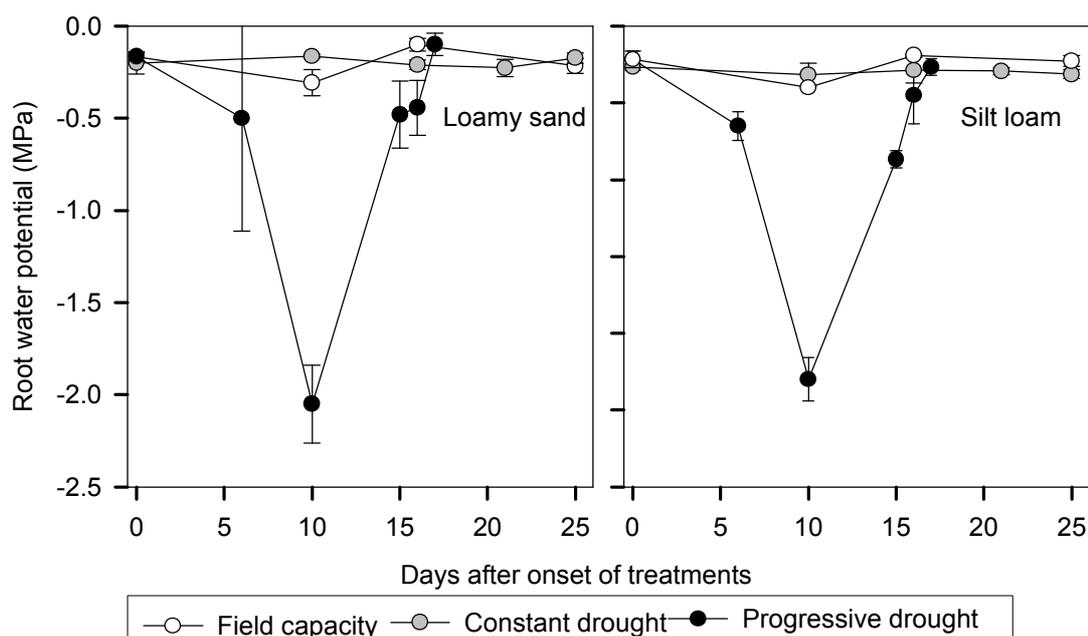
Figure 6: Time course of root water potentials for sorghum planted on loamy sand and silt loam under different moisture regimes. (Bars indicate SE of means, n = 3).

5.4.2 Leaf water potential

At the onset of drought treatments, no significant difference in LWP was found between L1 and L2 on loamy sand (p = 0.236), but the LWP of L2 was significantly (p = 0.037) higher than L1 on silt loam. No significant differences in LWP were found between L1 and L2 subjected to FC (p = 0.223), CD (p = 0.200) and PD (p = 0.223).

Ten days after starting progressive drought, LWP ranged from -2.35 MPa (PD on silt loam) to -0.49 MPa (FC on silt loam) for L1 and from -2.63 MPa (PD on silt loam) to -0.69 MPa (FC on silt loam) for L2. LWP, for either of the two leaves sampled, did not differ significantly among soil types. However, it differed significantly among the different moisture treatments for both leaves. The mean LWP of the leaves from pots subjected to FC was significantly higher than that of the leaves from pots subjected to either of CD and PD. On the other hand, the mean LWP of leaves from pots subjected to CD was significantly higher than that of those subjected to PD. In other words, LWP decreased with moisture regime in the order of FC, CD and PD.

LWP differed significantly, among the combined effects of soil type and moisture regime, for both L1 and L2. In pots filled with loamy sand, LWP of L1 was decreased,

from -1.33 MPa (FC) to -1.43 Mpa and -1.92 MPa by CD and PD respectively. On silt loam, the LWP of L1 was decreased from -0.49 MPa (for FC) to -1.32 MPa and -2.35 MPa by CD and PD respectively. LWP of L2 was reduced by CD and PD from-1.17 MPa (for FC) to -1.53 MPa and -1.95 MPa respectively on loamy sand, and from -0.69 MPa (for FC) to -1.21 MPa and -2.63 MPa respectively on silt loam. At this point in time (ten days after onset of treatments) LWP did not differ significantly between L1 and L2 for both soil types and moisture regimes.

Sixteen days after the onset of drought (two days after re-watering PD pots), LWP ranged from -1.58 MPa to -0.36 Mpa for L1 and from -1.44 MPa to -0.22 MPa for L2. For both leaves, LWP did not differ significantly among soil types, but the differences in LWP among moisture regimes were significant for both leaves. CD and PD reduced the LWP for L1 from -0.44 MPa for FC to -1.32 MPa and -1.44 MPa respectively. For L2, the LWP of -0.37 MPa for FC was significantly reduced by CD and PD to -1.12 MPa and -1.78 MPa respectively. The reduction in LWP of L2 was significantly higher under PD than under CD.

LWP differed significantly among the combined effects of soil type and moisture regime for both L1 and L2. LWP for both L1 and L2 were significantly reduced by CD and PD, compared to FC, in the all the pots at this point in time (sixteen days after starting drought). On loamy sand, CD reduced LWP for L1 and L2 from -0.53 MPa (for FC) to -1.34 MPa and -1.19 MPa respectively. PD on the other hand, reduced LWP for L1 and L2 from -0.53 MPa (for FC) to -1.29 MPa -1.44 MPa respectively. On silt loamy, LWP of L1 was reduced, by CD and PD, from -0.36 MPa (for FC treatment) to -1.30MPa and -1.58MPa respectively, whiles the respective reductions for L2 were from -0.22 MPa to -1.04 MPa and -2.11 MPa.

LWP differences between L1 and L2 were not significant on both loamy sand and silt loam. For FC and PD treatments, LWP differences between L1 and L2 were not significant, but LWP for L1 was significantly higher than that of L2 under CD treatment.

It was clear that the leaves had different sensitivity to changes in root zone water content; with L1 being more sensitive than L2, and the responses in pots filled with loamy sand lagged a little behind those in pots filled with silt loam.
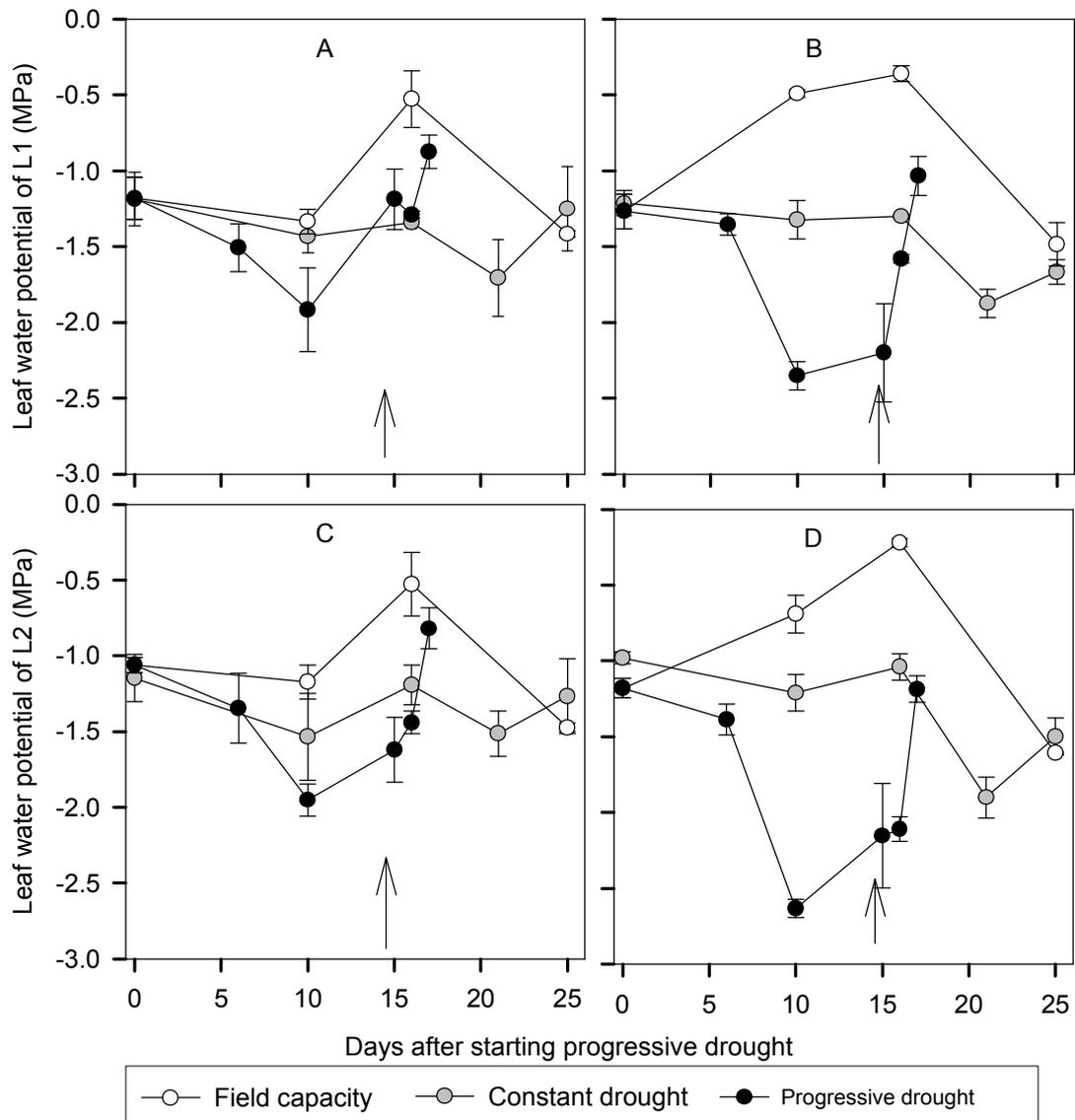
Figure 7: Time course of leaf water potentials for the youngest fully extended leaf (L1) and the third youngest fully extended leaf (L2) of sorghum grown on loamy sand (A&C) and silt loam (B&D) under three different moisture regimes. (Bars indicate S.E. of means, n = 3) Arrows indicate rewatering.

5.4.3 Leaf Osmotic Potential

The time course of leaf osmotic potential (LOP) of the youngest fully extended leaf, as affected by different moisture regimes on loamy sand or silt loam is presented in Figure 8. On loamy sand, LOP did not differ significantly among the moisture regimes at

the onset of drought treatments. LOP was lower for CD conditions in the pots filled with silt loam, at this point in time, but the differences were not significant.

Ten days into the drying cycle, LOP was similar for CD and FC conditions on both soils, with PD conditions having lower LOP, but the differences were also not significant. One day after re-watering the pots subjected to PD conditions, LOP was restored to a level higher than even for the pots subjected to FC conditions on loamy sand, but LOP for the pots filled with silt loam and subjected to PD conditions were still lower at this point. By the third day after re-watering, LOP was at FC levels in both CD and PD treated pots on the two soil types. The trend observed in the dynamics of LOP did not differ much from that observed for LWP, except for the fast restoration of water status in the pots filled with loamy sand.
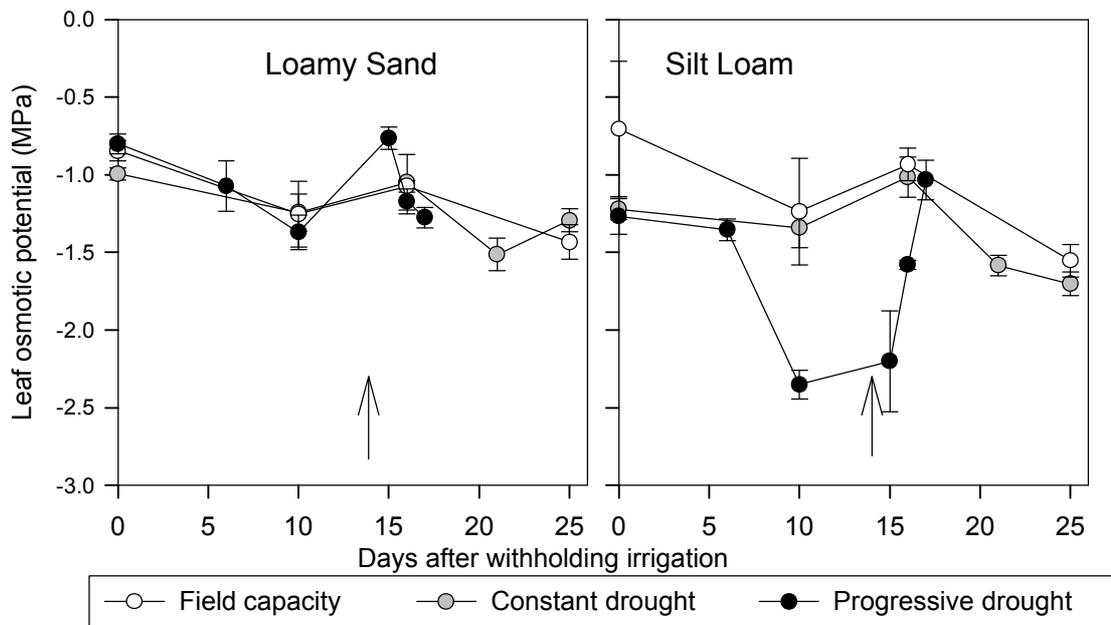
Figure 8: The time course of osmotic potential of the youngest fully extended leaf, as affected by three different moisture regimes in pots filled with loamy sand or silt loam. (Bars indicate S.E of mean, n=3). Arrows indicate days of re-watering pots subjected to PD conditions.

5.5 Gas exchange

5.5.1 Net photosynthesis rate

The net photosynthesis rates per unit of leaf area, on the sampling dates, as influenced by moisture regime in pots filled with loamy sand or silt loam are presented on Table 7.

At the onset of progressive drought, net photosynthesis rates ranged between 6.50 μmol m^{-2}s^{-1} and 9.95μmol m^{-2}s^{-1}. Net photosynthesis was similar for the two soils, but differed significantly among the moisture regimes. Plants under FC conditions (same as PD at this point) had significantly higher net photosynthesis than those subjected to CD conditions. The interactive effects of soil type and moisture regime did not affect photosynthesis rate differentially at this point in time.

Ten days after the onset of drought, net photosynthesis rates ranged between 4.42μmol m^{-2}s^{-1} and 11.91μmol m^{-2}s^{-1}, was similar for the two soils, but differed significantly among moisture regimes. Net photosynthesis rates under CD and PD were similar, but significantly lower than those under FC conditions. Net photosynthesis rates did not differ significantly among the interactive effects of soil types and moisture regimes.

Table 7: Net photosynthesis rate (μmol m^{-2} s^{-1}) of sorghum, on sampling days, as affected by moisture regimes on loamy sand and silt loam

Soil	Water	Onset		10DAWI		16DAWI	
		Mean	S.E	Mean	S.E	Mean	S.E
Loamy sand							
	FC	8.63	0.93	11.91	0.20	9.50	0.56
	CD	6.77	0.01	5.49	0.82	6.16	0.51
	PD	8.63	0.93	5.11	1.69	9.12	0.30
Silt loam							
	FC	9.95	0.69	8.82	2.17	7.13	0.81
	CD	6.50	1.53	4.54	0.47	7.13	1.31
	PD	9.95	0.69	4.42	0.68	6.45	2.22

Sixteen days after the onset of drought (i.e. two days after re-watering the progressive drought pots), net photosynthesis rates ranged between 6.16μmol m^{-2}s^{-1} and 9.50μmol m^{-2}s^{-1}. Net photosynthesis rates were significantly higher on loamy sand than on silt loam, but did not differ significantly among moisture regimes or the interactive effects of soil types and moisture regimes.

5.5.2 Transpiration rate

Table 8 shows the transpiration rates (mmol m^{-2} s^{-1}) on the sampling days, for each of the three moisture treatments on loamy sand and silt loam. At the onset of drought treatments, transpiration rates ranged between 1.8mmol m^{-2}s^{-1} and 2.9mmol m^{-2}s^{-1}. At this point in time, transpiration rate was significantly higher on loamy sand than silt loam and was already significantly reduced by CD conditions. Transpiration rates did not differ significantly among the interactive effects of soil type and water regime at this point.

Table 8: Transpiration rates (mmol m^{-2} s^{-1}) of sorghum, on sampling days, as affected by different moisture regimes on loamy sand and silt loam

		Day0		Day10		Day16	
Soil	Water	Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	2.9	0.1	2.4	0.1	2.6	0.2
	CD	2.1	0.1	1.8	0.3	1.9	0.1
	PD	2.9	0.1	1.6	0.7	1.8	0.1
Silt loam							
	FC	2.4	0.1	2.0	0.1	2.1	0.2
	CD	1.8	0.1	1.7	0.1	1.8	0.1
	PD	2.4	0.1	1.4	0.2	2.3	0.1

Ten days after imposing drought, transpiration rates ranged from 1.4mmol m^{-2}s^{-1} to 2.4mmol m^{-2}s^{-1}. Transpiration rate was reduced by both CD and PD conditions on both the soil types. However, differences in transpiration rates were not significant for either soil type or any other factor at this point in time.

On the sixteenth day after starting drought treatments (two days after re-watering the pots subjected to PD conditions), transpiration rates ranged from 1.8mmol m^{-2}s^{-1} to 2.6mmol m^{-2}s^{-1}. At this point, transpiration rates for both CD and PD conditions were still lower than that for FC conditions on both soil types used. No significant differences in transpiration rates were found among the soil types or the among the moisture regimes. However, differences in the combined effects of soil types and moisture regimes on transpiration rates were significant at this point in time.

5.5.3 Stomatal conductance

Table 9 shows the of stomatal conductance (mol m^{-2}s^{-1}) of sorghum, as affected by different moisture regimes in pots filled with loamy sand and silt loam, for the days on which sampling was made on all the treatments. At the onset of progressive drought (Day 0), stomatal conductance ranged from 0.06mol m^{-2}s^{-1}to 0.08mol m^{-2}s^{-1}. At this stage, stomatal conductance was reduced by CD conditions on loamy sand only, but there were no significant differences among any of the factors tested (soil type, moisture regime and the combined effects of soil type and moisture regime).

Ten days after imposing the progressive drought treatment, stomatal conductance ranged from 0.03 of a mol m^{-2}s^{-1} (PD on silt loam) to 0.09 of a mol m^{-2}s^{-1} (FC on loamy sand). At this point in time, both CD and PD conditions reduced stomatal conductance, but the differences among soil types were not significant. Transpiration rate for pots subjected to PD conditions was significantly lower than for those subjected to CD or FC conditions.

Two days after re-watering the pots subjected to PD conditions (after a fourteen day drying cycle), stomatal conductance ranged from 0.05mol m^{-2}s^{-1} to 0.07mol m^{-2}s^{-1}. At this point in time, stomatal conductance was generally decreased slightly by CD and PD conditions but did not differ significantly among the soil types or among any other factor tested.

5.5.4 Stomatal resistance

The kinetics of stomatal resistance, of sorghum plants treated with 3 different moisture regimes in pots filled with loamy sand and silt loam, are presented in Table 10.

Data for the onset, ten days after starting drought treatments and sixteen days after starting drought treatments are presented. These were the days on which sampling involved all the treatments.

Table 9: Time course of stomatal conductance of sorghum as affected by 3 different moisture regimes in pots filled with loamy sand and silt loam.

		Onset		10 DAWI		16DAWI	
Soil	Moisture	Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	0.08	0.01	0.09	0.01	0.07	0.02
	CD	0.06	0.01	0.07	0.01	0.06	0.01
	PD	0.08	0.01	0.04	0.01	0.07	0.01
Silt loam							
	FC	0.07	0.01	0.09	0.01	0.07	0.02
	CD	0.07	0.02	0.08	0.04	0.06	0.01
	PD	0.07	0.01	0.04	0.01	0.05	0.01

Table 10: Kinetics of stomatal resistance of sorghum treated with 3 different moisture regimes in pots filled with loamy sand and silt loam.

		Onset		10 DAWI		16DAWI	
Soil	Moisture	Mean	SE	Mean	SE	Mean	SE
Loamy sand							
	FC	13.44	2.71	12.05	1.44	13.92	2.81
	CD	18.63	0.84	16.09	0.62	19.88	4.81
	PD	13.44	2.71	19.58	2.98	16.99	1.09
Silt loam							
	FC	15.82	1.17	12.26	1.77	15.63	2.32
	CD	16.02	3.38	15.84	5.14	16.45	0.74
	PD	15.82	1.17	21.04	1.26	17.37	1.38

At the onset of drought treatments, stomatal resistance ranged from 13.44 m^2s mol-1 to 16.02 m^2s mol-1. No significant differences in this parameter were found among the effects of any of the factors studied.

Ten days after imposing drought, the stomatal resistances of the plants ranged from 12.00 m^2s mol-1 to 21.04 m^2s mol-1. Stomatal resistance was increased by both CD and PD conditions compared to FC conditions. Differences among effects of soil types on stomatal resistance were not significant. Stomatal resistance for CD and FC conditions did not differ significantly, but pots subjected to PD conditions was significantly lower than for pots exposed to FC and CD conditions. The combined effects of soil type and moisture regime did not influence stomatal resistance differentially at this point in time.

Sixteen days after the drought treatments were initiated (two days after re-watering PD pots to control levels) stomatal resistances ranged from 13.92 m^2s mol^{-1} to 19.88 m^2s mol^{-1}. At this point in time stomatal resistance was slightly increased by CD and PD conditions, but differences among the effects of the factors studied were not significant.

5.6 Treatment effects on ABA content of Xylem sap

Figure 9 shows the time course of xylem ABA concentration as influenced by moisture regimes on loamy sand and silt loam.

On sand, CD increased the ABA concentration in xylem sap from a level of 58 pmol ml^{-1} (under FC conditions) to 680 pmol ml^{-1} and PD increased it to 3445 pmol ml^{-1} ten days into the drying cycle. At this point in time, respective relative available soil moisture figures for CD and FC conditions were 60.2% and 6.1%.

On silt, the ABA concentration in the xylem sap increased from a FC level of 80 pmol ml^{-1} to 173 pmol ml^{-1} under CD conditions ten days after starting drought treatments. No xylem sap could be extracted from the plants under PD conditions, and the respective relative soil moisture availability figures for CD and PD conditions were 79.7% and 5.9% at this point in time.

Fourteen days after starting drought treatments, when the relative available soil moisture figures for PD were 3.0% on loamy sand and 2.4% on silt loam,

no xylem sap could be extracted from any of the plants due to the severe moisture deficits. At this point in time, sampling was not done on plants under FC or CD conditions.

ABA concentrations in xylem sap returned to near-FC levels two days after re-watering the pots subjected to PD treatments. At this point in time, ABA concentrations on loamy sand were 25 pmol ml^{-1}, 51 pmol ml^{-1} and 33 pmol ml^{-1} under FC, CD and PD conditions respectively. The respective concentrations of ABA in the xylem sap of plants, on silt loam, were 440 pmol ml^{-1}, 63 pmol ml^{-1} and 36 pmol ml^{-1} under FC, CD and PD conditions. There was a sudden leap in the concentration of ABA in the xylem of plants in pots filled with silt loam and subjected to FC conditions.
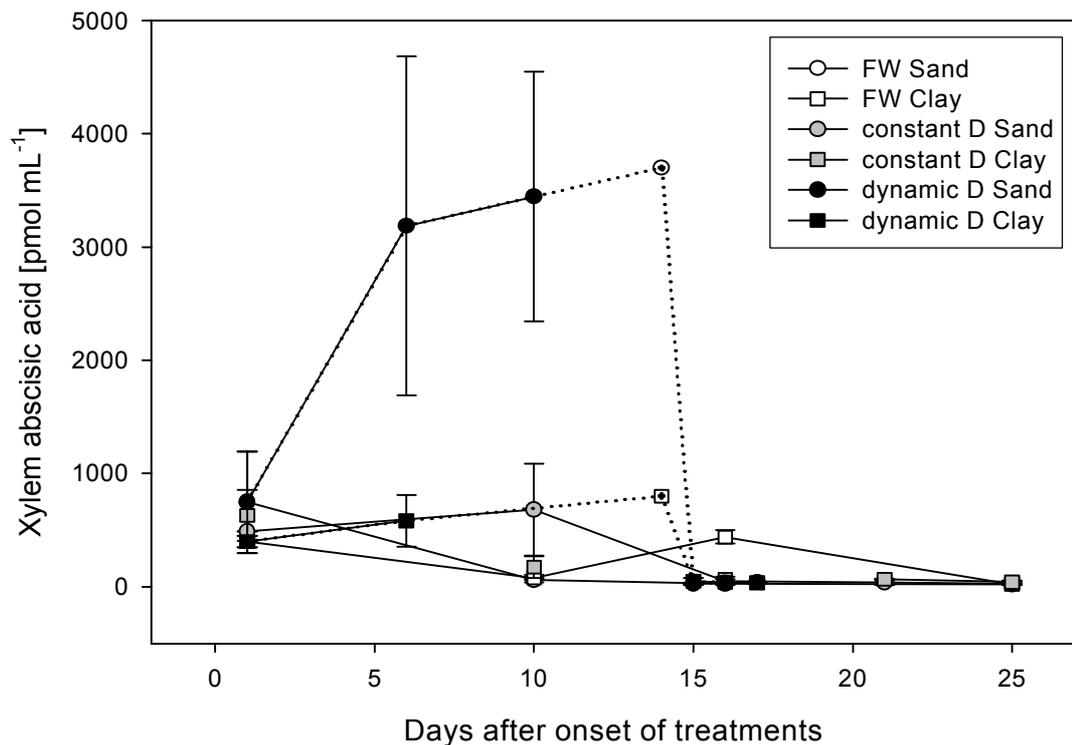
Figure 9: The time course of xylem ABA content as influenced by three different moisture regimes on loamy sand (circles) and silt loam (squares). Bars indicate SD). Vertical arrow indicates re-watering in progressive drought treatments. Dotted lines represent linear extrapolation for dates when there was no sap due to the severity of soil moisture deficit.

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5.7 Treatment effects on moisture and root distribution patterns

Figure 10 is a graphical presentation of the distribution patterns of moisture and roots, as affected by the treatments, within the four compartments of the pots. The distribution pattern for moisture has already been presented in the section "vertical distribution of moisture". The highest proportion of root dry matter was found in the top compartment (0.000 - 0.125m) for almost all the sampling days but the proportions were higher for pots subjected to FC and CD than for those subjected to PD. Within the remaining lower compartments (0.126 – 0.500m), root distribution was skewed towards the third and fourth (0.375 – 0.500m) compartments; with the second compartment (0.126 – 0.250m) having the lowest proportion of roots.

On loamy sand, similar patterns of root distribution were observed in the pots subjected to FC or CD conditions; with root distribution among the last three compartments being more or less even (Figure 10a, c). Root distribution in the pots filled with loamy sand and subjected to PD did not follow any well defined or discernable pattern, but was generally skewed towards the lower compartments (Figure 10e).

On silt loam, root distribution patterns within the three lower compartments were even for pots subjected to FC conditions (Figure 10b). For pots subjected to CD or PD conditions, root distribution was similar within the two central compartments but a little bit more in the last compartment (Figure 10d, f).

5.8 Treatment effects on relative growth rate and partitioning coefficients.

To ascertain whether the patterns of root growth were due to changes in overall growth or due to adaptive changes in dry matter partitioning between organs, mean partitioning coefficients were calculated for daily changes in dry matter of each organ. Figure 11 shows the time courses of partitioning coefficients for roots, leaves and stems, as well as the relative growth rate of sorghum grown in pots filled with loamy sand and silt loam and subjected to three different moisture regimes.
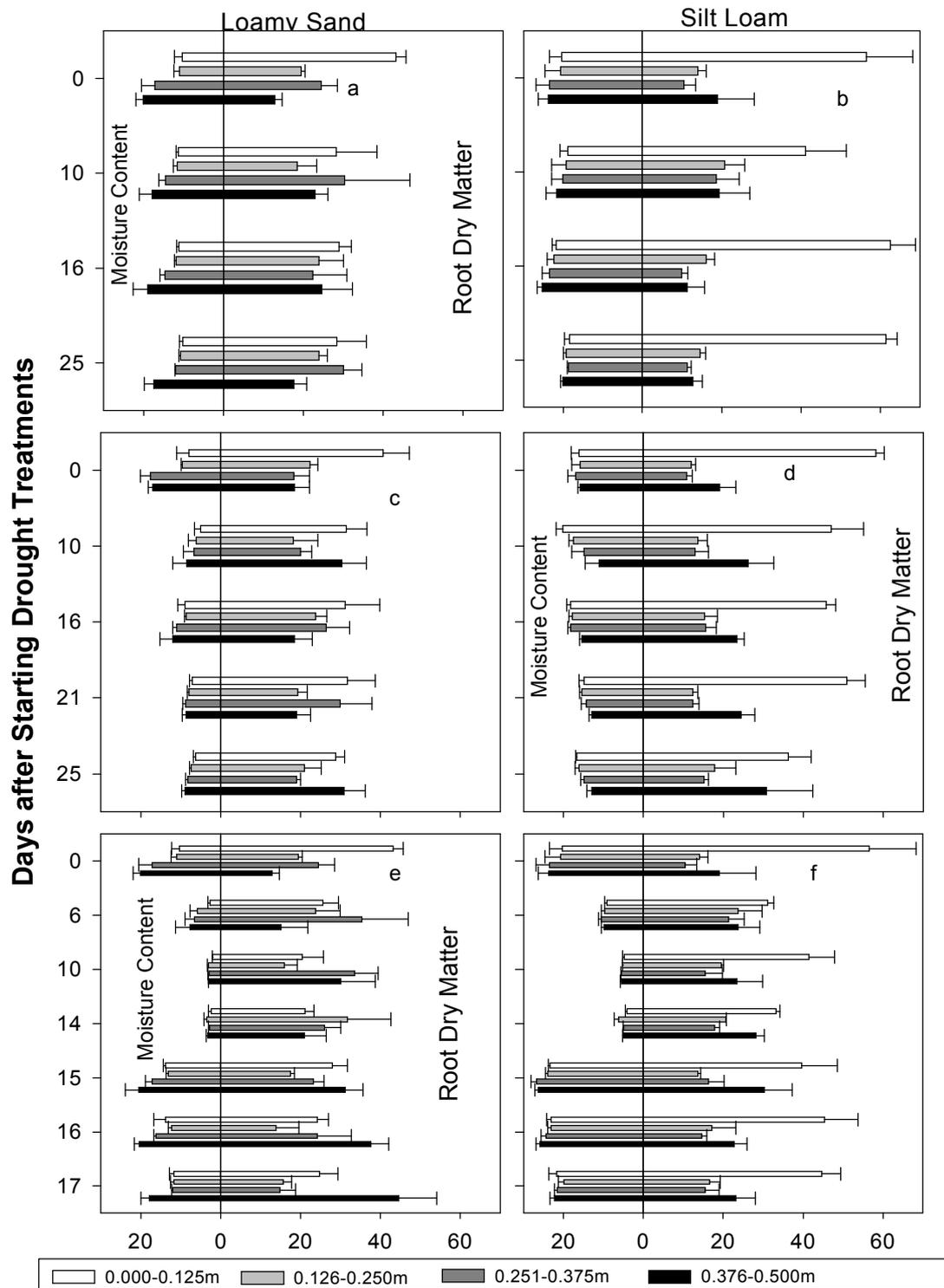
Figure 10: Kinetics of soil moisture and sorghum root distribution as affected by field capacity (a & b), constant drought (c & d) and Progressive drought (e & f) moisture regimes in pots filled with loamy sand (a, c, & e) and silt loam (b, d & f).

Field capacity conditions

Under FC conditions, relative growth rate (RGR) of the plants was between 5.6% (56 mg g-1 d-1) and 3.6% (36 mg g-1 d-1) in loamy sand and between 5.4% (54 mg g-1 d-1) and 2.3% (23 mg g-1 d-1) in silt loam. In both soils, RGR decreased with time, and as the plants developed (Figure 11a, d). Under this same moisture regime, mean partitioning coefficient (PC) for roots generally increased over time in both loamy sand and silt loam (Figure 11a, d). On loamy sand, it started from 0.36 and increased (linearly with time) to 0.41 over the twenty-five day data collection period (Figure 11a). On silt loam, PC for roots started with 0.34 and also increased linearly with time to 0.55 (Figure 11d). The PC for stems increased linearly with time from 0.33 to 0.49 on loamy sand (Figure 11a). On silt loam PC for stems increased from 0.43 to 0.45 during the first ten days, and then decreased thereafter to 0.32 at the end of data collection (Figure 11d). PC for leaves generally decreased over time on the two soils; from 0.31 to 0.12 (in loamy sand), and from 0.22 to 0.13 (in silt loam) (Figure 11a, d).

Constant drought conditions

Under CD conditions, RGR of the plants was between 3.5% (35 mg g-1 d-1) and 7.0% (70 mg g-1 d-1) in loamy sand and between 2.7% (27 mg g-1 d-1) and 4.3% (43 mg g-1 d-1) in silt loam. In loamy sand, RGR initially increased linearly with time from 3.5% (35 mg g-1 d-1) to 4.2% (42 mg g-1 d-1) by the fifteenth day, increased rapidly to 7.0% (70 mg g-1 d-1) on the seventeenth day, and decreased thereafter to 5.6% (56 mg g-1 d-1) at the end of the study (Figure 11b). In silt loam, RGR initially reduced from 4.3% (43 mg g-1 d-1) to the lowest 2.7% (27 mg g-1 d-1) by the fourteenth day and increased thereafter to 3.5% (35 mg g-1 d-1) at the end of the study (Figure 11e). Under this same moisture regime, PC for roots was between 0.26 and 0.44 in loamy sand. It was between 0.43 and 0.44 during the first fifteen days of the experiment, decreased sharply to the lowest (0.26) by the seventeenth day, and increased linearly thereafter to 0.30 at the end of the study (Figure 11b).

In silt loam, PC for roots was between 0.29 and 0.44; increasing from the initial 0.32 to a peak of 0.44 fourteen days into the study and decreasing almost linearly thereafter to the lowest (0.29) at the end of the study period (Figure 11e). PC for stems

was between 0.31 and 0.51 in loamy sand, increased initially from 0.47 to 0.51(the peak) during the first fifteen days, decreased rapidly to the lowest (0.31) by the seventeenth day, and increased again thereafter as the plants developed (Figure 11b). In silt loam, PC for stem, which was between 0.28 and 0.51 had a very similar trend to that for roots; increasing initially from 0.28 to the peak (0.51) by the fifteenth day, and decreased slightly thereafter as the plants developed (Figure 11e). PC for leaves was between 0.05 and 0.43 in loamy sand. It decreased from the initial 0.10 to the lowest (0.05) during the first fifteen days, increased rapidly to the highest (0.43) by the seventeenth day, and decreased thereafter (but stayed above 0.33) as the plants developed (Figure 11b). In silt loam, PC for leaves was between 0.06 and 0.39; initially decreasing (almost linearly) with time from the highest (0.39) to the lowest (0.06) within the first fourteen days, and thereafter increased almost linearly to 0.27 at the end of the study period (Figure 11e).

Progressive drought conditions

Under PD drought conditions, when the soil was allowed to dry slowly, RGR in loamy sand was between 0.2% (2 mg g-1 d-1) and 6.2% (62 mg g-1 d-1). It decreased initially from the highest 6.2% (62 mg g-1 d-1) to 1.5% (15 mg g-1 d-1) by the tenth day, increased sharply to a second peak of 5.4% (54 mg g-1 d-1) when the soil moisture fell below 7%, then finally decreased to the lowest (0.2% (2 mg g-1 d-1) when the soil moisture content was almost at permanent wilting point (Figure 11c). In silt loam, RGR decreased linearly during the drying cycle, from 5.4% (54 mg g-1 d-1) to almost 0% when the soil moisture fell lower than 6% (11 days into the drying cycle). Growth resumed only two days after the plants were re-watered (Figure 11f). Under this same moisture regime, the patterns of PC during the study differed with soil type. In loamy sand, there were hardly any differences in PC for roots stems and leaves until the soil moisture fell below 7%. At this point (nine days into the drying cycle) PC for roots increased, PC for stems remained constant, whiles partitioning to leaves had ceased (Figure 11c). By the fourteenth day, when the moisture content was nearly at permanent wilting point, PC was similar for roots, stems and leaves (Figure 11c). After re-watering, partitioning to roots ceased immediately whiles PC for stems and leaves increased, but the increase in PC was more pronounced in leaves than in stems (Figure 11c). In silt loam, PC was almost constant for each of roots, stems and leaves until the soil moisture

fell below 10% (ten days into the drying cycle). At this stage there was a slight increase in PC for roots and leaves, whiles PC for stems decreased slightly (Figure 11f). After re-watering, there was a rapid decrease in the PC for roots and a rapid increase in that for stems, but partitioning to leaves remained constant (Figure 11f).
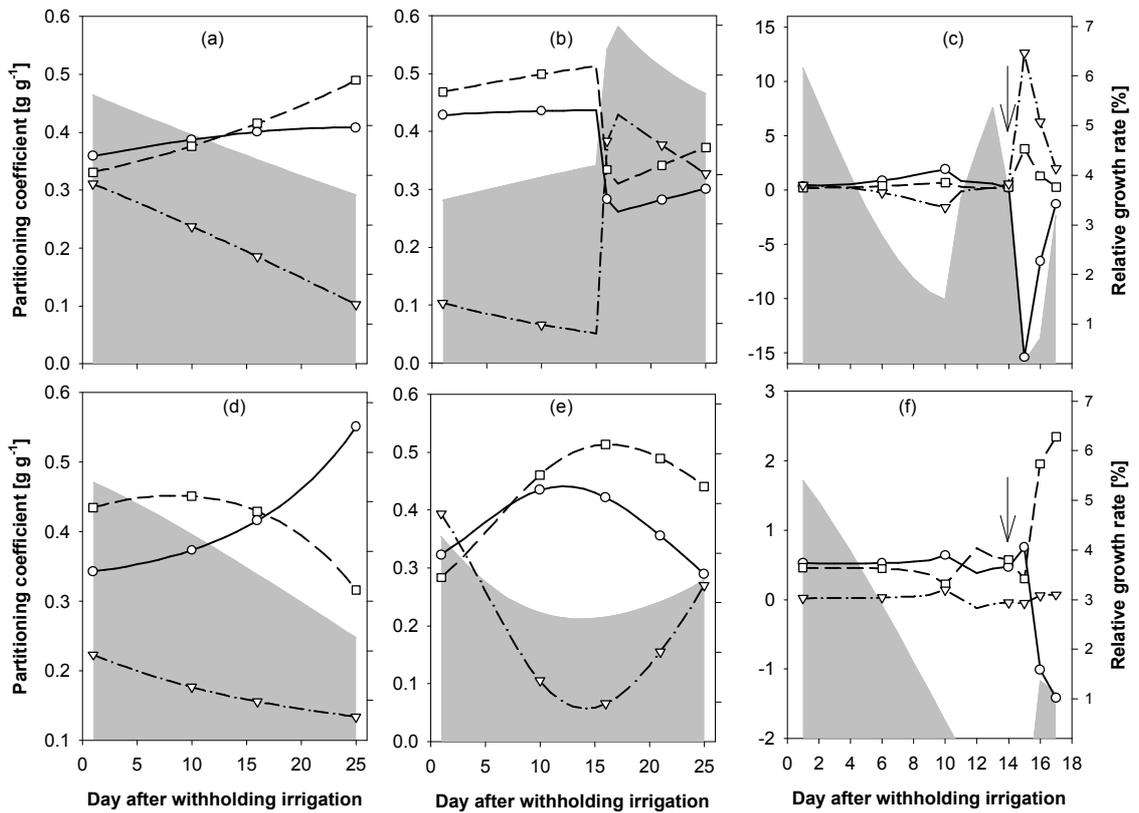
Figure 11: Time courses of partitioning coefficients for roots (circles), leaves (triangles) and stems (squares) and relative growth rate (grey shaded areas) of sorghum grown in pots field with loamy sand (a-c) or silt loam (d-f) under FC (a, d), CD (b, e) and PD (c, f) conditions. Arrows (in c, f) indicate point of re-watering.

6 Discussion

The current study was conducted on a sorghum crop with a well-developed root system extracting water in all layers of the pot during the later part of the drying cycle, thus, the discussion of the results will focus on responses of sorghum subjected to various levels of soil moisture deficit during the middle-to-late vegetative phase.

6.1 Experimental set-up and moisture distribution

A pot experiment was set up in a greenhouse using the factorial of two soil types (loamy sand and silt loam) and three moisture regimes (field capacity (FC), constant drought (CD) and progressive drought (PD)) as treatments.

The treatments were not intended to simulate situations in the field, but were fully artificial, to investigate sorghum responses in carbon partitioning and rooting patterns, assuming that changes in dry matter partitioning or rooting pattern would probably not occur in the field if they did not occur under these more severe, artificially controlled conditions.

Soil induced drought stress was established in three intentionally different ways: (1) no moisture deficit (FC), constant moisture deficit at a sub-lethal level (CD) and a transient drought stress including the stress relief period after re-watering (PD). For FC and CD moisture levels in the profile were intended to be constant, however, moisture distribution both among and within the compartments of a pot could be skewed, even when the average soil moisture for the whole soil column was constant. Moisture lost through evapo-transpiration was replenished via a perforated tube. This way soil closest to the tube would tend to be saturated, whereas zones farther away from the tube may not receive any moisture. To reduce this undesirable effect, the perforated tube was inserted diagonally (e.g. from the upper right to the lower left), instead of vertically through the column, ensuring that any concentration of moisture from irrigation was shifted across the column, instead of being vertically beneath each other.

In both loamy sand and silt loam under FC and CD conditions slightly lower moisture contents were found in the top layers than the lower ones, but the differences in moisture content between the compartments were not significant. Under PD conditions, typical field conditions prevailed; with a faster drying of top soil layers in

comparison with lower layers (Figure 4). Similar patterns, where soil dried faster at the top than the bottom under progressive drought, were reported by some authors for lysimeter experiments (e.g. Jensen *et al*., 1998; Ali *et al*., 1999).

Under all the moisture regimes and during all sampling dates, moisture was uniformly distributed within the individual compartments (visual assessment) indicating that inserting the perforated tube diagonally helped eliminate the uneven moisture distribution envisaged at the start of the study.

6.2 Soil moisture status as influenced by treatments content

Under FC conditions, soil water content above 19% in loamy sand and above 27% in silt loam by replenishing evapotranspiration daily. Soil water potential for the whole soil profile, was generally maintained closed to field capacity in loamy sand (0.01MPa to -0.02MPa) and a little below field capacity in silt loam (-0.03MPa to -0.05MPa), but the average values were all close to field capacity on both soils (Figure 2c, d).

Under CD conditions, soil water content was maintained above 11% in loamy sand and above 17% in silt loam by replenishing evapotranspiration daily. Soil water potentials in loamy sand and silt loam were generally between -0.04MPa and -0.17MPa on all the sampling dates (Figure 1c, d). The CD condition could be taken as a mild or moderate drought because despite its lower soil water potentials than FC conditions in both soils, on all sampling dates, the differences were not significant (Figure 2e, f).

Under PD conditions, typical field conditions (with a faster drying of top soil layers compared with lower layers) prevailed in both soils. Soil water potential reduced faster on silt loam than on loamy sand. Soil water potential was significantly reduced by PD conditions as compared to both FC and CD conditions after six days and five days into the drying cycle in loamy sand and silt loam respectively (Figure 2). The significant differences in soil water potential persisted until re-watering.

It was observed that the plants in silt loam were generally bigger than those on loamy sand (Table 6 and Figure 5a, b), and used more water, hence the more negative water potential each morning.

6.3 Drought effects on growth, biomass accumulation and green leaf area development

Growth, the increment in dry mass, volume, length and area, is a consequence of the interaction of processes such as photosynthesis, long-distance transport, respiration, and mineral nutrition, which are all influenced directly or indirectly by soil and plant water relations (Lambers *et al*., 1998). Plants depend on the availability of water for growth and development and have to tightly control the internal water balance to survive under drought stress (Maurel, 1997). The level of drought tolerance depends in most crops on the crops' development stage when the stress occurs. This adds another factor to be aware of in the characterization and study of drought tolerance (Mitchell *et al.*, 1997). At the vegetative stage, sorghum responds to progressive drought with reductions in shoot dry matter and leaf area (Salih *et al*., 1999; Tsuji *et al*., 2003).

Total dry matter

In this study, total dry matter production as well as plant height were influenced by the moisture regime (increasing with soil moisture content); they were greatest under FC condition and smallest under PD conditions on both soils (Figure 5a, b).

Total dry matter and plant height were both reduced by both CD and PD conditions on both soils (Figure 5a, b; Table **3**); with the reductions under CD conditions being similar on both soils, and being more pronounced on loamy sand than on silt loam under PD conditions. Compared to FC conditions, leaf area under CD conditions was reduced in pots filled with loamy sand, but was increased in those filled with silt loam (Table 6). The slower rate of water loss from the silt loam, could have permitted acclimation and hardening of the plants, leading to an over adjustment and enhanced performance. According to Leone *et al*, (1996) the response of the plant to soil drying depends on the extent and rate of water loss; a slow rate may permit acclimation to the water deficit and limit the extent of injury, while a rapid rate of loss may preclude acclimation.

Under PD conditions, trends observed in the reductions in leaf area were similar to those observed for total dry matter on both soil types. Similar responses, as for PD conditions in this study (where total dry matter, plant height, and leaf area were

reduced), were found by Salih *et al.,* (1999) and Tsuji *et al.* (2002) for some sorghum cultivars in one soil type under a drying cycle similar to PD condition in this study. The inconsistency of the response of leaf area, in pots filled with silt loam and subjected to CD conditions in this study, with that found by Salih *et al.,* (1999) could be attributed to the differences in drought patterns, and to some extent, the differences in soil types used during this study and theirs.

Root dry matter and rooting depth

Under drought conditions, change of rooting pattern is one of the discrete mechanisms plants employ to avoid low tissue water potentials. Drought avoidance by increased root growth draws considerable interest since it does not unduly hamper the productive processes, unlike reduction in leaf area or stomatal closure.

In this study, root biomass production was generally higher under FC conditions than under CD conditions in the pots filled with loamy sand, whereas the opposite was true when plants were grown in silt loam. Root biomass production was increased under progressive drought conditions, increasing with the severity of drought (Figure 5c, d). The results in this study, especially from conditions of progressive drought, confirm the assertions of Daie (1996) as well as Matsui and Singh (2003) that under drought stress, changes in partitioning most often favour root growth, which are reflected in increased root-shoot ratios, but contrast the findings of Rice (1979) that assimilate partitioning to roots of sorghum decreases under progressive drought. Both results from those contrasting situations (this study and that found by Rice, 1979) could be true due to genotypic differences in sorghum root systems noted by some authors (e.g. Blum *et al.* 1977a; Jordan *et al.* 1979).

The patterns of root biomass production under all the three moisture regimes were consistent with their respective total dry matter (Figure 5a, b). Consistency of rooting pattern with total dry matter (where root dry matter increases with increasing total dry matter and vice versa) has been reported by Asch *et al.* (2004) who worked on rice in one soil type under different patterns of drought.

In this study, root-shoot ratios under FC and CD conditions were almost constant, and did not differ significantly over the entire period on both loamy sand and silt loam (Figure 5e, f). Under PD conditions, root-shoot ratios increased significantly,

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compared to FC conditions, on both soils (Figure 5e, f). The results of root-shoot ratio under PD conditions further collaborates the assertions of Matsui and Singh 2003, but contrasts the findings of Asch *et al*. 2004 for rice under progressive drought conditions where no additional assimilates were partitioned in favour of roots. The contrast can be attributed to differences in species used (rice and sorghum).

Partitioning coefficients for roots were relatively higher than for stems and leaves during the drying cycle on both soils. In some instances there were clear cases of remobilization of assimilates from leaves in particular (Figure 11c, f). Water deficit is not the only possible candidate for the observed pattern of assimilate partitioning under progressive drought, as the availability of nutrients, especially nitrogen and phosphorus, could also be reduced under PD conditions and thus trigger an enhanced partitioning to the roots while maintaining either a constant or reduced partitioning to the shoot. Several authors have reported that the deficiency of nitrogen or phosphorus triggers enhanced partitioning to roots by plants, in order to exploit larger soil volumes and increase uptake of the nutrient (e.g. Bowman, 1991; Lynch *et al*., 1991; Smolders and Merckx, 1992; McDonald *et al*., 1996). Reports by Cechin, (1997) and Rafael *et al*., (2002), who investigated the effects (on sorghum) of nitrogen and phosphorus respectively, indicated that more assimilates were partitioned to roots under deficiency conditions of nitrogen or phosphorus. The linkage between these and the present study is the inadequate moisture, under PD conditions to keep the nutrients in solution, hence making them unavailable and thus perceived as deficient by the plants. Many authors have also reported that in drying soil, nutrient availability and uptake to the root system may decrease and, in turn, alter the physicochemical properties of the xylem sap (Chapin, 1991; Bacon *et al*., 1998; Schurr and Schulze 1996).

6.4   Drought effects on gas exchange

It has been reported that at the whole plant level, the effect of stress is usually perceived as a decrease in photosynthesis and growth (Cornic and Massaci, 1996). Tsuji *et al*, (2003) planted three sorghum cultivars under fully watered conditions, and the respective ranges for net photosynthetic rates, stomatal conductance and transpiration rate were 23 μmol m^{-2} s^{-1} to 25 μmol m^{-2} s^{-1}, 0.13 mol m^{-2} s^{-1} to 0.19 mol m^{-2} s^{-1} and 1.93 mmol m^{-2} s^{-1} to 2.12 mmol m^{-2} s^{-1} at the late vegetative stage. Compared

to the above findings, the net photosynthetic rate (7.13 μmol m^{-2} s^{-1} to 11.91 μmol m^{-2} s^{-1}), stomatal conductance (0.07 mol m^{-2} s^{-1} to 0.09 mol m^{-2} s^{-1}) and transpiration rate (2.0 mmol m^{-2} s^{-1} to 2.9 mmol m^{-2} s^{-1}) obtain under FC conditions in this study could be accepted as normal, since there were occasional cloud cover during measurements, which could reduce gas exchange.

Drought stress has also been reported by some authors to reduce photosynthesis, stomatal conductance, and transpiration in sorghum (e.g. Premachandra *et al*. 1994; Massacci *et al*. 1996) and for grain sorghum, a positive correlation has been found between leaf photosynthesis and total biomass under both well-watered and water-limited conditions (Peng *et al*. 1991). In this study, net photosynthesis, transpiration rate, and stomatal conductance were already reduced by CD at the onset of drought treatments, as it took some time of drying to attain the require moisture content for CD. Ten days after starting drought treatments CD and PD conditions reduced net photosynthesis transpiration rate and stomatal conductance (Table 7,Table **8** and Table 9). These results are consistent with those for total dry matter (Figure 5a, b). The results of the gas exchange parameters are consistent with the previous findings of Premachandra *et al*., (1994) and Massacci *et al*., (1996). It has been suggested that ability to acclimate and maintain positive net photosynthesis during a slow developing drought is related to survival and recovery following a drought (Kruger and van Rensburg, 1995).

6.5 Drought effects on xylem ABA concentration.

ABA is a plant hormone known to act as a root-shoot-signal under conditions of soil moisture deficit. It is suggested to be a central component in the co-ordination of whole plant responses to drought (Jones, 1990). Based on the report of Zhang and Davies (1987) that ABA is produced in large quantities in water stressed tissues, especially in roots, in drought situations, it was expected in this study that ABA concentrations in the xylem sap will be more under CD conditions than under FC conditions, and will also increase with increasing soil moisture deficit under PD conditions. Relatively mild soil drying may enhance the concentration of ABA in the xylem stream by perhaps two orders of magnitude (Macdonald and Davies 1996) which makes ABA a likely main signal molecule in these circumstances (Davies *et al* 1994).

Discussion

The increase in xylem ABA concentration, as a result of soil drying was rapid and more pronounced in the pots filled with loamy sand than in the pots filled with silt loam. This could have resulted from the higher drying rate of loamy sand than silt loam, especially from the sixth day to the tenth day after withholding irrigation (Figure 9).

Six days into the drying cycle, when soil water potential had decreased (significantly) to -0.43MPa and 0.90MPa on loamy sand and silt loam respectively, xylem ABA concentrations increased and stomatal conductance decreased (Figure 2 and Figure 9; Table 9). At this stage, stomatal conductance was similar on the two soils (0.06 mol m^{-2} s^{-1}), but xylem ABA concentration for plants grown in loamy sand (3186 pmol ml^{-1}) was higher than for those grown in silt loam (582 pmol ml^{-1}). A similar trend was found ten days into the drying cycle and also at the end of the drying cycle (fourteen days after withholding water in the pots subjected to PD conditions). However, ten days after starting drought, the ABA concentration in the pots filled with loamy sand and subjected to CD conditions was abnormally higher than the concentrations for this same treatment sampled on other dates. This could be caused by several reasons like the use of not exactly the same pressure and/or the same length of time during xylem sap sampling, maybe the transfer between freezing states interfered, or maybe the ELISA was not running well. Which of these is the actual cause is not possible to decipher.

Fourteen days into the drying cycle, irrespective of the soil type no more xylem sap could be extracted from plants subjected to PD, due to the severity of the soil moisture deficit. However, assuming that no more sudden changes in xylem ABA would occur at these drought levels, linear extrapolation of the response curve allowed the estimation of the xylem ABA level just before re-watering (Figure 9).

The sharp differences in ABA concentration between loamy sand and silt loam under PD conditions could be attributed to differences in the soil moisture contents between the two soils, as lower soil water contents were found in the loamy sand than in the silt loam at all times of the drying cycle and rate of drying was faster in loamy soil (Figure 2a, b). The roots in dry soil in the upper layers (greater in loamy sand than silt loam) could probably trigger the production of drought signal molecules. These results may thus confirm the earlier findings of Gowing *et al*., (1990), in split-root experiments in a growth chamber, that ABA was produced when only part of the root system

experienced desiccation. These results also corroborate the findings of Zhang and Davies, (1989) on sunflower and the suggestion of Davies *et al*. (1994) that ABA concentration and, therefore, stomatal behavior are a reflection of the access that roots have to soil water rather than a reflection of the soil water status alone, but oppose what Tardieu *et al*. (1992a) found in field experiments in maize where there was no reduction in leaf conductance and no appreciable increase in xylem ABA concentration with partial drying of the upper parts of the root system in the soil profile.

The extent to which roots were pot-bound (greater in loamy sand than silt loam) could have also enhanced the production of signal molecules. Tardieu *et al*. (1992b) reported that mechanical impedance to root growth (caused by compacted soils) induced a similar increase in xylem ABA concentration of maize. Lambers *et al* (1998 also reported that the effects of plants that grow in compacted soil are similar to those of plants that are pot-bound because the roots somehow sense the walls of the pots to be impenetrable soil, and leaf expansion is reduced even when sufficient water and nutrients are provided. Similar responses were reported by Hartung *et al.* (1994).

On the sixteenth day (two days after re-watering the pots subjected to PD conditions), xylem ABA concentration under PD conditions returned to the levels for FC conditions in both soils, except for pots filled with silt loam and subjected to FC conditions which had extremely high concentrations of ABA. The reason for this observation could be same as that given for the situation of pots filled with loamy sand and subjected to CD conditions on the tenth day.

6.6 Drought effects on plant water household

Water potential and its components are generally considered reliable indices of the water status of plant tissue. Total leaf water potential, leaf osmotic potential and relative water content relate directly or indirectly to plant response to drought stress (Brown, 1995), and are all, in theory, potential water stress resistance screening criteria (Matin *et al*., 1989).

Results from this study indicated that there was little variation in root water potential (RWP) among the pots subjected to FC on both loamy sand (-0.3 MPa to -0.1 MPA) and silt loam (-0.40 MPa to -0.19 MPa). The variation in RWP, among the pots subjected to CD conditions was also very little in both loamy sand (-0.23 MPa to -0.16

Discussion

MPa) and silt loam (-0.32 MPa to -0.27 MPa). RWP did not differ significantly between these two moisture regimes (FC and CD) throughout the period of the experiment. With similar RWP for plants under FC and CD conditions, it was expected that LWP would also not differ significantly between these moisture regimes if there was no differential accumulation of compatible solutes. However significantly lower LWP were measured under CD (-1.21 MPa to -1.87 MPa) compared to FC (-0.53 MPa to -1.48 MPa) on both soils (Figure 7). LWP under FC and CD conditions appeared to be influenced more by the ambient temperature of the air (Figure 1), judging from the similarity in the trends of ambient temperature of the air and LWP under these conditions (Figure 1, Figure 7), rather than by differences in soil type or leaf position. Leaf osmotic potential (presented for only L1 because of high senescence in L2) did not differ among plants under FC and CD conditions at all times (Figure 8). Thus, either the moisture content for the CD conditions was not sufficiently different (lower) from FC to have any effect on RWP, or it was balanced due to the accumulation of compatible solutes under CD conditions (osmotic adjustment). Reductions in LWP by PD conditions varied with leaf position and soil type (Figure 7).Ten days into the drying cycle, the number of leave positions present were lower under PD (8 leaves on both soils) than under both CD (11 leaves on loamy sand; 14 leaves on silt loam) and FC (11 leaves on loamy sand; 13 leaves on silt loam) conditions. L2 was not fully functional in almost all cases because more than 30% of the leaf surfaces were fired and/or senesced, particularly from the tips and leave sap could not be extracted from most of these leaves to determine osmotic potential. Very little senescence of firing was observed on L1.

PD reduced RWP significantly on both soils after ten days into the drying cycle (Figure 6). Any earlier significant differences in root water were not recorded due to the sampling frequency. LWP was also significantly reduced under PD conditions (from -1.33 MPa to -1.92 MPa on loamy sand and from -0.49 MPa to -2.35 MPa on silt loam). LOP were lower under PD conditions than both FC and CD conditions, but did not differ significantly among the water regimes. During the drying cycle, RWP, LWP and LOP were higher on silt loam than on loamy sand. The reduction in both LWP and LOP were relatively greater in plants grown in silt loam than in loamy sand (Figure 6 and Figure **7**), and was similar to reactions of wheat (Rascio *et al.*, 1988) and alfalfa (Pennypacker *et al.*, 1990).

Discussion

Re-watering resulted in an immediate, visible stress relief in all plants. Physiological parameters such as RWP, LWP, osmotic potential, net photosynthesis rate, stomatal resistance stomatal conductance and xylem ABA approximated control values within one to four days (Figure 6-9; Tables 7-10)

After re-watering the pots subjected to PD conditions, restoration of RWP to FC levels was faster in pots filled with loamy sand than those filled with silt loam. Three days after re-watering, RWP in the pots filled with loamy sand was restored to the same levels observed under FC conditions (Figure 6a), whereas in the pots filled with silt loam RWP increased only to the levels observed under CD conditions (Figure 6b). The differences in water holding capacities of the two soils could account for the trend observed during the drying cycle (Kramer and Boyer, 1995), whiles the trends observed after re-watering could be due to silt loam having a slower rate of infiltration than loamy sand. Bahrun et al. (2002) also reported that effects of progressive drought were more pronounced on maize plants in coarser soil (sand) than those in a finer soil (loam).

Two days after re-watering, LWP of L1 under PD conditions (-1.29 MPa in loamy sand; -1.58 MPa in silt loam) was still lower than LWP of L1 under FC (-0.53 MPa in loamy sand; -0.36 MPa in loamy sand) conditions. A similar trend was observed for LWP of L2 under PD conditions (-1.44 MPa in loamy sand; -2.44 MPa in silt loam), which were also lower than LWP under FC conditions (-0.53 MPa in loamy sand; -0.22 MPa in silt loam). LWP for plants in silt loam was lower than for those in loamy sand (Figure 7). LWP for the plants grown in pots filled with silt loam and subjected to PD conditions lagged behind in their restoration of LWP. The leaves seemed to react with different sensitivities to changes in root zone moisture content. In all cases, the older leaves (L2) (Figure 7b, d) seemed to have weaker sensitivities than the younger leaves (L1) (Figure 7a, c), and this could probably be attributed to the differences in age, degree of senescence and activity of the two leaves. Variations in the reactions of leaves at different positions on the plant was found by Busch et al, (1996) who reported differences in assimilation rates of wheat leaves at different positions, even at the same photon flux densities.

7 Conclusion(s) and Outlook

The different soil types (loamy sand and silt loam) affected the components of soil water differentially. Silt loam holds more water than loamy sand, but the soils had similar relative available soil moisture during the drying cycle. Higher soil water potentials were generated in loamy sand than in silt loam.

Sorghum reacted to drought stress with reductions in height leaf area and biomass production and changes in rooting pattern. Assimilate partitioning was not affected by constant drought, but it was shifted in favor of roots under progressive drought until FC conditions were re-established. A higher percentage of the root dry matter was channeled to the production of nodal roots, especially on silt loam, whereas more of the seminal-root dry matter was found in the deeper layers of the soil column. The apparent distribution of root dry matter was not related to the moisture distribution within the soil column.

Abscisic acid concentration in the xylem increased with increasing soil moisture deficit. Gas exchange of sorghum was affected, to varying degrees, by different patterns of drought stress. Plant reactions depended on drought pattern and also severity, especially under progressive drought. Plant response to drought was related to soil water content rather than to soil water potential.

The results of this study need to be developed into a model of drought response for sorghum and should be validated in field trials and for a wider range of genotypes.

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