Water stress effects on growth, yield and quality of wheat (*Triticum aestivum* L.)

by

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DECLARATION

I, Zwidofhelangani Aubrey Mbave, confirm that this dissertation submitted for the degree M.Inst.Agrar: Agronomy is my own work, and has never been submitted by me at any other university.

Signed ________________________________
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ABSTRACT

Understanding the effects of water stress on wheat growth, yield and quality is essential for good irrigation management. In South Africa most of the wheat production areas are vulnerable to drought stress during crop development. That causes substantial reduction in grain yield, depending on the developmental stage at which water stress occurred. Supplemental irrigation is the main strategy for adaptation and stabilisation of yield under water stress. However, agriculture is the leading single water-use sector locally, consuming about 60% of total available water. Therefore, the need to improve water use efficiency (WUE) in crop production is clear, since South Africa is classified as a water-scarce country. Experiments were conducted under a rain shelter at Hatfield Experimental Farm, University of Pretoria, in the 2010 and 2011 seasons. The main objective of the study was to evaluate the effects of water stress at different stages on growth, yield, and quality of three wheat cultivars, namely Duzi, Steenbras and SST 843. Water stress was imposed by withholding water at either of three growing stages. The first treatment was stressed during tillering stages to flag leaf (stem elongation (SNN)), followed by water stress from flag leaf to the end of flowering (flowering stage (NSN)), and lastly water stress from grain filling to physiological maturing (grain-filling stage (NNS)), whereas optimal supply of water was maintained throughout the season by weekly irrigating to field capacity for the control treatment (NNN). Irrigation treatments and cultivars influenced growth, yield and quality, depending on the developmental stage at which irrigation was withheld. The control treatment (NNN) and the treatment stressed in the flowering stage (NSN) had highest and lowest grain yield respectively in both seasons. Water stressed treatment NSN reduced grain yield by 33% and 35% in the 2010 and 2011 seasons respectively, when compared with the control treatment (NNN). Reduction of grain yield due to stress in the flowering stage (NSN) was ascribed to reduction in the number of seeds per ear, number of ears per unit area, ear length, and flag-leaf photosynthesis rate (Pn). In the flowering stage (NSN) water stress reduced Pn by 59%

which was due to increased leaf temperature because of lower transpiration (E) and stomatal conductance (g_s). The water stress treatment NSN reduced transpiration by 72% and stomatal conductance by 84% in the flowering stage. Plant height was reduced by 23% because of water stress imposed in the flowering stage (NSN), which consequently decreased biomass yield by 29% in the 2011 season. Growth and yield parameters showed dramatic recovery when stress was terminated during the flag-leaf stage (SNN). The cultivar Steenbras had lower yield reduction under stress, whereas Duzi and SST 843 had higher yield potential under the well-watered conditions (NNN). In the 2011 season SST 843 had higher WUE of 14.2 kg ha^{-1} mm, which corresponded to higher grain yield of 7210 kg ha^{-1} and higher ET of 509 mm. Water-stress treatment SNN gave the highest WUE of 14.9 kg ha^{-1} mm, which corresponded to a total water use (ET) of 451 mm and grain yield of 6738 kg ha^{-1}. Water stress treatments SNN and NNS reduced ET by 27% and 17%, respectively, which translated to 173 mm and 105 mm water saved by each treatment correspondingly. Grain protein content (GPC) was reduced most by the treatment exposed to stress in the stem elongation stage (SNN). However, the GPC was acceptable (>12%) in all treatments in both seasons. Hectolitre mass was reduced most by water stress imposed during grain filling (NNS). Water stress treatment NNS lowered the hectolitre mass by 3% and 4% in the 2010 and 2011 seasons respectively. Generally all quality parameters in the present study were acceptable for all irrigation treatment and cultivars. The hypothesis that water stress in the stem elongation and grain-filling stages will have little effect on yield and improve WUE was accepted. Therefore it can be recommended that supplemental irrigation should be applied from flag leaf to end of flowering (NSN) stages of wheat in order to minimise grain yield losses in the absence of rainfall. Further research should focus on extrapolation of these results to other production regions using crop models.

Key words: water stress, water use, water use efficiency, wheat growth stages, quality, yield and yield components

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LIST OF ABBREVIATIONS AND SYMBOLS

ARC-SGI	Agricultural Research Council, Small Grains Institute
α	Alpha
cm	Centimetre
Ci	Intercellular CO_2 concentration (µmol CO_2mol^{-1})
CO_2	Carbon dioxide
DAFF	Department of Agriculture, Forestry and Fisheries
DAP	Days after planting
DI	Deficit irrigation (mm)
DM	Dry matter production (t ha^{-1})
Dr	Drainage below the bottom of the root zone (mm)
E	Transpiration rate(mmol H_2O m^{-2} s^{-1})
EL	Ear length (cm)
ET	Water use (mm)
ETo	Reference evapotranspiration (mm day^{-1})
FAO	Food and Agricultural Organisation (United Nations)
FN	Falling number(s)
g	gram
g_s	Stomatal conductance (mol H_2O m^{-2} s^{-1})
GY	Grain yield (t ha^{-1})
GYi	Mean grain yield of stress treatment (t ha^{-1})
Gyp	Mean grain yield of well-irrigated treatment (t ha^{-1})
GPC	Grain protein content (%)
HI	Harvest index (%)
hl	Hectolitre

HLM	Hectolitre mass (kg hl^{-1})
H_2O	Water
I	Irrigation (mm)
iWUE	Instantaneous water use efficiency(µmol mol^{-1})
kg hl^{-1}	kilogram per hectolitre
LAI	Leaf area index (m^2 m^{-2})
LSD^c	Least significant differences of cultivars
LSD^I	Least significant differences of irrigation
$LSD^{I×C}$	Least significant differences of interaction effect between irrigation and cultivars
LWP	Leaf water potential (MPa)
m	metre
m^2	metre square
mm	milimetre
MJ	Megajoule
MPa	Mega Pascal
NEM	Numbers of ears (m^2)
NKE	Number of kernels per ear
NNN	Non-stressed control treatment
NNS	Treatment stressed in the grain-filling stage
NSN	Treament stressed in the flowering stage
P	Precipitation / Rainfall (mm)
PAW	Plant available water (mm)
PH	Plant height (cm)
Pn	Photosynthesis rate (µmol CO_2 m^{-2} s^{-1})

R	Runoff (mm)
RH	Relative humidity (%)
Rs	Solar radiation (MJ m^2 d^{-1})
s	Seconds
SI	Supplemental irrigation (mm)
SNN	Treatment stressed in the stem elongation stage
SWB	Soil water balanceequation
Tave	Average temperature (°C)
TDM	Total dry matter (t ha^{-1})
TKM	Thousand kernel mass (g)
Tmax	Maximum temperature (°C)
TOL / YR	Stress tolerance / Yield reduction (t ha^{-1})
t ha^{-1}	ton per hectare
U	Wind speed (m/s)
USA	United States of America
USDA	United States Department of Agriculture
WUE	Water use efficiency (kg ha^{-1} mm^{-1})
YSI	Yield stability index (t ha^{-1})
*	Significant at 5% probability
**	Significant at 1% probability
ΔS	Change in soil water storage (mm)
ºC	Degrees Celcius
%	Percentage
µmol	Micro-mol

CHAPTER 1: GENERAL INTRODUCTION

Water plays an important role in the world's development. However; its increasing scarcity imposes the need to optimise water use in all human activities, particularly in irrigation, the foremost water-use sector worldwide. Globally, agriculture uses about 75% of the total water (FAO, 2005). About 40% of wheat production regions in the USA, Canada, Australia, China, Middle East and most African countries are prone to global aridity (Deng *et al.*, 2005). Generally, drought or water stress is a meteorological term, which is usually defined as a period without significant rainfall (Simpson, 1981). Plants experience water stress whenever absorption of water by the crop is lower than the evaporative demand of the atmosphere, especially when 50% of available water is depleted (Blum, 1996). The major processes involved in water relations include crop water absorption which is controlled mainly by root characteristics and the physical properties of the soil. The crop water use or evapotranspiration (ET) depends mostly on atmospheric properties, particularly net radiation and vapour pressure deficit, and crop characteristics such as crop ground cover and stomatal conductance (Acevedo *et al.*, 2002). In wheat ET is positively and linearly related to grain yield, therefore water stress certainly decreases yield (Zhang & Oweis, 1999).

Several authors have reported that water stress is common in arid and semi-arid regions, and is a major factor in preventing the realisation of maximum crop yields (Zhang & Oweis, 1999; Deng *et al.*, 2005). Water stress limits the productivity of the world's most important staple cereal crops, including rice, wheat and maize (Ji *et al.*, 2010). It is the most detrimental environmental factor limiting crop production (Blignaut *et al*. 2009; Anjum *et al.*, 2011), and has been amplified by the ever-changing climatic conditions worldwide (Ji *et al.*, 2010). Blignaut *et al*. (2009) indicated that climate change has led to an increase in water use in South Africa, due mainly to the increased hot and dry conditions experienced over the last two decades. Currently most agricultural production areas of major grain crops in South Africa are under threat of drought due to low and unreliable rainfall, (Gbetibouo & Hassan, 2005), as the total annual average rainfall is about 495 mm, which is far below the world's average of 860 mm per year (FAO, 2005). Furthermore, the rain is distributed unevenly across the country with sub-tropical conditions in the east and dry desert conditions in the west (Blignaut *et al.*, 2009). That makes water stress the most harmful ecological stress, limiting yield in both winter and summer wheat production regions (ARC-SGI, 2009).

It is estimated that the country will run out of surplus water for irrigation at about 2025, and the irrigation sector may be forced to sacrifice its water to other sectors (FAO, 2005). Therefore, water use efficiency (WUE) in crop production in South Africa must be improved, since agriculture uses more than 60% of total available water (Gbetibouo & Hassan, 2005; Blignaut *et al*., 2009). Innovative soil water management techniques should be introduced in order to achieve higher productivity (Oweis & Hochum, 2006). Some wheat farmers have switched over to full irrigation in summer rainfall areas of South Africa. Such a practice helps to reduce the risk of crop failure, resulting in higher and more sustainable yields (Gbetibouo & Hassan, 2005). However, the challenge facing irrigation farmers is to know the growth stages for a specific cultivar that are less sensitive to water stress so that water can be saved at that stage without reducing yield and quality significantly, hence saving water and costs of irrigation.

The solution is to optimise water application at any specific growth stage in order to save water, but minimise loss of yield and quality from water stress. Therefore it is important to increase knowledge of the interaction between crop development, grain yield and water use to face the climate change-driven increase in global aridity (Gbetibouo & Hassan, 2005; Blignaut *et al*., 2009). Maximising grain yield is the main aim of crop production. However, the physiological and agronomical responses to drought stress conditions influence grain yield (Jatoi *et al*., 2011). The growth and yield responses of winter wheat to available soil water differ, depending on the intensity of the stress and the developmental stage at which water stress occurs (Bogale & Tesfaye, 2011). Water stress during certain growth stages may have less effect on grain yield and quality than similar stress at other growth stages (Ozturk & Aydin, 2004). Therefore, it is important to understand the consequences of water stress at each developmental stage in relation to growth and yield potential for better irrigation management (Zhang & Oweis, 1999). In agricultural production, supplemental and deficit irrigation have been proposed as strategies to conserve water under limited water supply conditions (Zhang & Oweis, 1999; Ali *et al*., 2007). Crops can be deficit irrigated at certain crop growth stages without reducing crop yield significantly, whereas supplemental irrigation can be applied in the absence of rain in most sensitive stages (Oweis & Hochum, 2006). Many researchers have concluded that deficit and supplemental irrigation are economically viable options to follow under conditions of limited water supply (Zhang & Oweis, 1999;

Shamsi *et al*., 2010). They are suitable methods for saving water while maintaining acceptable yield under water shortage conditions (Ali *et al*., 2007).

1.1 Hypotheses

$H_0$1: Three South African wheat cultivars will respond differently to water stress at various developmental growth stages, namely stem the elongation, flowering and grain-filling stages

$H_0$2: Water stress imposed at various growth stages of wheat will improve water-use efficiency, but have minimal effect on growth, yield and quality

1.2 General objectives/ aims

The purpose of the study was:

(i) To determine the growth and physiological sensitivity of three wheat cultivars (Duzi, Steenbras and SST 843) to water stress imposed at various growth stages, namely the stem elongation, flowering and grain-filling stages (Chapter 4)

(ii) To identify the growth stages at which limited water supply will improve water use efficiency, but have minimal effect on yield and quality of wheat (Chapter 5)

The present dissertation is subdivided into six chapters. The first chapter constitutes the general introduction, which highlights the effects of water (drought) stress on wheat yield, and also emphasises the need to improve water-use efficiency, specifically in South Africa, through the use of supplemental irrigation at the most sensitive growth stages. Chapter 2 provides a general literature review of wheat production, the effects of water stress on growth, photosynthesis, yield and quality, as well as the physiological adaptations of wheat and the use of irrigation as a strategy to control water stress. General materials and methods are summarised in Chapter 3. The results and discussion on the physiological and growth responses of wheat cultivars to water stress are presented in Chapter 4. Chapter 5 discusses the results obtained on the effects of stress on water use, water use efficiency, the yield and quality of wheat cultivars stressed at various growth stages. Finally the general discussion, conclusions and recommendations are compiled in Chapter 6.

CHAPTER 2: LITERATURE REVIEW

2.1 Origin and botanical description of wheat

Wheat is among the first cereals known to have been domesticated. It is believed that all Triticeae species, including wheat and barley, originated in the semi-arid region of South-West Asia in the area known as the Fertile Crescent (Deng *et al.*, 2005; Matsuoka, 2011). Several authors reported that wild einkorn and emmer wheat were domesticated as part of the origins of agriculture about 10,000 years ago, and they are regarded as the mothers of all wheat species (Matsuoka, 2011; Peng *et al.*, 2011). Through repeated cultivation and harvesting, mutant forms with tough ears and large grains that remained attached to the ear at harvest were chosen. Preference for these traits was an important reason for crop domestication (Peng *et al.*, 2011). However, selection of the best varieties for domestication took place over many centuries in many regions (Deng *et al.*, 2005). Thus, the origin of cultivated hexaploid wheat is controversial (Matsuoka, 2011). It is concluded that only wild wheat species (wild einkorn and emmer) were subject to domestication selection, but common or bread wheat was not derived directly from a wild progenitor through domestication (Peng *et al*, 2011). Wheat (*T.aestivum* L.) is a hexaploid form of the free-threshing wheat genome AABBDD that is believed to have resulted from current hybridisation about 8,000 years ago between *Triticum turgidum* L. (allotetraploid wheat of AABB genome) and the diploid (wild species of DD genome) *Aegilops tauschii* var. strangulata (Matsuoka, 2011).

Cultivated wheat and its close wild relatives belong to the genus *Triticum L.*, a member of the Triticeae tribe (Matsuoka, 2011). Wheat is a tall, annual grass with an average height of 1.2 m (Deng *et al*., 2005). The leaves are flat and narrow, and can extend to 38 cm long; the stems are hollow in most varieties; and the heads are composed of flowers, ranging from 20 to 100 (DAFF, 2010). The flowers are grouped together in the spikelets, where they are fertilised to produce grains (Deng *et al*., 2005). Today the most important wheat’s are *Triticum aestivum* L. for making bread, followed by *T.durum* L. for pasta (macaroni and spaghetti) and lastly *T. comactum* L., a soft type of wheat that is used for making cakes, crackers, cookies and flours. However, this review will focus most on *Triticum aestivum* L. owing to the nature of the objectives. Bread or common wheat (*Triticum aestivum* L.) is the most widely cultivated wheat today, accounting for about 95% of all consumed wheat in the world (Peng *et al.*, 2011). In South Africa wheat is called by various names such as *koring* in Afrikaans, *korong* in Sesotho (DAFF, 2010) and *goroi* in Tshivenda.

2.2 Overview of wheat production in South Africa

The largest wheat-producing countries of the world are China, USA and Russia. However, extensive wheat production is also carried out in India, Western Europe, Canada, Argentina and Australia (Deng *et al.*, 2005). In South Africa, wheat is the second most important grain crop after maize (Gbetibouo & Hassan, 2005) and is consumed daily as bread, cakes, cookies, livestock feeds and alcoholic beverages (DAFF, 2010). South Africa is a net importer of wheat, having imported roughly 2 million tons in the 2010 season, mainly from Argentina, USA and Australia (DAFF, 2012). The major production areas of wheat include Western Cape, Free State and Northern Cape, which account for more than 70% of total production. However, wheat is produced in other provinces as well (Figure 2.1).

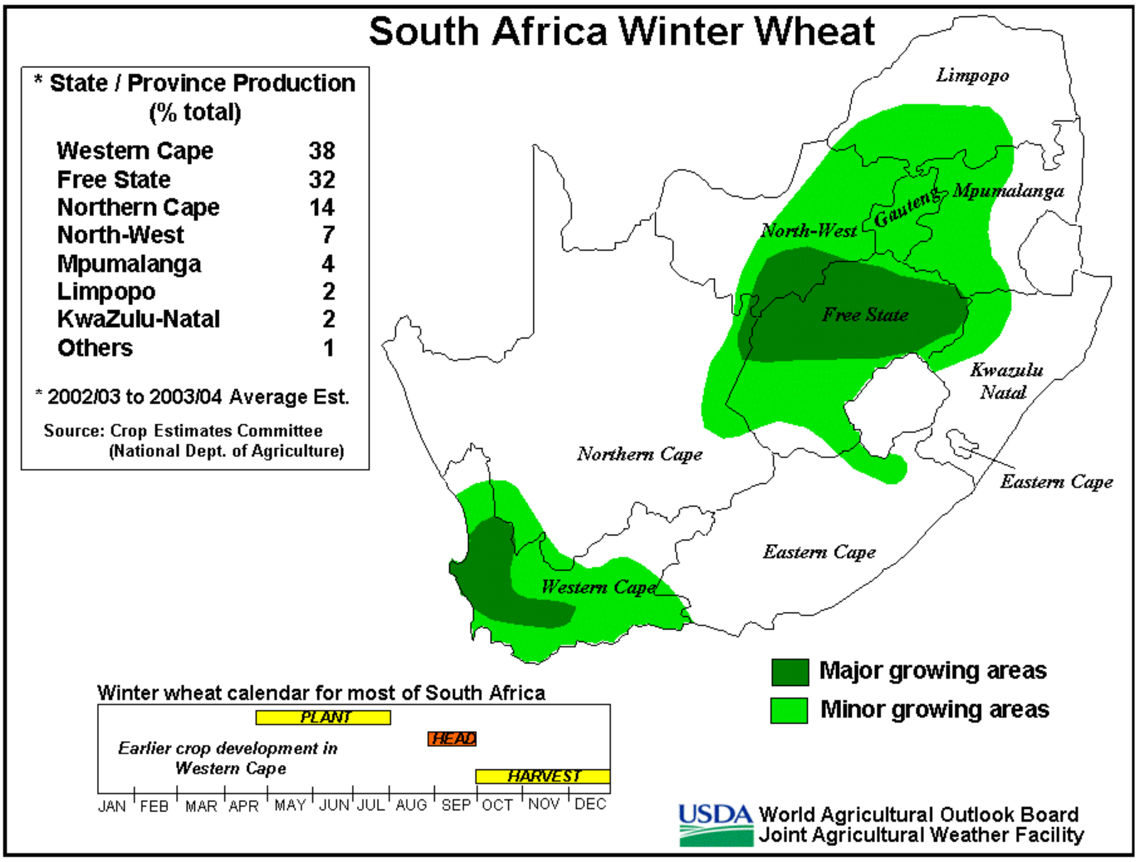

Figure 2.1 Major wheat production areas in South Africa (USDA, 2003)

According to Sun *et al*. (2006) high grain yield of 6.5 t ha^{-1} requires about 680 mm of water for bread wheat. Doorenbos and Kassam (1979) reported that water requirements for wheat range from 450 mm to 600 mm per annum. Furthermore Sun *et al*. (2006) found that optimal water consumption by wheat was about 453 mm without water stress. Deng *et al*. (2005) reported that wheat can be grown successfully under dryland conditions, with an average rainfall of 500 mm per annum. In South Africa, wheat is produced in both the summer and winter rainfall regions (ARC-SGI, 2009). It is grown as a dryland crop mostly in the winter rainfall regions, and under both irrigation and dryland in summer production regions (ARC-SGI, 2009; DAFF, 2010). The production environment of wheat locally can be divided into three regions. The first is the Mediterranean region around the Western Cape. This area is characterised by a wet subtropical winter with rainfall of about 400 mm and 150 mm in summer (Gbetibouo & Hassan, 2005). According to Slafer and Whitechurch (2001), this region is suitable for spring-winter-type genotypes. The second is the dryland environment in the Free State, which is characterised by average summer rainfall of 400 mm and winter rainfall of 150 mm, with dry cold winters (Gbetibouo & Hassan, 2005). The wheat cultivars are winter types, varying in vernalisation requirements and day-length sensitivity (Slafer & Whitechurch, 2001). The last type comprises the irrigation areas around the country, especially in Northern Cape, North West, Limpopo, Mpumalanga, Gauteng and Eastern Cape (Figure 2.1).

In the regions described above, annual wheat production over the past five years has ranged between 1.4 to 2.1 million tons at the average rate of 2 to 3.1 t ha^{-1} under dry land and about 5 to 7 t ha^{-1} under irrigation (DAFF, 2010; ARC-SGI, 2009). In South African, about 80% of wheat is grown under dryland whereas 20% grown under irrigation. In the last decade, wheat yields were very low with dramatic drops in area under production despite an increase in consumption (DAFF, 2012). However, yields are variable because of drought stress and heat which pose a risk in crop productivity (Blignaut *et al*., 2009). Due to climatic changes, most production areas of South Africa are under threat of aridity, as the total annual rainfall (495 mm) seems to become lower and more erratic (Gbetibouo & Hassan, 2005). Figure 2.2 indicates the rainfall distribution in is South Africa. Blignaut *et al*. (2009) reported that rain is distributed unevenly across the country with sub-tropical conditions in the east and dry desert conditions in the west (Figure 2.2).

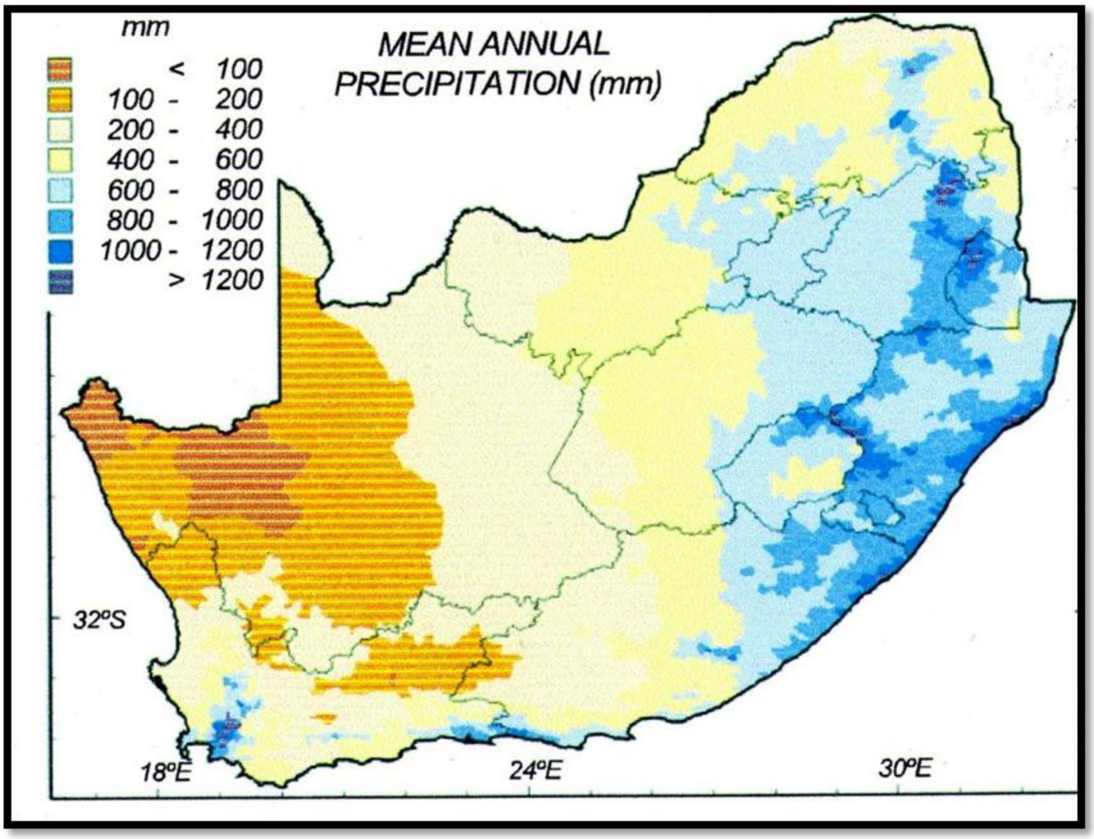

Figure 2.2 Mean annual rainfall distribution in South Africa (Gbetibouo & Hassan, 2005)

Water stress is most limiting in the summer production region, mainly because the crop is planted in winter when there is low rainfall (150 mm) and dry cool conditions (Gbetibouo & Hassan, 2005). Wheat is sown in autumn and harvested in early summer in the winter rainfall regions of South Africa. The window period for planting is mainly between mid-April and mid-June (DAFF, 2010). In the summer rainfall areas wheat is often planted between mid-May and the end of July, depending on the cultivar (DAFF, 2010, ARC-SGI, 2009). The seeds can be sown at a depth of 2 cm to 4 cm under irrigation and 5 cm to 8 cm in dry soil (Doorenbos & Kassam, 1979). In the soils that are dry at the beginning of the season, seeds should be planted at greater depth, so that they will not germinate until sufficient moisture is available through rainfall or irrigation (Acevado *et al*., 2002). That is referred to as dormancy, and is viewed as a drought-resistant mechanism (Blum 1996). Row spacing also depends on water availability, ranging from 30 cm to 100 cm (DAFF, 2010). In dryland farming, wider rows are preferred, whereas under irrigation, narrow rows can be used (Deng *et al*., 2005). According to the ARC-SGI (2009), the planting density of wheat ranges from 20 to 100 kg ha^{-1}, depending on the type of cultivar and the moisture availability.

2.3 Temperature requirements

Wheat is a temperate crop that can be cultivated in a wide range of climatic conditions, including subtropical and tropical zones (Deng *et al*., 2005) of both the Southern and Northern hemispheres (Peng *et al*, 2011). It is favoured by cool temperatures at the vegetative stage, whereas grain-filling occurs under warmer conditions (Acevado *et al*., 2002). The optimal air temperature for the wheat crop is about 20°C and any temperature above 35°C is not tolerated (Deng *et al*., 2000). In South Africa, warm temperatures of 22°C to 34°C are suitable for wheat in summer rainfall production regions, whereas cool temperatures between 5°C and 25°C are appropriate in winter rainfall areas. An ideal climate for planting wheat can be described as cool and moist, followed by a warm dry season for harvesting (DAFF, 2010).

Temperature mainly affects the wheat development rate and the duration of each stage. Generally increased temperature accelerates development, which leads to a shorter growth period (Slafer & Rawson, 1994). Wheat adapts to the various growing conditions mainly through vernalisation and photoperiod (Slafer & Whitechurch, 2001). Vernalisation refers to the minimum temperature that is required before the initiation of the reproductive parts (inflorescence). The photoperiod is the amount of light and the temperature required by the plant to influence any change in its development and that is affected by day length (Slafer & Rawson, 1994). Wheat only flowers after the completion of the cold period (Acevado *et al*., 2002). The double ridge stage is not reached until the chilling requirements have been met, consequently the vegetative stage is prolonged (Figure 2.3). The period from sowing to heading is sensitive to temperature. As the temperature increases, the duration to heading is reduced (Slafer & Whitechurch, 2001). Acevado *et al*. (2002) reported that winter wheat requires temperature of 0°C to 7°C for about 30 to 60 days for vernalisation. However, sensitivity depends on the response of a cultivar (Slafer & Rawson, 1994). Some cultivars require particular day length to flower, which is collectively referred to as the ‘photoperiod’. Generally wheat is a long-day plant. It flowers fast when day length increases, but does not require a specific day length to induce flowering (Deng *et al*., 2005).

Several authors reported that higher temperatures and limited water availability during wheat growth period modifies overall growth and development by affecting vital physiological processes such as photosynthesis and water uptake (Deng *et al*., 2000; Pradhan *et al*., 2012). Acevedo *et al*. (2002) reported that an optimum temperature for photosynthesis is 25°C;

whereas temperatures above 30°C negatively affect photosynthesis (Deng *et al*., 2000; Zhang *et al*., 1998). Leaf temperature can be used as an indirect indicator of leaf water status (Deng *et al*., 2000). It is assumed that when water stress increases, the stomata close partially, restricting water loss (which cools down the leaf), which leads to an increased temperature (Simpson, 1981).

Other factors that affect the productivity of wheat are frost and hail. Ear formation is affected negatively by frost, whereas hail in the summer rainfall regions of South Africa may also pose yield loss threats (DAFF, 2010). Rainfall and wet conditions towards harvesting may lead to disease prevalence and quality deterioration of grains (Biddulph *et al*., 2008). Wet conditions, particularly in the grain-filling stage, affect the falling number through pre-harvest sprouting (discussed in detail under quality in subsection 2.4.3)

2.4 Sensitivity of wheat to water stress

2.4.1 Photosynthesis

Photosynthesis is the basic determinant of plant growth and productivity, therefore productivity is determined mostly by the ability of the plant to maintain the rate of carbon assimilation under environmental stress (Anjum *et al*., 2011). Water stress causes reduction of the photosynthesis area, which limits the availability of assimilates (Saint Pierre *et al*., 2008). Siddique *et al*. (1999) found that plants subjected to drought at the vegetative stage recovered quickly to show a greater rate of photosynthesis at anthesis. Deng *et al*. (2005) reported that the physiological adaptation of wheat plants is attributed to closure of stomata in response to low soil water potential. However those genotypes that can keep their stomata open during water stress have higher yields when exposed to stress (Acevedo *et al*., 2002). Flexas *et al*. (2004) reported that stomatal closure is the early indication of stress which results in agreat reduction of the CO_2 flux into the leaf and water out of the leaf. Water transpiring through the stomata provides a means of cooling the plant and thereby avoiding temperature stress (Deng *et al*., 2005). Photorespiration may be an adaption for plants growing under water stress conditions by regulating and avoiding photochemical damage (Deng *et al*., 2005).

2.4.2 Growth and development

To understand how wheat growth, yield and quality respond to the availability of soil water, one first needs to explore how wheat develops (Figure 2.3). Crop development is often referred as the progressive development of stages towards maturity (Slafer & Rawson, 1994). Wheat growth stage development is distinguished by organ differentiation. Over the past decades, different scales and codes have been developed as a way of understanding and quantifying how wheat develops. Such knowledge is useful for crop management through observation and monitoring (Zadoks *et al.*, 1974). Physiologically, the following stages are usually distinguished: germination, emergence, tillering, floral initiation or double ridge, terminal spikelet, first node or beginning of stem elongation, boot, spike emergence, anthesis grain-filling and physiological maturity (Figure 2.3). The developmental stages of wheat are mostly divided into three phases, namely the vegetative, reproductive and grain-filling periods (Slafer & Whitechurch, 2001). The vegetative stage includes stages from emergence to double ridge; the reproductive stage covers stages from double ridge to anthesis, whereas grain-filling period starts at anthesis until physiological maturity or harvesting (Figure 2.3). Several authors indicated that wheat adapt to a wide range of climatic conditions (Slafer & Whitechurch, 2001; Deng *et al*., 2005). However, the shortage of water at some growth stages may affect growth, yield and quality (Ozturk & Aydin, 2004).

Water stress at the vegetative stage affects wheat growth and establishment, which affects both leaf elongation and expansion. This is mainly affected because leaves continue to emerge until the flag leaf appears, thereafter the stems grow actively, and the demand of assimilates increases significantly (Slafer & Whitechurch, 2001). Therefore, leaf expansion is most sensitive to water stress during the early vegetative stage (Acevedo *et al*., 2002). As a result, leaf area development is the physiological process that is most affected during the vegetative stage (Blum, 1996; Abayomi & Wright, 1999). However, plasticity in the leaf area is an important means by which a water stressed crop maintains controls over water use (Blum, 1996). Water stress at any growth stage decreases leaf area index (LAI) development due to a reduction in the number of leaves per plant, leaf expansion and leaf size (Zhang *et al*., 1998; Abayomi & Wright, 1999). Consequently severe water stress accelerates the death of leaves, which then reduces the interception of solar radiation (Blum, 1996). Cultivars that show little reduction in leaf area can still maintain good leaf area for photosynthesis (Jatoi *et al*., 2011).

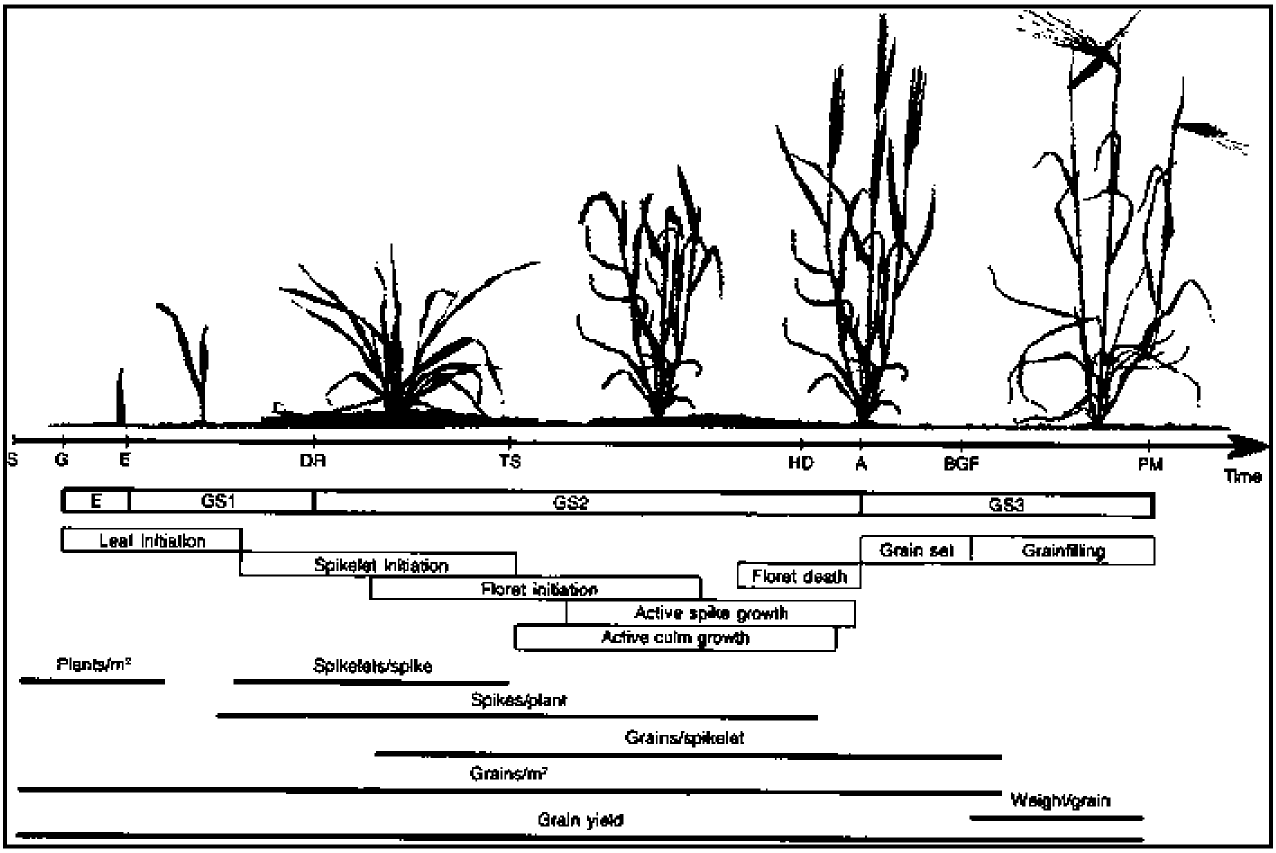

Figure 2.3 Various developmental phases of wheat (Slafer & Rawson, 1994). *S: sowing; G: germination; E: emergence; DR: double ridge appearance; TS: terminal spikelet initiation; HD: heading; A: anthesis; BGF: beginning of grain-filling period; PM: physiological maturity; GS: growth stage*

According to Slafer and Whitechurch (2001) the reproductive period can be sub-divided into early and late reproductive phases. Early reproductive period is from floret initiation to terminal spikelet initiation, whereas late reproductive phase includes stages from spikelet initiation to anthesis (Slafer & Whitechurch, 2001). Water stress at the early reproductive stages had little effect on yield due to irrigation at later reproductive stages (Doorenbos & Kassam, 1979). Abayomi and Wright (1999) found that water stress reduces grain yield most due to stress at late reproductive stages as compared to early stress and stress in the grain-filling stage. Several authors found that water stress at reproductive stage impairs the number of tillers, the number of leaves per plant, plant height, the number of ears and number of kernels per ear, which ultimately leads to a reduction in yield compared to stress at other stages (Abayomi & Wright, 1999; Qadir *et al*., 1999).

In bread wheat, Shamsi *et al.* (2010) found that grain yield was reduced most when 80% of water was depleted in the soil profile from stem elongation up to the end of the season, compared with 80% depletion from the booting and grain-filling stages. Water stress from stem elongation to maturity affects stem and spike growth mainly because that period covers most of the reproductive phases (Slafer & Whitechurch, 2001). Slafer and Whitechurch (2001) reported that the reproductive stage is characterised by active growth of stem and spikes. The same authors explained that during this period there is competition for resources due to high demand for assimilates and most yield components are determined. Bogale and Tesfaye (2011) found that the treatment exposed to stress from tillering to maturity reduced yield more than the treatment stressed from flowering and grain filling to maturity of wheat. Lower yield due to stress at the tillering stage could be attributed to the death of young tillers. Slafer and Whitechurch (2001) reported that the period from terminal spikelet initiation to anthesis is considered the most crucial in determining yield potential and most of the young tillers may die owing to limited resources. Abayomi and Wright (1999) found that withholding irrigation of wheat from booting to flowering reduced yield more than stress from stem extension to booting and stress from grain filling to maturity.

Wheat grain yield under water stress is determined by the response of yield components. Yield components that determine the final grain yield include the number of spikes “ears” per square metre, number of kernels per spike, and grain weight (Jatoi *et al*., 2009). Most of these yield components are determined at the reproductive stage (Figure 2.3). Ji *et al*. (2010) indicated that water stress at the reproductive stage of wheat leads to spikelet sterility, which significantly decreases the number of kernels per spike (Mirzaei *et al*., 2011). Grain number decreases sharply when water stress occurs during the spike growth period (Agenbag & De Villiers, 1995).

According to Slafer and Whitechurch (2001), grain-filling period starts from anthesis to maturity. This period is characterised by endosperm cells developed which mostly take place during early grain filling and serve as the main sinks for the accumulation of assimilates during the next phase of active grain filling (Slafer & Whitechurch (2001). Furthermore, Slafer and Rawson (1994) reported that potential size and maximum dry weight are determined after flowering to maturity. Water stress during grain-filling does not affect the number of fertile tillers; however, grain weight is reduced, due to a shortening of the grain-filling period, resulting from accelerated senescence (Bogale & Tesfaye, 2011).

2.4.3 Quality

The quality of wheat is influenced by the genotype (cultivar), environmental factors, and the interaction of the genotype and the environment (Agenbag & De Villiers, 1995). Water stress is one of the most important environmental factors that may influence the end-use quality of wheat (Saint Pierre *et al*., 2008). Saint Pierre *et al*. (2008) noted that appropriate soil water status during grain development, is of key importance for the accumulation of starch and protein in grains, and thus the formation of grain yield, kernel weight, diameter and quality. In South Africa, wheat grading systems take into account the grain protein content (GPC), falling number (FN) and hectolitre mass (HLM) (Table 2.1).

Several authors have indicated that there is an increase in GPC under drought stress as compared with well-watered conditions (Ozturk & Aydin, 2004; Zhao *et al.*, 2005). Zhao *et al.* (2005) found that water stress during the grain-filling phase increased the protein content. Related results were obtained by Ozturk and Aydin (2004), who found that continuous water stress increased protein content by 18% compared with well-irrigated treatments. Furthermore, Agenbag and De Villiers (1995) found that total protein during the milk stage (21 days after anthesis) was increased from 15.46% to 15.99% by the unstressed treatment (control), but decreased at 35 and 49 days after anthesis. Therefore the protein content is influenced by the duration and intensity of stress after the flowering stage. Under water stress, high GPC has been associated with low yield, and decreased kernel weight (Ozturk & Aydin, 2004). According to Zhao *et al.* (2005) water deficits in late stages of wheat growth negatively affect the conversion of sucrose to starch, but generally have less effect on protein deposition in the grain. Consequently, water stress can result in small pinched kernels that are high in protein and low in flour yield (Zhao *et al.*, 2005).

Doorenbos and Kassam (1979) reported that wheat grain yield and quality under limited water supply are not linearly related. Ozturk and Aydin (2004) also found that grain protein of wheat was significantly negatively correlated with grain yield. Saint Pierre *et al*. (2008) also found that the treatment that obtained higher grain protein produced lower grain yield. The positive effect of water stress on GPC is through reduction in the synthesis and storage of carbohydrates, which allows more concentration of nitrogen (N) per unit starch accumulated in the grain (Saint Pierre *et al*., 2008). The effect of nitrogen on GPC is reduced more under moderate or optimal water supply than in water limited conditions, although both yield and protein are higher under optimal conditions (Doorenbos & Kassam, 1979). Oweis *et al*. (1999) found that an increase in N fertiliser induces an increase in protein content of both straw and grain, whereas irrigation reduces the protein percentage. Protein is also influenced by temperature during grain filling; consequently higher temperatures induce an increase in protein content (Slafer & Whitechurch, 2001). In South Africa, grains of lower protein content (<12%) are penalised by a lower price per ton in the bread industry. According to the ARC-SGI (2009), higher GPC (>12%) in the bread and milling industry is considered as the first grade (Table 2.1).

Table 2.1 Grading system of bread wheat in South Africa (ARC-SGI, 2009)

Wheat bread – class B			
Grade	Minimum protein 12% moisture basis	Minimum hectolitre mass (kg/ha)	Minimum falling number (seconds)
B1	12	77	220
B2	11	76	220
B3	10	74	220
B4	9	72	200
Utility	8	70	150
Other classes:	Do not comply with these or other grading regulations		

The soil water deficit and heat stress during the grain-filling period induce a decrease in hectolitre mass (HLM) (ARC-SGI, 2009). Reduction of HLM in grain-filling stage is mainly due to the percentage of small malformed and broken kernels, which results in a reduction of thousand kernel mass (TKM) (Mirzaei *et al*., 2011). Furthermore, Manley *et al*. (2009) concluded that reduced HLM was due to unclean wheat which could be due to the roughness of bran and swollen kernels. Generally when HLM drops, the percentage of small, malformed, and broken kernels usually increases (Barnard *et al*., 2002). Hectolitre mass gives a direct indication of the potential flour extraction of the grain sample. Flour extraction is a critical parameter for the miller as it largely influences his profitability (ARC-SGI, 2009).

Hectolitre mass is therefore part of the grading regulations by the South African bread industry (Table 2.1).

Other than grain protein content and hectolitre mass, falling number (FN) is also an important quality parameter in wheat grading (Table 2.1). According to the report of ARC-SGI (2009), conversion of enzymes has an effect on falling number. Alpha-amylase enzyme activity determines the degree of falling number which has effect on flour quality. High α-amylase activity (low falling number) is an indication that the starch molecules have to a large extent been broken down to sugars (maltose in particular), and such grain is unacceptable for commercial milling and baking in South Africa (ARC-SGI, 2009) and Australia (Biddulph *et al*., 2008). However, this is common under rainy conditions prior to harvesting of wheat grain; consequently grains may begin to germinate, a phenomenon known as pre-harvest sprouting (Biddulph *et al*., 2008). Flour made from sprout-damaged wheat can have a falling number of 100 seconds or lower. In South Africa bread with an average α-amylase activity has a falling number of about 220 seconds (Table 2.1) (ARC-SGI, 2009). The upper limit for the falling number test is about 400 seconds, which occurs for flour devoid of α-amylase activity. The addition of malt or α-amylase from another source also affects falling numbers. Consequently, this test can be used as a means to monitor and control these additions (Barnard *et al*., 2002).

2.5 Wheat adaptation to water stress

Blum (1996) defined plant adaption as an adjustment of structure or habits by certain species mainly to improve the conditions of their environment, and stated that it is often hereditary. Araus *et al*. (2008) reported that the key factor that will determine the future severity of the effects of climatic change on food production is crop adaptation. Several authors indicated that the most important factors that determine severity of water stress on crop are the duration, intensity and (time) growth stage at which water stress occurs (Blum, 1996; Bogale & Tesfaye, 2011). Therefore, it is important to understand the mechanism of crop response to drought or water stress for better breeding (Araus *et al*., 2008) and agronomic management (Deng *et al*., 2005).

Physiological and morphological characters that confer drought resistance can be classed according to their association with water absorption or water loss by the crop (Blum, 2005).

Plants restrict cell water loss through partial closure of the stomata (Flexas *et al*. 2004). The closure of stomata due to water stress greatly reduces the flux of CO_2 into the leaf and of water out of the leaf (Shun *et al*., 2012). Araus *et al*. (2008) reported that water loss out of a leaf, which is collectively referred to as transpiration, provides a means of cooling the plant, and thereby avoiding other environmental stresses such as temperature or heat stress (Deng *et al*., 2005). The avoidance and tolerant strategies of wheat under water stress are discussed in sub-section 2.5.1 and 2.5.2 respectively; whereas the last section (2.5.3) give a brief review on management of water stress through irrigation strategies.

2.5.1 Avoidance strategy

It is well documented that plants normally resist drought stress through dehydration avoidance and tolerance mechanisms (Simpson, 1981; Blum, 2005). Dehydration avoidance can be through mechanisms that allow the plant to minimise water loss while maximising water uptake. Generally, stressed plants minimise water loss through the closure of stomata, which consequently reduces stomatal conductance, leaf size and LAI (Zhang *et al*., 1998). Deng *et al*. (2005) reported that plants with higher root density and deep rooting systems are associated with higher water absorption. Therefore, crops with a deep rooting system are favoured where deep soil water is available in the profile (Blum, 2005).

In nature, plants are exposed to slow developing water deficits, which usually take days, weeks or months, or perhaps face short-term water shortages. Plants adapt or resist slow developing water deficits by shortening their crop cycle, which is referred to as an 'escape avoidance mechanism' (Araus *et al*., 2002). Geerts and Raes (2009) reported that drought stress decreases the crop cycle length in wheat. Shortening of the crop cycle reduces the total demand for water and avoids severe terminal stresses, mainly because of the shorter period in the field (Araus *et al*., 2008).

At management level, farmers can use escape strategies by shifting the planting dates or switching to an existing tolerant crop variety (Araus *et al*., 2008). However, shifting the planting dates (early or late planting) affects the duration of the growth season. Therefore short growth duration or early maturing cultivars can be used if this strategy is followed. Short growth duration cultivars are generally defined by early flowering or heading, and may escape drought (Araus *et al*., 2002), particularly for conditions characterised by drought stress towards the end of the season (Araus *et al*., 2008). Early heading cultivars complete a greater fraction of the grain-filling duration earlier in the season when air temperatures are lower and generally more favourable. However, they tend to produce fewer total leaves per tiller, but retain more green leaves and lose fewer leaves to senescence at anthesis than later heading cultivars (Blum, 1996). On the other hand, longer growth duration cultivars are often associated with high yield potential (Blum, 1996). Consequently, using drought escape as a solution may have negative effects of yield reduction (Araus *et al*., 2002). This is serious, especially where availability of rainfall is unpredictable and may vary to a large extent between years. Generally drought escape strategy can save water due to the shortened crop cycle, but also reduces the accumulated photosynthesis during the crop cycle (Blum, 1996).

2.5.2 Tolerance strategy

Blum (2005) defined dehydration tolerance as the relative capacity to sustain or conserve plant function in a dehydrated state. Dehydration tolerance is viewed as the second line of defence after dehydration avoidance (Simpson, 1981). Simpson (1981) indicated that most mesophytes species cannot tolerate water loss below 50% of saturated soil water content without injury or death. Other physiological mechanisms that enable plants to tolerate water stress include osmotic adjustment and related solute membrane stability (Deng *et al*., 2005). The osmotic adjustments help the plant to continue with cell function and growth. However, osmotic potential is the function of solute concentration that differs per species, but includes mainly organic acids and sugar (Simpson, 1981).

Dehydration tolerance as an effective drought-resistance mechanism in crop plants is rare, as it exists mostly in the seed embryo. Once the seed has germinated, the plant loses its tolerance (Blum, 1996). The only major exception that constitutes a form of effective dehydration tolerance mechanism in crop plants is stem reserve utilisation for grain-filling under drought stress (Blum, 1998). This is a coordinated whole-plant process that allows effective grain filling when whole-plant photosynthesis is inhibited by stress during grain-filling (Blum, 2005). Stem reserve utilisation has been found to be an effective yield-supporting mechanism under drought stress (Blum, 1996).

The major condition for stem reserves is sufficient storage of carbohydrate before grain filling (Blum, 1998). This may be partially linked to plant traits that promote high yield potential, at least during the pre-flowering growth stage (Blum, 2005). Although some stem reserve mobilisation may support grain-filling under non-stress conditions, reserve mobilisation is noticeably induced by drought stress during grain-filling (Blum, 1998). The signal for the induction of reserve mobilisation under drought stress is not clear, but is likely to involve hormones such as gibberellins and abscise acid (Blum, 1996; 2005).

To evaluate the tolerance of wheat cultivars to drought stress conditions, several indices are used namely: stress tolerance index (TOL), susceptibility index (SSI) and yield stability index (YSI) (Khan & Naqvi, 2011). Such indices provide meaningful measures under drought-stress conditions based on yield loss under stress compared with normal conditions (Golabadi *et al*., 2006). Higher TOL indicates relatively more sensitivity to stress, whereas a smaller value of TOL indicates high tolerance, due mainly to lower yield reduction. The use of SSI as a measure of yield stability depends on the time of the stress occurrence in relation to the phenology of specific cultivar (Bogale & Tesfaye, 2011). Cultivars with lower values of SSI are regarded as tolerant, whereas cultivars that have an SSI value of more than one are classified as susceptible (Khan & Naqvi, 2011). However, where there is a variation in yield potential between cultivars, a lower SSI value may not necessarily denote stress resistance, as it could be influenced by lower yield under optimal conditions (Khan & Naqvi, 2011). The YSI is obtained by dividing yield under stress by non-stress (GYs/GYp). The cultivars with the highest YSI produce lower yield under non-stress conditions and highest yield under stress condition (Khan & Naqvi, 2011).

2.5.3 Management of water stress through irrigation

Irrigation, where applicable, is one of the main strategies and an old method to alleviate or avoid water stress in crop production (Simpson, 1981). Araus *et al*. (2008) reported that intensification and stabilisation of income in agriculture were mostly due to extensive use of irrigation. Increase in cereal production at present will be optimised mainly under irrigation, through the diffusion of improved crop varieties, and agronomic practices suitable for specific ecosystems (Araus *et al*., 2008). The uses of deficit and supplemental irrigation are currently viewed as some of the practices that can alleviate water stress (Oweis & Hochum, 2006). Under these practices, water is applied at the most sensitive stages to sustain yield and improve water use efficiency (WUE), mostly in dry regions (Ali *et al*. (2007). Sections

2.5.3.1 and 2.5.3.2 below give a brief review on the uses of deficit and supplemental irrigation as a way of managing water stress.

2.5.3.1 Deficit irrigation

Deficit irrigation (DI) is an optimising strategy under which crops are deliberately allowed to sustain some degree of water deficit and yield reduction, through the application of less water than is required by the crop, mostly in drought seasons (Oweis & Hochum, 2006). Generally, DI aims to apply water at the most sensitive stages such as crop establishment, flowering and early grain filling, and to withhold irrigation at less sensitive stages such as the vegetative stage (Geerts & Raes, 2009). Ali *et al*. (2007) indicated that water saved in less sensitive stages can be used to irrigate other crops and also allows farmers to expand their production areas, which may consequently increase net farm income. The use of DI requires appropriate knowledge of crop water use and responses to water deficits, including the identification of critical crop growth stages, and of the economic impacts of yield reduction strategies (Geerts & Raes, 2009).

2.5.3.2 Supplemental irrigation

Supplemental irrigation (SI) is a management strategy in which a limited amount of water is applied to rainfed crops that can normally grow without irrigation. It is implemented mainly to increase and stabilise productivity (Oweis & Hochum, 2006). The WUE of supplemental irrigation is generally high if practised well (Zhang & Oweis, 1999). Geerts and Raes (2009) reported that SI practices and benefits differ, depending on the crop and production regions. Supplemental irrigation is often used to save, improve and stabilise yield in the event of unforeseen drought (Oweis *et al*., 1999). It is also practised to supplement the expected total seasonal rainfall (Zhang *et al*., 1998). This practice aims to maximise water productivity and to stabilise yield rather than maximise yield (Geerts & Raes, 2009). Supplemental irrigation influences not only yield, but more importantly water productivity. Yield and WUE under irrigation and rainfed conditions are improved when used simultaneously (Oweis *et al*., 1999). The high water productivity of SI water is attributed mainly to alleviation of water stress during the most sensitive stages of crop growth. Blum (2009) reported that an increase in WUE under water stress conditions may seem to be an ideal mechanism for drought resistance. It is viewed mostly as a conservative strategy that involves reduced transpiration. However, several authors indicated that the effect of these irrigation strategies on yields and related economic results depends on the irrigation scheduling, the irrigation system performance, production costs and yield values (Zhang & Oweis, 1999; Oweis & Hochum, 2006). Ali *et al*. (2007) also found that water stress in the grain-filling stage had little effect on yield compared with stress in the booting and heading stages.

Many researchers concluded that deficit and supplemental irrigation are economically viable options to follow under conditions of limited water supply (Zhang & Oweis, 1999; Shamsi *et al*., 2010). They are suitable methods for saving water while maintaining an acceptable yield under water shortage conditions (Ali *et al*., 2007). Shamsi *et al.* (2010) found that applying irrigation when 80% of water is depleted in the soil profile from grain filling to the end of the season improved WUE, compared with 80% depletion from stem elongation and flowering stages in bread wheat. Zhang and Oweis (1999) found that SI during booting to grain filling improving WUE when the chances of rainfall were low. Ali *et al*. (2007) found that SI in the early stages of wheat saved 68% of water, compared with the well-watered treatment. Zhang *et al*. (1998) found that single irrigation at the end of the second node extension improved WUE, compared with SI in four stages (one at first and second node extension, first and third weeks after flowering). Seghatoleslami *et al*. (2008) found that withholding irrigation in the vegetative stage improved WUE compared with stress in the ear emergence (heading) and grain-filling stages in millet.

CHAPTER 3: GENERAL MATERIALS AND METHODS

3.1 Site description

The experiments were carried out under a rain shelter during winter seasons of 2010 and 2011 at the Hatfield experimental farm, University of Pretoria, South Africa (Figure 3.1). The soil of the experimental site had a clay content of 26% and pH(H_20) of 6.7. According to Agricultural Research Council-Small Grain Institute, 2009 (ARC-SGI) Pretoria falls under the summer wheat production regions which is mostly characterised by production under irrigation.

Figure 3.1 Panoramic view of wheat (*Triticum aestivum* L.) trial at maturity in the 2011 cropping season

3.2 Cultural practices

To evaluate water stress effects at different growth stages, three wheat cultivars were used, namely SST 843, Duzi and Steenbras. SST 843 was released in 2009, Duzi in 2004, and Steenbras in 2001. All three cultivars are recommended for irrigated warmer production regions. The cultivars Duzi and Steenbras are on the preferred millers' list in South Africa

(ARC-SGI, 2009). Important dates and agronomic practices applied in the two successive growing seasons are summarised in Table 3.1.

Table 3.1 Important dates and agronomic practices applied in the two successive wheat growing seasons

Activity	**2010 season**	**2011 seasosn**
Planting date	17 July	07 June
Seeding rate	100 kg ha^{-1}	100 kg ha^{-1}
Row spacing	0.25 m	0.25 m
Harvesting	17 November	16 November
Total days	125	156

The targeted potential yield under irrigated production was 8 t ha^{-1} or higher. Fertilisers were broadcast according to the soil analysis results: 160 kg ha^{-1} N (in the form of LAN), 60 kg ha^{-1} P (as superphosphate) and 30 kg ha^{-1} K (as KCl) were applied before planting. Topdressing of LAN was done at different growth stages: 17 kg ha^{-1} N was applied during the vegetative stage and 8 kg ha^{-1} N during the flag-leaf stage, as recommended by the ARC-SGI (2009). Seeds were planted with a tractor drawn planter in rows spaced 0.25 m apart. The total area of each plot (experimental unit) was $4.5m^2$ and consisted of four rows oriented in an east-west direction. Weeds and diseases were controlled manually when needed, and bird nets were used to protect the crop from birds after planting and during the grain-filling stage.

3.3 Experimental design and treatments

A factorial experiment was conducted (wheat cultivars × water stress applied at different growth stages) in a split-plot completely randomised block design. The four irrigation treatments were: water stress from tillering to flag leaf (stem elongation (SNN)); from flag leaf to end of flowering (flowering stage (NSN)); and from grain filling to physiological maturity (grain-filling stage (NNS)); and an optimal supply of water was maintained by weekly irrigating to the field capacity for the control treatment (NNN). Treatments are summarised in Table 3.2. Irrigation treatments were allocated to the main plots while the three wheat cultivars to subplots, and the treatments were replicated three times, giving a total of 36 plots. The treatments were based on the morphological stages of wheat according to the

Zadoks scale and Joubert scale (South African scale) (Zadoks *et al*., 1974; ARC-SGI, 2009). However, decimal codes representing each stage were adopted from the Zadoks scale (Table 3.2). A dissecting microscope was used to establish the growth stage. The last irrigation in 2010 was on 95 DAP, whereas in 2011 it was on 127 DAP. Days to harvesting or duration of the seasons is presented in Table 3.1.

Table 3.2 Irrigation treatments and decimal codes of growth stages exposed to water stress in the 2010 and 2011 seasons

Irrigation Treatments	**Zadoks decimal code**	**Growth Stages Stressed**	**Time of stress (Days after planting-DAP)**	
			2010 Season	2011 Season
SNN	Z25-39	Tillering-flag leaf stage	51-63DAP	45-77DAP
NSN	Z39-69	Flag leaf-end of flowering	63-77DAP	77-105DAP
NNS	Z69-92	Grain-filling-maturity	77-125DAP	105-165DAP
NNN	-	well-watered	(control)	(non-stressed)

3.4 Data collection

In order to quantify the effects of water stress on three South African wheat cultivars, weather related data, physiological data and development data, soil water content, yield, and quality data were collected during the 2010 and 2011 season.

3.4.1 Weather data

Meteorological data was collected from an automated weather station installed close to the experimental site. Daily solar radiation, maximum and minimum relative humidity, maximum and minimum temperatures and wind speed were collected for the period of the trials (Table 3.3).

3.4.2 Leaf gas exchange parameters

Net photosynthesis (Pn), transpiration (E), stomatal conductance (g_s), leaf temperature (TL), and internal CO_2 concentration (Ci) were determined at various wheat growth stages using a portable gas exchange measuring system (Li6400, Li-Cor, USA). Instantaneous water use efficiency (iWUE) was calculated by dividing Pn by E (Pn/E) (Bogale *et al.*, 2011). Measurements were taken on five top leaves and flag leaves of the control (NNN), the treatment stressed at stem elongation (SNN), the flowering stage (NSN) and the grain-filling stage (NNS). Measurements were taken between 11:00 and 12:00 under atmospheric CO_2 and full sunlight conditions, as recommended by Changhai *et al*. (2010). Leaf gas exchange measurements were collected in the 2011 season only. During stem elongation, leaf gaseous exchange measurements were collected only from the stressed treatment (SNN) and the control treatment (NNN). The other treatments (NSN and NNS) were not exposed to water stress during stem elongation. It was assumed that they would not be different from the NNN treatment since they were irrigated to field capacity to avoid stress. During grain-filling, all leaf gas exchange measurements were collected from only two cultivars (Duzi and SST 843) owing to technical problems with the equipment.

3.4.3 Leaf water potential (LWP)

A portable pressure chamber was used to estimate leaf water potential (LWP). Fully developed leaves were placed in an aluminium foil leaf holder. Leaves were continuously protected by the leaf holder until the measurements had been completed. Pressure was released from the cylinder of compressed nitrogen gas until sap was forced out through the cut end. The measurements were taken only from the cultivar SST 843.

3.4.4 Plant growth measurements

To monitor the effect of water stress on wheat growth, four plants were harvested from an area of 0.06 m^2 at different growth stages (interval of two to three weeks). The number of leaves per plant was determined, and leaf area was measured using an LI 3100 belt-driven leaf area meter (LiCor, Lincoln, Nebraska, USA) and leaf area index (LAI) was calculated using equation 3.1. Thereafter samples were oven-dried (for about 24 hours) at 68 ºC until constant mass to determine dry matter yield (DM). The total above-ground dry yield was determined by adding together the dry mass of the leaves, stems and ears. Plant height was measured from 39 DAP for each cultivar and irrigation treatment in the 2011 cropping season, but in 2010 it was recorded only at harvesting.

$$LAI = \frac{measured\,total\,leaf\;area}{sampled\;area} \qquad (3.1)$$

3.4.5 Soil water content monitoring

Soil water content in the root zone was monitored twice a week using a neutron water meter (Campbell Pacific Nuclear Inc., USA, Model Hydroprobe) that was calibrated for the experimental site. Readings were taken at an interval of 0.20 m to a soil depth of 1m by lowering the radioactive source through an access tube that was installed in each sub-plot. After planting, sprinkler irrigation system was used for good plant establishment and thereafter a drip irrigation system was used for the rest of the season. Dripper pipes were placed at 0.25 m spacing between rows.

The drip irrigation system was pressure compensated with a discharge rate of 1.5*l* h^{-1} in the pressure range between 100 kPa and 120 kPa. Water meters were installed to quantify the amount of water applied to each plot. In the 2010 season, plots of the same water treatment, regardless of cultivar were irrigated simultaneously (from the same valve and water meter, for example the SNN treatment). In addition, the timing of the stress period was more accurate in 2011, as the growth stages and development were monitored through the use of a dissection microscope. In the 2011 season, each treatment per cultivar was irrigated individually. Irrigation was then applied, depending on the measured average soil water deficit per treatment of each cultivar to refill the soil profile to field capacity.

3.4.6 Grain yield and quality determination

Grain yield and yield components were determined by harvesting 1 m^2 at maturity. Plants were harvested by hand and threshed. The ear length from each cultivar and treatment was measured with a ruler, and the number of seeds per unit area harvested and the number of seeds per ear was counted. Thereafter grain moisture content was determined by oven drying, and yields and seed mass were reported on a 12% moisture basis according to standard procedures. Thousand kernel mass (TKM) was determined by weighing 1000 seeds from oven-dried grain samples harvested from each plot and adjusting the grain moisture content to 12% (Barnard *et al.*, 2002). The harvest index was calculated as the ratio of grain yield to total aboveground biomass at maturity (Ali *et al.*, 2007). Yield reduction (YR), stress tolerant (TOL) and yield stability index were calculated using equation 3.2 to 3.4.

$$\text{Stress tolerant or yield reduction (TOL / YR)} = (GYp - GYs) \qquad (3.2)$$

$$\text{Percentage (\%) yield reduction (YR)} = (GYp - GYs) / GYp * 100 \qquad (3.3)$$

$$\text{Yield stability index (YSI)} = GYs/GYp \qquad (3.4)$$

Where: GYp refers to mean grain yield of cultivar under irrigation condition, whereas GYs refers to mean grain yield of cultivar under water stress conditions (Khan & Naqvi, 2011).

Grain samples were collected from each plot and sent to the ARC-SGI laboratory for quality determination. GPC results were expressed as a percentage of the total sample mass. HLM is considered an important prediction of flour yield, and represents the mass of wheat per volume (ARC-SGI, 2009). HLM was determined by equipping the hectolitre device with a funnel that provides uniform packing, using a 500 ml measuring cup according to the South African grading system described by Manley *et al.* (2009). Falling number (FN) was recorded according to the standard method as described by Barnard *et al.* (2002).

3.4.7 Water use and water use efficiency calculation

Water use (ET) in mm was calculated using the soil water balance equation (3.5), and water use efficiency (WUE) in kg ha^{-1} mm^{-1} was calculated using equation 3.6.

$$ET = \Delta S + P + I - Dr - R \qquad (3.5)$$

$$WUE = (GY/ ET) \qquad (3.6)$$

Where GY is grain yield kg ha^{-1}
Where ΔS= the change in soil water storage (mm), P = rainfall (mm), I = irrigation (mm), Dr = drainage below the bottom of the root zone (mm), R= runoff (mm). P was considered to be

zero because the experiment was conducted under a rain shelter (Figure 3.1 in chapter), I was obtained from water meter readings, Dr+R was also assumed to be zero. ∆S was calculated from neutron probe measurements (Ali *et al*., 2007).

3.5 Statistical analysis

The analysis of variance was performed using Statistical Analysis System software (SAS 9.3 – 2010). The simple correlation co-efficiency between grain yield, yield components and quality parameters was also performed using SAS 9.3 (2010). Means were compared using the least significant differences (LSD) test at 5% probability level. Correlation between parameters were also computed (using Microsoft Excel 2010) when applicable.

CHAPTER 4: WATER STRESS EFFECTS ON PHYSIOLOGICAL PARAMETERS OF WHEAT CULTIVARS STRESSED AT VARIOUS STAGES

Abstract

The experiments were conducted to assess the physiological and growth response of three South African wheat cultivars, namely Duzi, Steenbras, and SST 843, which were stressed during the stem elongation (SNN), flowering (NSN), and grain-filling (NNS) stages, whereas the control treatment (NNN) was irrigated to field capacity throughout the season. Water stress treatments and cultivars significantly influenced leaf gas exchange parameters such as intercellular CO_2 concentration (Ci), net photosynthesis rate (Pn), transpiration rate (E) stomatal conductance (g_s) and leaf temperature. The response to water stress of growth and physiological parameters depends on the developmental stage at which water stress occurs. All growth parameters showed significant recovery when stress was terminated in the flag-leaf stage (SNN), whereas the period from flag leaf to end of flowering (NSN) was the most sensitive to water stress. Water stress in the flowering stage (NSN) decreased stomatal conductance by 84% compared with the control treatment (NNN), which could be attributed to partial closure of stomata owing to a drop in leaf water potential (LWP), which resulted in lower Ci and higher leaf temperature. The NSN water-stress treatment significantly reduced photosynthesis and transpiration by 59% and 72%, respectively, compared with the control treatment (NNN). Water stress imposed at any growth stage reduced the number of green leaves, the leaf area index (LAI), plant height and dry matter production compared with the control treatment. Reduction of physiological functions under water stress was due to lower LWP, which affects the formation and enlargement of leaves. The NSN treatment reduced leaf area the most, even after termination of stress in the grain-filling stage (131 DAP), which was because of the accelerated death of leaves. The cultivar SST 843 had higher Pn and LAI than the other cultivars. Plant height of all cultivars used in the present study responded similarly to water stress treatments at any growth stage. Water stress at any growth stage reduced plant height. Water stress imposed in the stem elongation stage (SNN) reduced plant height most by 25% compared to the control treatment. However, it recovered owing to irrigation thereafter in the flowering and grain-filling stages. The NSN treatment reduced final plant height most in the 2011 season. In the grain-filling stage (165 DAP harvest), the

NSN treatment reduced plant height by 19%, compared with 9% and 5% reduction of the NNS and SNN treatments. The NSN treatment also reduced dry matter production most, and it failed to recover when irrigated in the grain-filling stage. The NSN treatment reduced dry matter production by 59% in the flowering stage and in the grain-filling stage it reduced dry matter production by 18%, which was higher than the 11% reduction in the NNS treatment. The hypothesis that photosynthesis of different wheat cultivars will respond differently to water stress imposed at various growth stages was accepted. Significant reduction in physiological functions and growth components due to stress in the flowering stage (NSN) suggests that supplemental irrigation is more critical at this stage.

Key words: leaf area index, photosynthesis, stomatal conductance, transpiration, water stress, wheat growth stages,

4.1 Introduction

It is well documented that water stress is one of the most detrimental biotic stresses responsible for the impairment of wheat growth and development (Deng *et al*., 2000, Flexas *et al*., 2004). Water stress limits photosynthesis (Pn) which is the primary source of growth and development of the plant (Bogale *et al*., 2011). Anjum *et al*. (2011) reported that the future productivity of a crop will be determined mostly by the ability of the plant to maintain the rate of carbon (CO_2) assimilation under environmental stresses. Several authors noted that the rate CO_2 assimilation (photosynthesis) under water stress is attributed to closure of stomata (Flexas & Medrano, 2002; Flexas *et al*. 2004; Ahmed *et al*., 2012). The stomata partially close in mild or moderate water stress whereas it completely closes under severe stress (Flexas *et al*., 2004). Stomatal conductance (g_s) therefore serves as a good indicator of the rate at which water and CO_2 move in and out of the leaf in response to developing soil water stress (Shan *et al*., 2012). Stomatal closure due to reduction in soil water content lowers leaf water potential (LWP), which induce increase in leaf temperature, resulting in lower photosynthesis and transpiration rate (Deng *et al*., 2000). Water stress influences the intercellular CO_2 concentration (Ci), which decreases at the initial stage of stress (moderate) but increases when stress progresses (severe) (Flexas & Medrano, 2002). The decrease in intercellular CO_2 concentration owing to water stress indicates that reduction of photosynthesis rate is attributed mainly to stomatal limitation rather than metabolic limitations (Flexas & Medrano, 2002).

Leaf transpiration rate is the productive water loss that the plant pays in exchange for CO_2 uptake. In nature this is affected by several environmental stresses, including water stress. However, it may also be influenced by the time or growth stage at which the stress occurs (Bogale *et al*., 2011). Shan *et al*. (2012) found that water stress at the jointing stage of wheat significantly reduced the transpiration rate compared with the non-stressed treatment. Siddique *et al*. (1999) found that the photosynthesis rate of wheat cultivars exposed to water stress at the vegetative stage recovered at the anthesis stage after water stress was terminated. Leaf photosynthesis and transpiration rate may be used to quantify water use efficiency (WUE) at leaf level, which is defined mostly as instantaneous water use efficiency (iWUE) or transpiration efficiency (Changhai *et al*., 2010; Bogale *et al*., 2011). This is obtained by dividing net CO_2 assimilated by photosynthesis over water transpired in the same period (Bogale *et al*., 2011). The cultivars with higher iWUE under both water stress and well-irrigated condition produce higher yield due to higher photosynthesis assimilated per water loss through transpiration (Changhai *et al*., 2010). Wu and Bao (2011) found that maintaining 85% of water in the soil profile improves the photosynthetic rate of wheat compared with 55% field capacity (FC). However, the same authors found that 55% FC increased instantaneous water-use efficiency (iWUE). They concluded that cultivars grown under stress conditions have higher iWUE due to reduction of transpiration rate, which consequently has negative effects on the grain yield (Wu & Bao, 2011).

Reduction in transpiration rate under water stress results in a higher leaf temperature (Zhang *et al*., 1998), due to less leaf cooling. Gupta *et al*. (2001) found that increased leaf and air temperature due to water stress at anthesis had negative effects on grain yield and other yield attributes. Pradhan *et al*. (2012) also reported that higher air temperatures combined with water stress at the grain-filling stage decreased leaf chlorophyll content, which consequently accelerated leaf senescence and led to yield reduction. Siddique *et al*. (2000) indicated that higher leaf temperature under water stress was due to increased respiration and a lower transpiration rate because of stomatal closure. Acevedo *et al.* (2002) indicated that optimum air temperatures between 15ºC and 25ºC are required for photosynthesis, whereas air temperature above 30ºC negatively affects photosynthesis (Deng *et al*., 2000). It is important to increase knowledge of the physiological basis of photosynthesis and growth under water stress in order to be able to improve plant yield and to face the climate change-driven increase in global aridity (Anjum *et al*., 2011). Leaf gas exchange characteristics have been reported to be of prime importance among physiological attributes in screening crops for water stress tolerance at various growth stages (Bogale *et al*., 2011). Therefore, the aim of this study was to categorise the growth stage at which water stress would have minimal effect on photosynthesis of wheat cultivars and, secondly, to identify if some cultivars are better adapted to water-limited conditions.

The following hypotheses were tested:

> **$H_0$1**: Water stress will induce stomatal closure, which will restrict water loss, resulting in reduction of internal leaf CO_2 concentration, photosynthesis and transpiration rate,
>
> **$H_0$2**: Photosynthesis of different wheat cultivars will respond differently to water stress imposed at various growth stages.

4.2 Materials and methods

General methodology was discussed in chapter 3 of this dissertation.

4.3 Results and discussion

The first part of this section describes the weather conditions during the 2010 and 2011 growing seasons. Whereas, the second section discusses the effects of water stress on some physiological parameters of wheat associated with leaf gaseous, followed by the growth parameter related to yield. Lastly conclusions are drawn from all these sections.

4.3.1 Weather conditions during the growing periods

The 2010 season was characterised by higher temperatures, higher wind speed, and lower humidity and solar radiation in the early vegetative stages of the crop (June and July), whereas 2011 had favourable cool conditions.

Table 4.1 Mean monthly temperature (°C), relative humidity (RH, %), wind speed (m/s), solar radiation (MJ m^2 d^{-1}) and monthly average reference evapotranspiration (ET$_O$, mm day^{-1}) data for the 2010 and 2011 cropping seasons

Month	**Maximum temperature**	**Minimum temperature**	**Maximum RH**	**Minimum RH**	**Wind speed**	**Solar radiation**	**ET$_O$**
			…………2010 Season…………				
July	21.7	5.2	73.5	19.6	1.3	11.4	2.6
Aug	23.7	6.0	75.8	17.3	1.6	12.6	2.8
Sep	28.3	11.0	64.1	16.8	1.8	16.6	4.2
Oct	30.6	14.7	72.2	19.3	2.1	18.4	4.9
Nov	29.7	15.3	81.8	26.6	1.8	17.9	4.6
			…………2011 Season…………				
June	19.3	3.1	81.5	23.3	1.2	13.5	2.3
July	19.2	3.1	70.1	16	1.7	12.5	2.5
Aug	22	5.3	65.9	13.4	1.7	16.2	3.3
Sep	27	10.9	51.5	7.5	1.8	19.5	2.5
Oct	28.3	12.9	68.5	12.6	2.1	18.9	5.0
Nov	30.6	15.5	79.3	9.4	1.8	19.8	5.3

According to the Department of Agriculture, Forestry and Fisheries (DAFF, 2010) in South Africa wheat is mostly planted during cool and moist conditions, thus in winter months. In both seasons the evaporative demand increased as the growing season progressed (Table 4.1).

Higher temperatures and longer days favour flowering (Deng *et al*., 2005), therefore late planting in 2010 resulted in early flowering. The flowering period occurred on 65 DAP and 82 DAP in 2010 and 2011, respectively. This consequently shortened the 2010 season compared to the 2011 season (Tables 3.1 and 3.2). This is well supported by Araus *et al.* (2008), who reported that shifting the planting dates (early or late planting) affects the duration of the growth season. Due to late planting in 2010, less solar radiation was received during the growth season (Table 4.1), which consequently reduced productivity compared to the 2011 season.

4.3.2 Water stress effects on physiological parameters of wheat

4.3.2.1 Stomatal conductance

Stomatal conductance (g_s) indicates the rate at which water and CO_2 move in and out of the leaf, and it is an early indication of water stress in plants (Flexas *et al*., 2004). Therefore, measuring g_s may be useful in elucidating whether water stress induces closure of the stomata, leading to restriction of leaf gaseous exchange. The analysis of variance (Anova) results on stomatal conductance are summarised in Appendix A (Table A.1). Table 4.2 presents the effects of water stress on wheat cultivars at various growth stages, and Figure 4.1 presents the averages of the main factors (irrigation and cultivars). The results revealed that water stress imposed at various growth stages (SNN, NSN and NNS) significantly ($p \leq 0.01$) reduced stomatal conductance compared with the control (NNN) treatment (Table 4.2 and Figure 4.2a).

The interaction effect significantly influenced g_s only in the flowering and grain-filling stages (Table 4.2). However, during stem elongation (SNN), in the cultivar SST 843, g_s was reduced by 57%, compared with 77% and 70% reduction of g_s in Duzi and Steenbras, respectively. When stress was terminated, the SNN treatment of Duzi resulted in the lowest percentage g_s reduction compared with the other cultivars. Therefore, although Duzi was the most affected by water stress in the stem elongation stage, it exhibited better recovery at later stages. The

SNN treatment of Duzi showed a 32% reduction in g_s at the flowering and 9.7% in the grain-filling stages. Generally, the treatment exposed to water stress during the stem elongation stage (SNN) showed greatest recovery, as it was not significantly different from the NNN treatment during the grain-filling stage (Figure 4.1a).

Table 4.2 Water stress effects on stomatal conductance of wheat cultivars stressed at various growth stages in the 2011 season

Stomatal conductance (mol CO_2 m^2 s^{-1})				
Interaction effect		**Growth stage**		
Irrigation	***Cultivar***	*Stem elongation*	*Flowering*	*Grain filling*
SNN	Duzi	0.04c	0.29d	0.28c
	Steenbras	0.06bc	0.32cd	-
	SST 843	0.06bc	0.32cd	0.47b
NSN	Duzi	-	0.09e	0.13de
	Steenbras	-	0.08e	-
	SST 843	-	0.08e	0.20cd
NNS	Duzi	-	0.28d	0.07e
	Steenbras	-	0.47b	-
	SST 843	-	0.47b	0.23cd
NNN	Duzi	0.18a	0.43bc	0.31c
	Steenbras	0.20a	0.48b	-
	SST 843	0.14ab	0.63a	0.57a

Means in a column followed by the same letter are not significantly different at $p \leq 0.01$*; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

At the grain-filling stage, a 15% reduction in g_s was observed for the SNN treatment compared with 61% and 66% for the NNS and NSN treatments, respectively (Figure 4.1a). Comparable results were found by Siddique *et al*. (1999), who noted that g_s was more severely affected by water stress in the flowering stage than the vegetative stage of wheat. Therefore, the results in this study are in agreement with those of Siddique *et al*. (1999).

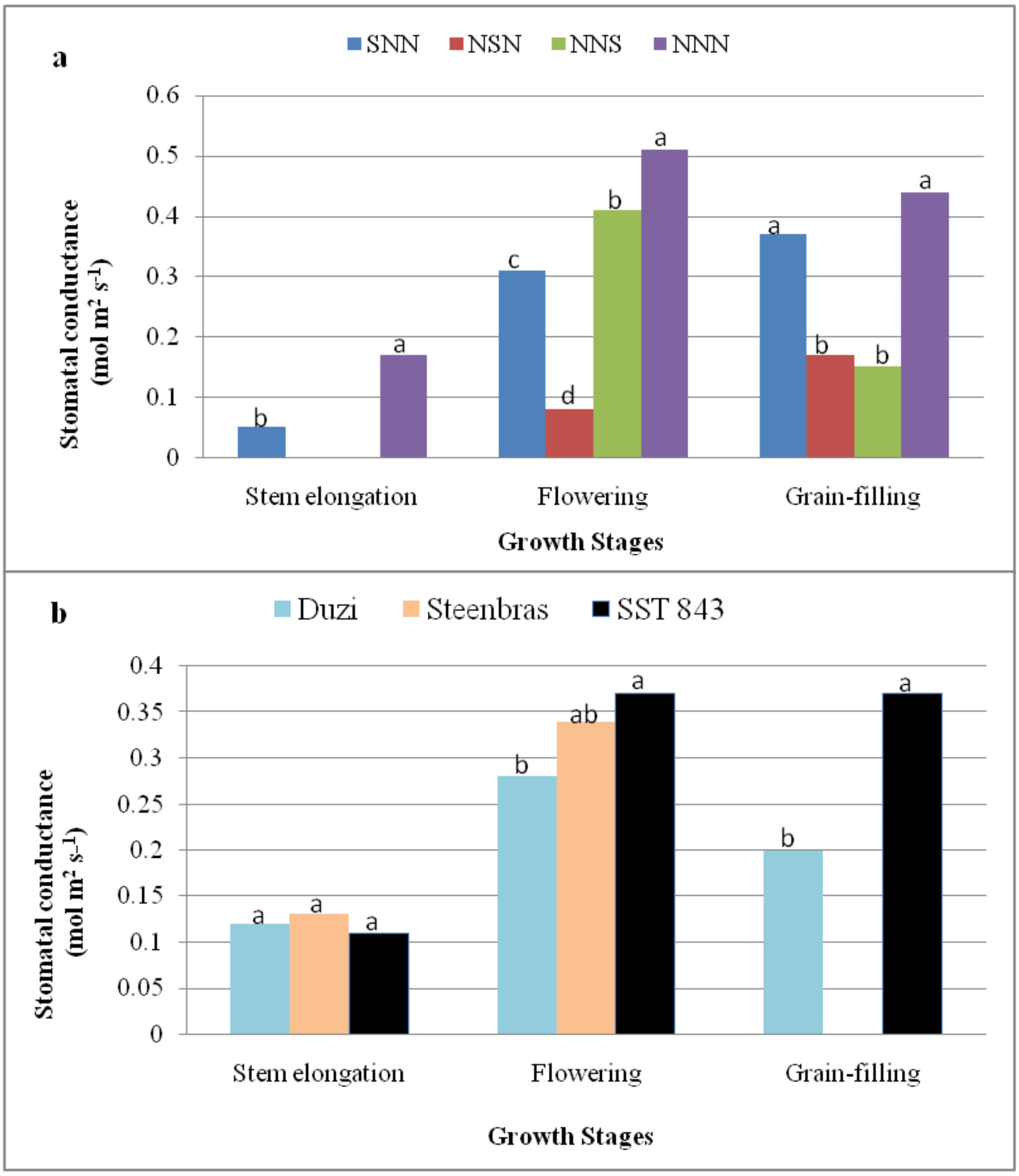

Figure 4.1 Water stress and cultivar effects on stomatal conductance in plants exposed to stress at various growth stages in 2011 season. Bars with the same letters per growth stage are not significantly different at p≤0.01; *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

The more pronounced reduction in g_s due to water stress in the flowering stage, compared to vegetative stage (Table 4.2), could also be explained by higher atmospheric evaporative demand (higher air temperature and lower relative humidity) later in the season (Table 4.1). This is well supported by the findings of Deng *et al.* (2000), who found that g_s decreased most due to stress in flowering and grain-filling stages compared to stress in the jointing and booting stages of wheat. They also found that reduction in g_s at any growth stage was due to increased air temperature and vapour pressure deficit in progression of the growth season. The interaction results revealed that the g_s of the NSN treatment amongst cultivars was not significantly different during the flowering (stress period) and the grain-filling periods. This implies that the cultivars responded similarly to water stress imposed in the flowering stage (NSN) (Table 4.2). The difference in g_s during the grain-filling stage was also attributed to cultivar effect (Figure 4.1b).

Generally, SST 843 had higher g_s compared to other cultivars in the flowering and grain-filling stages (Table 4.1). On average, g_s was reduced by 71% owing to water stress in the stem elongation stage (SNN), whereas reduction in g_s was 84% and 66% in the flowering (NSN) and grain-filling (NNS) stages, respectively, compared with the control treatment (NNN) (Figure 4.1a). Stomatal conductance was reduced most by water stress in the flowering stages (NSN). Significant reduction of g_s due to water stress in the flowering stage (NSN) corresponded with lower photosynthesis and transpiration rates (Figure 4.1a and Figure 4.2a). Blum (1998) indicated that water stress in wheat led to limited production of new photosynthetic products, mainly because of a decrease in leaf stomatal conductance. The results of this study confirm that lower stomatal conductance (Table 4.2) limits the photosynthesis rate under water-stress conditions in wheat (Table 4.4). Decreased g_s under water stress limit CO_2 assimilation due lower diffusion of CO_2 into the leaf, resulting in lower intercellular CO_2 concentration (Ci) inside the leaf (Ahmed *et al*., 2012).

4.3.2.2 Intercellular CO_2 concentration

Intercellular CO_2 concentration (Ci) is important in regulating leaf gaseous exchange attributes such as photosynthesis, stomatal conductance and the transpiration rate. It is one of the important physiological attributes in screening crops for water-stress tolerance at different growth stages (Bogale *et al.,* 2011). Flexas and Medrano (2002) reported that under severe water stress conditions Ci increases whereas under moderate stress it decreases, compared to well-irrigated conditions. Table 4.3 presents the mean effects of water stress on Ci of wheat cultivars stressed at various growth stages, whereas Anova results are presented in Table A.1 (Appendix A). The results revealed that water stress imposed at any growth stage significantly ($p \leq 0.01$) reduced the Ci compared with the control treatment during stress periods (Table 4.3). Water stress during stem elongation (SNN) did not result in significantly different Ci levels between cultivars, although the cultivar Duzi showed the 18% reduction in Ci at this stage, compared with a reduction of 36% for Steenbras and 30% for SST 843. The Ci of the SNN treatment was not significantly different from the NNN treatment when stress was terminated in the flowering and grain-filling stages (Table 4.3).

Table 4.3 Water stress effects on intercellular CO_2 concentration of wheat cultivars stressed at various growth stages

Internal CO_2 concentration (μmol mol^{-1})				
Interaction effect		***Growth stages***		
Irrigation	***Cultivars***	*Stem elongation*	*Flowering*	*Grain filling*
SNN	Duzi	190.96bc	307.32a	303.50ab
	Steenbras	167.59c	295.97ab	-
	SST 843	168.96c	295.58ab	315.89ab
NSN	Duzi	-	274.30b	263.94d
	Steenbras	-	187.55d	-
	SST 843	-	228.08c	269.31cd
NNS	Duzi	-	291.82ab	293.80bcd
	Steenbras	-	291.82ab	-
	SST 843	-	297.90a	289.35bcd
NNN	Duzi	232.78ab	313.78a	298.82abc
	Steenbras	260.43a	303.01a	-
	SST 843	243.88a	311.52a	326.25a

Means in a column followed by the same letter are not significantly different at $p \leq 0.01$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

The cultivar effect significantly influenced Ci in the flowering stage (NSN) (Table 4.3). At this stage, the cultivar Steenbras exhibited the greatest reduction in Ci, compared with the other cultivars. Generally, for Steenbras Ci was reduced by 38%, which was significantly higher, compared with the 13% and 26% reduction in Ci for Duzi and SST 843 at the same stage. On average, water stress treatments increased instantaneous water use efficiency (iWUE) (Table 4.6), compared with the well-irrigated treatment, which shows that stress reduced the transpiration rate more than photosynthesis. Comparable results were found by Wu and Bao (2011), who noted that applying irrigation after depletion of 75% water in the soil profile induced higher iWUE compared with 45% and 25% depletion. The same authors found that higher iWUE corresponds with lower Ci. Therefore results in the present study agree with those of Wu and Bao (2011).

Intercellular CO_2 concentration of the three wheat cultivars did not differ significantly in response to water stress in the grain-filling stage (NNS). However, the mean per irrigation treatment shows that the NSN treatment reduced Ci most during grain filling. On average, the NSN irrigation treatment had significantly lower Ci of 266.6 µmol mol^{-1}, compared with 291.6 µmol mol^{-1}, 309.7 µmol mol^{-1} and 312.5 µmol mol^{-1} of the NNS, SNN and NNN treatments, respectively. Siddique *et al.* (1999) found that water stress in the vegetative and anthesis stages induced an increase in Ci of wheat cultivars. The results of the present study therefore contradict those of Siddique *et al.* (1999). In the current study, water stress imposed at any growth stage decreased Ci. Flexas and Medrano (2002) reported that the decrease in Ci due to water stress indicates that Pn reduction is attributed mainly to stomatal limitation rather than metabolic limitations. Therefore, the results of this study are in agreement with those of Flexas and Medrano (2002). Thus, in this study, decreased g_s, Pn and E were caused mostly by stomatal closure, which consequently limited Ci.

4.3.2.3 Photosynthetic rate

Photosynthesis is considered the most important physiological process controlling plant growth and consequently yield. Bogale *et al.* (2011) found that wheat photosynthetic rate was correlated well with grain yield. Therefore, Pn measurements can be used to assess the effect of water stress on yield, mainly with the hypothesis that water stress will induce stomatal closure, leading to a rise in leaf temperature, which consequently reduces the photosynthetic and transpiration rates. In the current study, water stress significantly ($p \leq 0.01$) reduced flag leaf photosynthesis in any growth stage exposed to stress, compared with the control treatment (NNN) (Table 4.4; Appendix A, Table A.1). During stem elongation (SNN), the interaction effect (treatment combination) was not significant among the cultivars, although for Duzi there was 41% reduction in Pn, while for Steenbras and SST 843 there was a 39% and 32% reduction in Pn, respectively (NNN) (Table 4.4).

Table 4.4 Water stress effects on photosynthesis of wheat cultivars stressed at various growth stages in the 2011 season

Photosynthetic rate (µmol CO_2 m^{-2} s^{-1})				
Interaction effect		**Growth Stages**		
Irrigation	***Cultivars***	Stem elongation	Flowering	Grain filling
SNN	Duzi	8.61bc	12.77cde	11.01bc
	Steenbras	7.85c	13.83bcd	-
	SST 843	7.75c	12.10cde	14.29ab
NSN	Duzi	-	6.26f	8.79c
	Steenbras	-	8.70def	-
	SST 843	-	7.54ef	12.1abc
NNS	Duzi	-	17.85ab	4.03d
	Steenbras	-	19.78a	-
	SST 843	-	12.74cde	9.12c
NNN	Duzi	14.63a	15.66abc	12.74ab
	Steenbras	12.96a	18.65ab	-
	SST 843	11.32ab	20.83a	14.57a

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$: SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

The interaction effects significantly influenced photosynthetic rate in the flowering (NSN) and grain-filling (NNS) stages only (Table 4.4). The treatment combination of NSN × Steenbras had a higher photosynthetic rate than other cultivars during the flowering stage. For Steenbras there was a 53% reduction in Pn, although that was not statistically different from the 60% and 64% in Pn reduction of Duzi and SST 843, respectively. However, when stress was terminated in the grain-filling stage, Pn was reduced more for NSN × Duzi (31%) than SST 843 (14%). Unfortunately, the Pn measurements were not made for Steenbras, owing to technical problems encountered with the instrument (Table 4.4 and Figure 4.2b).

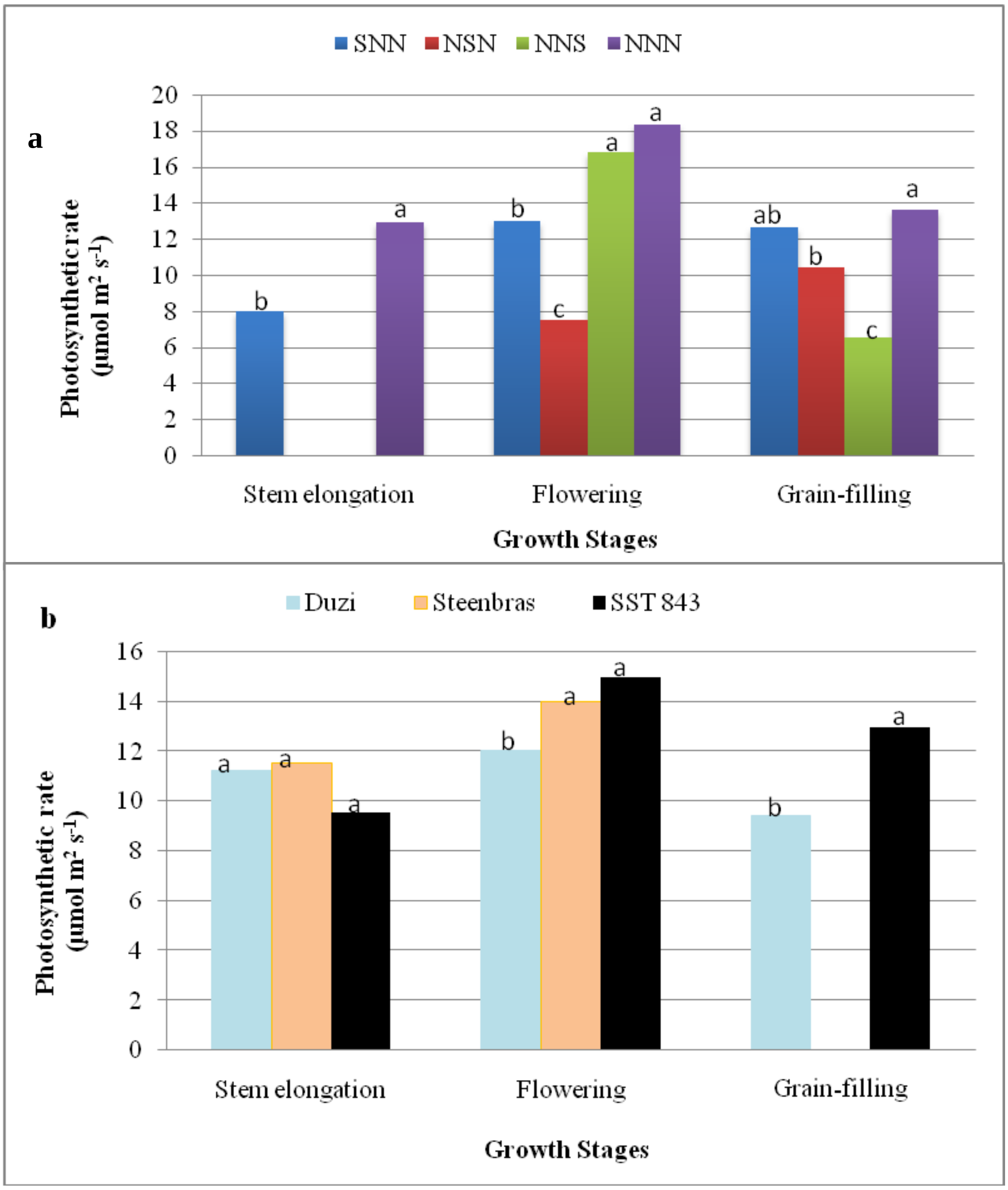

Figure 4.2 Effects of irrigation treatments and cultivars on photosynthesis at various growth stages in the 2011 season. Means of the same letters per growth stage are not significantly different at $p \leq 0.01$: *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

The average Pn significantly differed amongst cultivars in the flowering and grain-filling stages only (Figure 4.2b). The cultivar SST 843 had a lower photosynthetic rate than other cultivars in the stem elongation stage, although the difference was not statistically significant. However, at later stages (flowering and grain filling) the cultivar SST 843 had a significantly higher photosynthetic rate than other cultivars (Figure 4.2b). The interaction effect during the grain-filling stage (NNS) shows that the cultivar SST 843 had the highest Pn compared with NNS × Duzi. Unfortunately, measurements were not taken for NNS × Steenbras owing to technical problems with the equipment (Table 4.4).

Generally, the cultivar SST 843 seemed to have better performance under stress at the grain-filling stage, as Pn was only reduced by 37% compared with a 68% reduction for Duzi. The higher Pn of the cultivar SST 843 could be ascribed to higher g_s and E, compared with Duzi (Figure 4.1b and Figure 4.3b). These results are in agreement with those of Changhai *et al*. (2010), who found that cultivars that have higher Pn also had higher g_s and E. On average during stress period, water stress imposed during stem elongation (SNN) significantly ($p \leq 0.01$) reduced photosynthesis by 38%, whereas water stress in the flowering (NSN) and grain-filling (NNS) stages lowered Pn by 59% and 52%, respectively (Figure 4.2a). Photosynthesis failed to recover fully when irrigation was applied after the termination of the stress for the SNN and NSN treatments, compared with the well watered control (NNN) treatment. However, the SNN treatment showed greater recovery than the NSN treatment. Generally photosynthesis was reduced most when water stressed in the flowering stage (NSN) compared with other stages. Comparable results were found by Siddique *et al*. (1999), who reported that the photosynthetic rate of wheat cultivars exposed to water stress in the vegetative stage recovered at the flowering stage after water stress was terminated.

4.3.2.4 Transpiration rate

Leaf transpiration rate is the productive water loss that the plant pays in exchange for CO_2 uptake. Table 4.5 shows the mean effects of water stress on the transpiration rate of wheat cultivars, and Figures 4.3a and 4.3b show the effects of irrigation and type of wheat cultivar on the transpiration rate, whereas anova results on transpiration rate are summarised in Appendix A.1 (Table A.1). The results revealed that water stress in the stem elongation stage (SNN) significantly reduced transpiration, compared with the control treatment (NNN). The interaction was not significant during stem elongation. For the cultivar SST 843 E was reduced by 47%, compared with 63% and 71% for Steenbras and Duzi, respectively (Table 4.5). However, E showed significant recovery for the SNN treatment when stress was terminated, to the extent that it was not significantly different from NNN at the flowering and grain-filling stages. Good recovery for SNN treatment could be due to short-term avoidance of loss of water through partial closure of stomata. This is well supported by several authors

(Lu & Zhang, 1999, Deng *et al*., 2000), who indicated that a decrease in the transpiration rate of wheat under water stress is caused by partial stomatal closure, which results in higher leaf temperatures and a reduction in the photosynthesis rate.

Table 4.5 Water stress effects on transpiration rate of wheat cultivars stressed at various growth stages in the 2011 season

Transpiration rate (mmol H_20 m^{-2} s^{-1})				
Interaction effect		**Growth stages**		
Irrigation	***Cultivars***	Stem elongation	Flowering	Grain filling
SNN	Duzi	0.89d	4.69d	7.15b
	Steenbras	1.28cd	6.78b	-
	SST 843	1.22d	6.57b	11.51a
NSN	Duzi	-	2.06e	4.00c
	Steenbras	-	2.24e	-
	SST 843	-	2.23e	6.89b
NNS	Duzi	-	4.75cd	2.23c
	Steenbras	-	8.62a	-
	SST 843	-	6.72b	6.42b
NNN	Duzi	3.02ab	6.24bc	7.24b
	Steenbras	3.49a	8.62a	-
	SST 843	2.30bc	8.37a	12.34a

Means in a column followed by the same letter are not significantly different at p≤0.01; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

On average, water stress imposed in the flowering stage (NSN) significantly reduced the transpiration rate by 72% and the same treatment failed to recover after termination of stress when irrigated in the grain-filling stage, compared with the SNN treatment (Figure 4.3a).

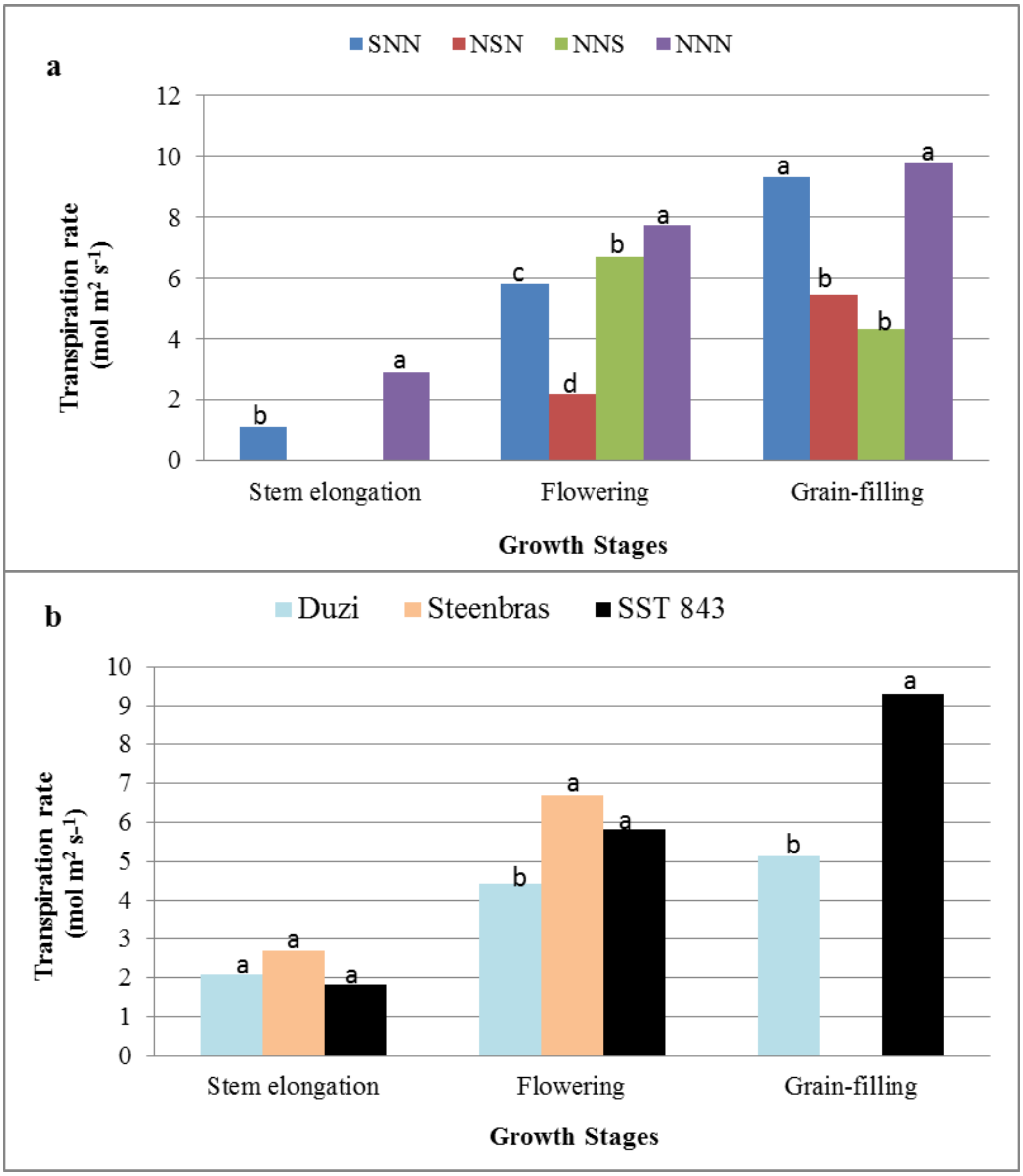

Figure 4.3 Effects of irrigation treatments and cultivars on transpiration rate at various growth stages in 2011 season. Means of the same letter per growth stage are not significantly different at p≤0.01; *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

The interaction effect of water stress imposed during the flowering stage was not significant for the treatment stressed in this stage (NSN). However, the cultivar Duzi had the lowest E reduction of 67% compared with 73% and 74% for Steenbras and SST 843, respectively (Table 4.5). When stress was terminated, NSN of Duzi, had significantly lower E than SST

843 in the grain-filling stage. However, both cultivars showed a 44% transpiration rate reduction in that stage.

Water stress treatment NNS lowered the transpiration rate in the grain-filling period by 56%, followed by 44% for the NSN treatment, compared with the NNN treatment (Figure 4.3a). On average, SST 843 had a significantly higher transpiration rate than Duzi in the grain-filling stage, which reduced E by 69%, compared with 47% for SST 843 (Figure 4.3b). Lu and Zhang (1999) indicated that reduction in transpiration rate of wheat under water stress is due mainly to stomatal closure, which results in higher leaf temperatures, leading to reduction in the photosynthetic rate. Similar results on photosynthesis (Table 4.4) and leaf temperature (Table 4.7) were found in this study.

Generally, irrigation treatments influenced E highly significantly in all the growth stages exposed to stress (SNN, NSN, and NNS) compared with the control (NNN) treatment. On average NSN reduced transpiration rate most by 72%, compared to 62% and 44% for SNN and NNS during the stress period respectively (Figure 4.3a). Therefore, the flowering stage (NSN) showed to be a more sensitive period to water stress than other stages. Doorenbos and Kassam (1979) also indicated that the negative effects of water stress in the reproductive stage of wheat cannot be recovered by re-watering at the later stages. Therefore, these results agree with the reports of Doorenbos and Kassam (1979).

4.3.2.5 Instantaneous water use efficiency

At leaf or canopy level, water use efficiency (WUE) may be defined as net CO_2 assimilated by photosynthesis (Pn) over water transpired (E) in the same period. This is mostly defined as instantaneous water or transpiration use efficiency (iWUE) (Changhai *et al*., 2010; Bogale *et al*., 2011). The analysis of variance results on iWUE are summarised in Appendix A (Table A.1).The results revealed that iWUE was not significantly influenced by cultivar effect in the stem elongation stage only (Table 4.6). However, in general water stress imposed in any growth stage increased iWUE compared to the control treatment (Figure 4.4). During stem elongation (SNN), Duzi had the highest iWUE compared with other cultivars. Generally, iWUE for Duzi was increased by 45%, whereas for Steenbras and SST 843 iWUE was increased by 27% and 41% respectively in the stem elongation stage. The interaction of irrigation treatment and cultivars was only significant in the flowering stage (Table 4.6; Table A.1).

Table 4.6 Water stress effects on instantaneous water use efficiency of wheat cultivars stressed at various growth stages in the 2011 season

iWUE (μmol mol^{-1})				
Interaction effect		**Growth stages**		
Irrigation	***Cultivars***	*Stem elongation*	*Flowering*	*Grain filling*
	Duzi	9.19a	2.69cd	1.55b
SNN	Steenbras	7.22ab	2.01f	-
	SST 843	6.78ab	2.17ef	1.24c
	Duzi	-	3.01bc	2.21a
NSN	Steenbras	-	3.93a	-
	SST 843	-	3.22b	1.77ab
	Duzi	-	2.75bcd	1.55bc
NNS	Steenbras	-	2.27def	-
	SST 843	-	2.65cde	1.81ab
	Duzi	5.03bc	2.46def	1.81ab
NNN	Steenbras	3.82c	2.16ef	-
	SST 843	4.94bc	2.49def	1.18c

Means in a column followed by the same letter are not significantly different at p≤0.05; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control

Water stress in the flowering stage resulted in a significant increase in iWUE for the cultivar Steenbras (45% increase), which was significantly higher compared to the 18% and 23% increase for the cultivars Duzi and SST 843 respectively. The NSN treatment had higher iWUE than other treatments during the stress period and even after termination of stress in the grain-filling period (Figure 4.4). Instantaneous water use efficiency of the NSN × Duzi treatment combination was also significantly higher than that of the stressed treatment in the grain-filling period (NNS) and other treatments of Duzi (SNN and NNN) (Table 4.6).

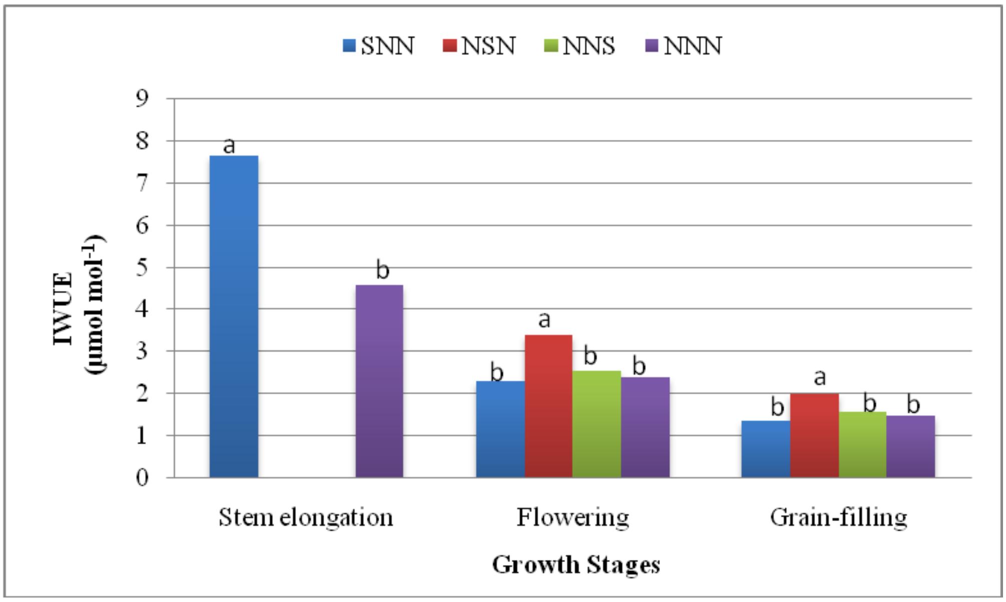

Figure 4.4 Water stress effect on instantaneous water use efficiency of wheat plants exposed to stress at various growth stages in the 2011 season. *Bars with the same letter per growth stage are not significantly different at p≤0.05; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

On average the NSN water stress treatment significantly (p≤0.01) increased iWUE measured in the grain-filling stage by 26%, whereas the iWUE of stressed treatment at this stage (NNS) increased by only 5.7% when compared with the NNN treatment (Figure 4.4). The results are in agreement with those of Bogale *et al.* (2011), who indicated that an increase in iWUE was due to greater reduction in E than Pn by water stress. Therefore, higher iWUE for NSN treatment was because of a more pronounced reduction in E (Figure 4.3) during the flowering stage relative to the reduction in Pn in the same stage (Figure 4.2).

4.3.2.6 Leaf temperature

The physiological components or functions of leaf gaseous exchange are affected by continual changes in the prevailing climatic conditions, such as external CO_2, air temperature and leaf to air vapour pressure deficit (Anjum *et al.*, 2011). Several authors reported that higher temperatures and limited water availability during the crop growth period may modify overall growth and development by affecting vital physiological processes such as photosynthesis and water uptake (Ahmed *et al*., 2012; Pradhan *et al*., 2012). Leaf temperature can be used as an indirect indicator of leaf water status, mainly with the hypothesis that when water stress increases, the stomata close partially, restricting water loss which may lead to an increase in leaf temperature (Simpson, 1981). The results revealed that both irrigation and cultivar effects influenced leaf temperature at all stages imposed to stress, whereas the interaction effect was only significant in the flowering and grain-filling stages (Appendix A.1, Table A.1). Table 4.7 presents the mean irrigation treatment and cultivar effect on leaf temperature measured at various growth stages.

Table 4.7 Mean irrigation and cultivars effect on leaf temperature measured at various growth stages during the 2011 cropping season

		Leaf temperature (°C)		
Main effect		Growth stages		
		Stem elongation	*Flowering*	*Grain filling*
Irrigation	SNN	23.75b	27.58b	24.75b
	NSN	-	28.32a	25.65a
	NNS	-	26.67c	25.23ab
	NNN	22.95a	26.46c	23.73c
Cultivars	Duzi	23.96a	26.34c	23.98b
	Steenbras	23.91a	28.41a	-
	SST 843	22.23b	26.98b	25.65a

Means in a column followed by the same letter are not significantly different at p≤0.01: SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain-filling stage; and NNN refers to the control treatment

On average, the SNN treatment significantly ($p \leq 0.01$) increased leaf temperature by 3%, whereas NSN and NNS both increased leaf temperature by 4% during the stress period compared with the control treatment (NNN). Leaf temperature of all irrigation treatments and cultivars increased most during flowering and grain-filling stages (Table 4.7). This is in agreement with the reports of Pradhan *et al*. (2012), who indicated that the reproductive stage is the most sensitive to drought and high temperature stresses. Therefore, the results in the present study concur with those of Pradhan *et al*. (2012) in the sense that water stress in the flowering (NSN) and grain-filling (NNS) stages significantly increased leaf temperature because of higher air temperature at those stages (air temperature is presented in Table 4.1), as well as due to lower transpiration rate of the stressed treatment, resulting in less leaf cooling. This is well supported by Deng *et al*. (2005) who reported that water transpiring through the stomata provides a means of cooling the plant and thereby avoiding temperature stress.

Higher leaf temperature for stressed treatments (SNN, NSN and NNS), compared with NNN in all cultivars during stress period could also be attributed to lower LWP (Figure 3.6), which consequently reduced g_s, Pn and E. This is well supported by Deng *et al*. (2000), who indicated that water stress at any growth stage of wheat reduces LWP, which leads to partial closure of stomata and higher leaf temperature, resulting in lower leaf net CO_2 concentration. Gupta *et al*. (2001) found that higher leaf temperature was negatively correlated with grain and biological yield. In this study, grain yield trends (Chapter 5) followed the leaf temperature trends in the grain-filling stage (Table 4.7). Therefore, leaf temperature, and stomatal conductance serves as a good indicator for screening water stress tolerance. Acevedo *et al.* (2002) indicated that an optimum air temperature of wheat required for photosynthesis is between 15ºC and 25ºC, and a temperature of more than 30ºC reduces photosynthesis. In the flowering and grain-filling stages, the leaf temperature of the NSN treatment exceeded the optimum temperatures reported by Acevedo *et al.* (2002), but never reached the uppermost limits of 30ºC (Table 4.7). Generally, plants in the well-watered control (NNN) had lower leaf temperatures at all growth stages compared with the water stressed treatments, which corresponded with higher Pn, E and g_s. These results are well supported by reports of Araus *et al*. (2008), who indicated that lower leaf temperature implies higher transpiration cooling and stomatal conductance, which favours a high photosynthesis rate.

4.3.2.7 Leaf water potential

It is well documented that leaf water potential (LWP) is related to other physiological parameters such as stomatal conductance, transpiration and photosynthetic rate (Deng *et al*., 2000) and consequently related to yield (Gupta *et al*., 2001). Figure 4.5 shows the effects of water stress on the LWP of wheat measured on different days after planting (DAP). The results reveal that water stress in SNN reduced LWP by 40%, 53% and 43% at 59, 63 and 77

DAP respectively, compared to the NNN treatment (Figure 4.5a). Figure 4.5b shows the effects of water stress on LWP measured at grain-filling stage (115 DAP). The leaf water potential was reduced most during the grain-filling stage irrespective of treatment (Figure 4.5a and 4.5b). Comparable results were found by Deng *et al*, (2000), who found that LWP was reduced most due to water stress in the flowering and grain-filling stages compared to stress in earlier stages of wheat. Reduction in LWP in the flowering and grain-filling stages of wheat is mostly attributed to lower soil water content under water stress conditions, compared to irrigated conditions (Zhang *et al*., 1998).

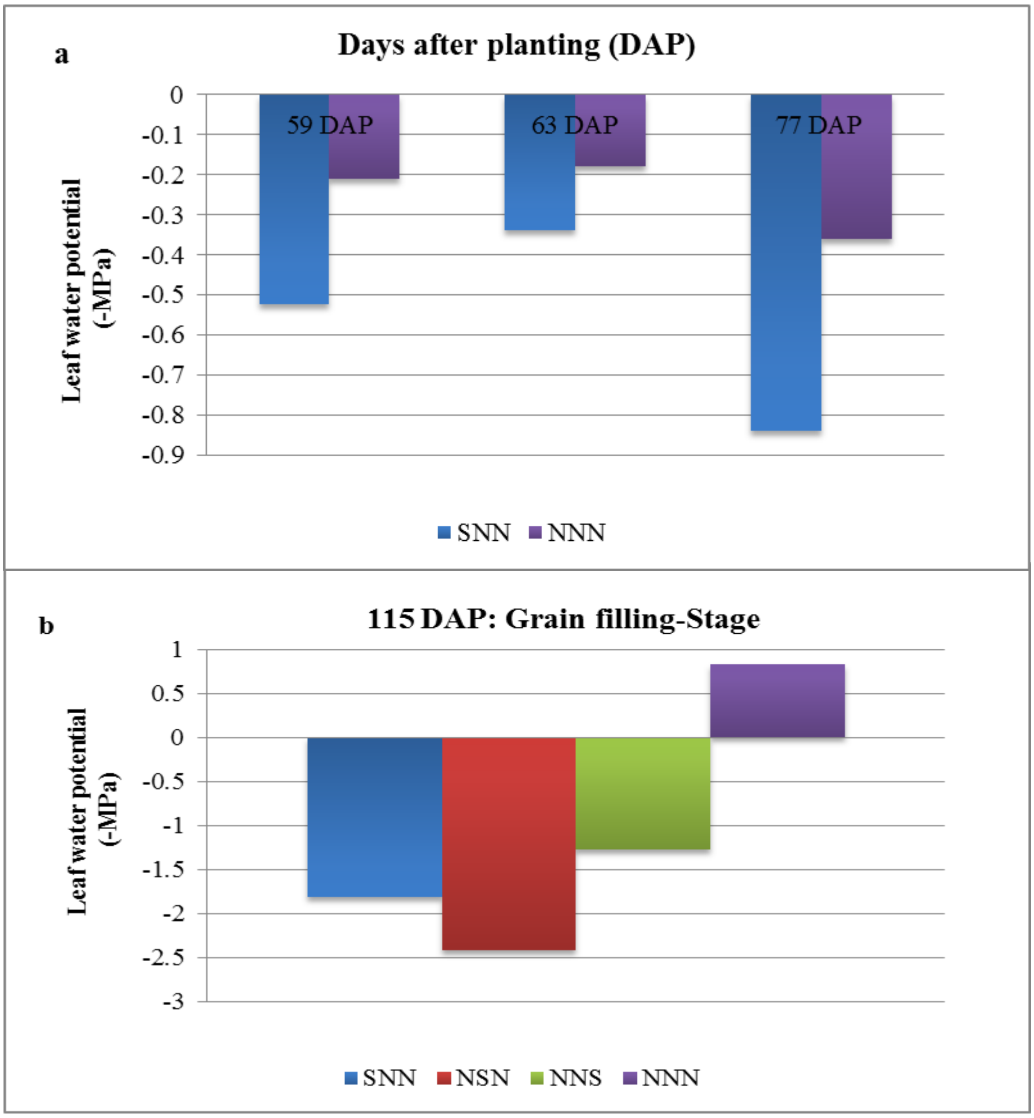

Figure 4.5 Water stress effect on leaf water potential measured at different days after planting in the 2011 season. *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain-filling stage; and NNN refers to the control treatment*

In the present study the NSN treatment reduced LWP most even after termination of stress (12 days after stress termination) in the grain filling stage. The NSN treatment reduced LWP by 66% in the grain-filling stage compared with 54% and 35% reduction of SNN and NNS treatments respectively (Figure 4.5b). Reduction in LWP owing to water stress (SNN, NSN and NNS) when compared with the control treatment (NNN) could be attributed to reduction in leaf functions such as lower conductance because of dehydration, and lower soil water content. Comparable results were reported by Zhang *et al.* (1998), who concluded that a reduction in LWP under non-irrigated conditions compared to well-irrigated conditions was due to lower soil water potential in the profile, which consequently affected leaf functions negatively. Zhang *et al.* (1998) reported that dryland wheat exhibited reduced stomatal conductance and leaf size, and significantly increased leaf temperatures, compared with a well-watered treatment. Comparable results in leaf temperature (Table 4.7) and stomatal conductance (Table 4.2) were found in the present study.

4.3.3 Water stress effects on wheat growth components

The anova tables on growth components are summarised in Appendix B (Table B.1 - B4).

4.3.3.1 Leaf area index

Leaf area index (LAI) is a growth parameter related to several physiological components, such as photosynthesis, leaf expansion, dry matter production, and grain yield (Blum, 1996). Table 4.8 indicates the effects of water stress on the LAI of wheat cultivars stressed in various growth stages. Figure 4.6a indicates the effect of irrigation treatments on LAI, and Figure 4.6b summarises the effect of cultivar on LAI. The LAI data collected on 75 DAP was in the stem elongation stage, 87 and 95 DAP were during the flowering stage, and 108 DAP to 131 DAP represent the LAI measurements taken during the grain-filling stage.

The results revealed that water stress imposed at any developmental stage significantly reduced LAI compared with the control treatment (Table B.1; Table 4.8 and Figure 4.6a). Reduction in LAI due to water stress is attributed to lower leaf area and leaf expansion (Zhang *et al*., 1998). Blum (1996) indicated that flexibility in leaf area is an important means by which a water stressed crop maintains control over water use. The lower LAI of the stressed treatment could be ascribed to the reduced number of leaves per plant, diminished leaf expansion and smaller leaf size (Abayomi & Wright, 1999). Therefore, the results agree with the reports of Abayomi and Wright (1999) in the sense that water stress imposed at any growth stage in the current study reduced the number of leaves per plant (Table 4.9).

Table 4.8 Water stress effects on leaf area index of wheat cultivars stressed at various growth stages

Leaf area index (m^2m^{-2})							
Interaction effect		**Days after planting (DAP)**					
Irrigation	***Cultivars***	75	87	95	108	124	131
SNN	Duzi	1.88b	3.55e	6.67d	3.80i	2.00e	0.85f
	Steenbras	2.44b	2.96e	3.51e	4.50efg	3.95c	0.68g
	SST 843	2.60b	3.60e	6.04d	4.76def	3.89c	3.01b
NSN	Duzi	4.66a	3.55e	3.86e	4.01ij	1.61ef	0.83f
	Steenbras	4.56a	4.81d	7.90c	2.65j	1.85ef	1.45e
	SST 843	4.65a	5.29d	8.09bc	4.14ghi	2.97d	1.54d
NNS	Duzi	4.80a	7.52c	8.09bc	4.42fgh	0.84gh	0.21h
	Steenbras	4.59a	7.19c	8.58bc	4.89de	0.51h	0.01i
	SST 843	5.37a	8.56ab	9.02ab	5.40c	1.22fg	0.24h
NNN	Duzi	5.27a	7.68bc	8.71abc	6.85b	4.94b	2.66c
	Steenbras	5.24a	7.59c	8.42bc	5.01cd	4.33bc	1.53d
	SST 843	5.01a	8.71a	9.55a	9.33a	6.64a	5.18a

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

The highest LAI for both irrigation treatment and cultivars was recorded in the flowering stage (95 DAP), whereas the lowest LAI was recorded in the grain-filling stage (131 DAP) in the present study (Figure 4.6). When water stress was terminated at the flag-leaf stage (SNN), LAI showed good recovery at flowering and grain-filling stage for all cultivars. This could be ascribed to maintenance of the number of green leaves, starting from 87 DAP (Table 4.9 and Figure 4.7). Though the LAI of the SNN treatment showed significant recovery in all cultivars, it never exceeded the LAI of the NNN treatment, but was higher than the NSN and NNS treatments towards the end of the season (124 DAP to 131 DAP) (Figure 4.6).

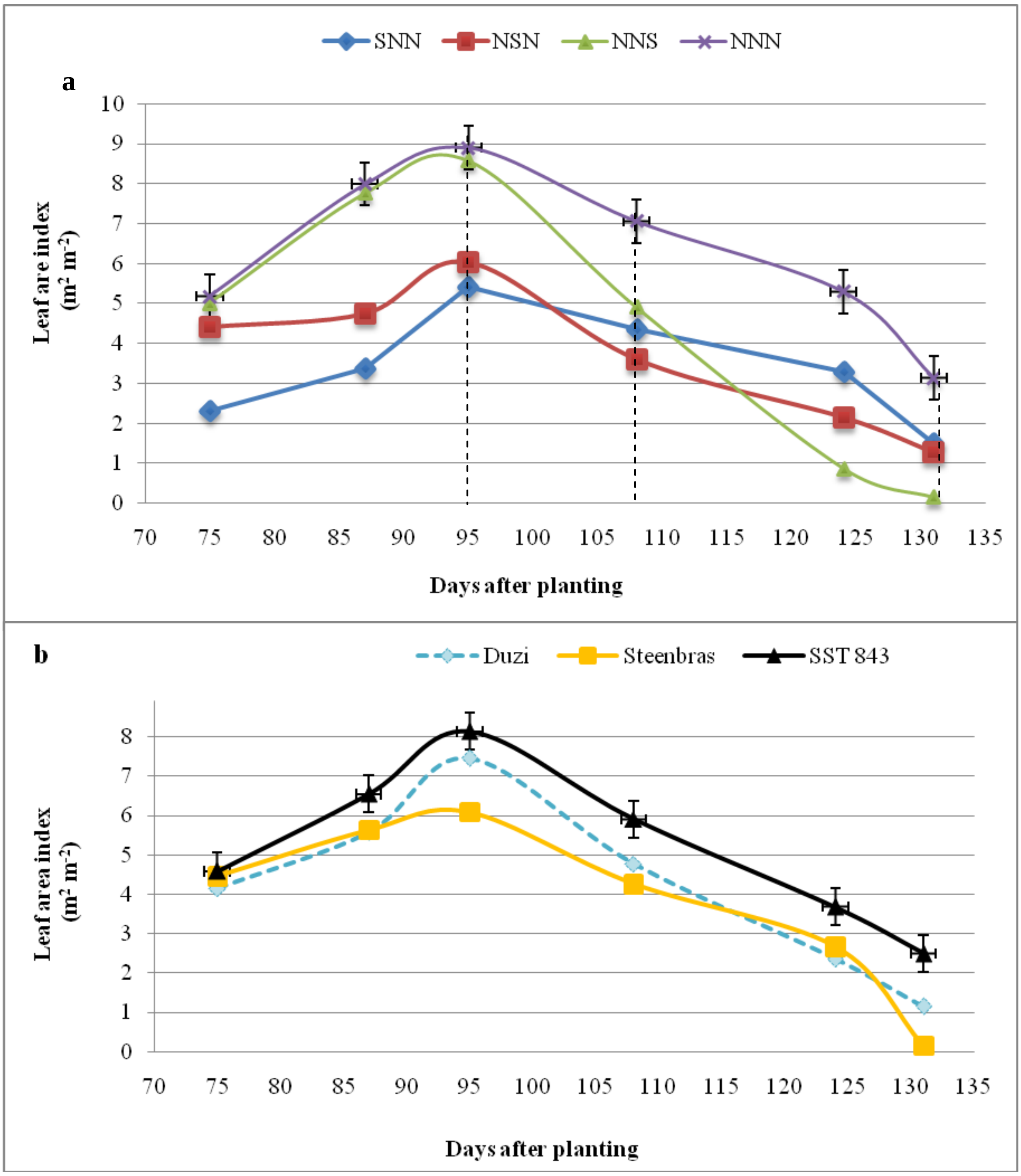

Figure 4.6 Effects of irrigation treatments and cultivars on leaf area index measured at various days after planting in 2011 season. Vertical bars indicate the LSD per day at p≤0.01; *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control. The dotted lines indicated the time of stress termination.*

The SNN treatment reduced LAI by 38%, which was significantly lower than the 60% and 84% reduction in LAI found in the NSN and NNS treatments at 124 DAP. Reduction of LAI in the flowering and grain-filling stages was because of the accelerated death of leaves (Table 4.9). The recovery of LAI for SNN treatment could be due to new leaves formed from newly developed tillers after termination of the stress period at the flag-leaf stage. The results are in agreement with the findings of other researchers (Mogensen *et al*., 1985; Abayomi & Wright, 1999), who indicated that the recovery of LAI could be due to new leaves from late tillers that develop if stress is terminated before the boot stage. However, the number of tillers was not recorded in this study.

Stress during the flowering stage (NSN) significantly reduced LAI, starting from 87 DAP (12 days stressed) (Figure 4.6a). The NSN treatment significantly decreased the number of leaves per plant (Figure 4.7a), which led to a reduction in the LAI from 87 DAP (Figure 4.6a). This result is well supported by Blum's (1996) reports, which indicated that lower LAI and interception of radiation under water stress after flowering is ascribed to a decrease in leaf expansion. At the start of the water stress during the grain filling period (NNS), the LAI of the plants in this treatment (during stem elongation to flowering stages, i.e. 75 to 95 DAP) were not significantly different from the LAI of the control treatment (NNN). However, the NNS treatment significantly reduced LAI from 108 DAP to 131 DAP, compared with other treatments. The LAI of the NNS treatment was reduced by 95% at 135 DAP, compared with the NNN treatment (Table 4.8and Figure 4.6a).

Generally, the reduction in LAI after flowering could be as a result of higher atmospheric demand (Table 4.1), which accelerated the death of leaves. These results are well supported by Blum's (1996) reports, which indicated that reduction in LAI due to water stress after flowering is because of accelerated leaf senescence. The LAI of wheat cultivars differed significantly ($p \leq 0.01$) in response to water stress applied at different growth stages (Table 4.8). On average, SST 843 had the highest LAI when exposed to water stress in the flowering and grain-filling stages, compared with other cultivars (Figure 4.6b). That implies that SST 843 was more resistant to water stress than other cultivars. Wheat cultivars that maintained higher LAI under water stress sustained good yield, as they had relatively higher photosynthesis per leaf (Jatoi *et al*., 2011). Consequently SST 843 had higher flag-leaf photosynthesis than other cultivars (Table 4.4 and Figure 4.2b). The cultivar Steenbras had the lowest LAI in the grain-filling stage. This was due to early maturity compared with other cultivars. Consequently it started losing leaves a week earlier than other cultivars, which led to lower LAI at the last measurement date (Table 4.8 and Figure 4.6b). The number of leaves per treatment and cultivars are discussed in the next section.

4.3.3.2 Number of leaves

Blum (1996) reported that the number of leaves per plant determines the potential radiation interception for photosynthesis per unit leaf area. However, the production of new leaves depends on the availability of water. The anova results on number of leaves at various DAP are summarised in Table B.2 (Appendix B.2). Table 4.9 presents the effects of water stress on the number of leaves of various wheat cultivars, and Figure 4.7 summarises the mean irrigation and cultivar effect on the number of leaves per plant recorded at different DAP in the 2011 season. The number of leaves recorded at 75 DAP was during the stem elongation stage (SNN), whereas 87 and 95 DAP were during the flowering stage (NSN) and leaves recorded from 108 and 124DAP were in the grain-filling stage (NNS).Irrigation treatment significantly ($p \leq 0.01$) reduced the number of leaves during the stem elongation and grain-filling stages. The interaction effect shows that cultivars were not significantly different in the number of leaves owing to water stress at stem elongation (SNN), but the SNN treatment had significantly lower number of leaves compared with control treatment (NNN) (Table 4.9). The control treatment (NNN) of Duzi had a significantly higher number of leaves per plant in the stem elongation stage (75 DAP).

Though the cultivars were not significantly different as a result of water stress at stem elongation (SNN), the cultivar Duzi had 50% less leaves at the grain-filling stage and leaf number was reduced in SST 843 and Steenbras by 44% and 35% compared with their own control treatments (NNN). Therefore, the cultivar Steenbras had a lower reduction in the number of leaves per plant compared with the control treatment in the stem elongation stage (Table 4.9). The treatment combinations stressed during grain filling (NNS) were not statistically different from each other. The NNS treatments of Duzi and Steenbras were not significantly different from their own control treatments (NNN) at 108 and 124 DAP, whereas SST 843 differed significantly from the well-watered control 124 DAP (Table 4.9). The mean of the NNS treatment was not significantly different from the well-watered control on 108 and 124 DAP. However, the number of leaves of NNS was reduced by 13% and 4% on these measurement days, compared with the NNN treatment (Figure 4.76a).

Table 4.9 Water stress effects on number of leaves of wheat cultivars stressed at various growth stages

Number of leaves						
Interaction effect		**Days after planting (DAP)**				
Irrigation	***Cultivars***	75	87	95	108	124
SNN	Duzi	12.58c	19.67bc	21.93b	13.42ab	1.83bcd
	Steenbras	13.17c	14.80d	16.20d	10.08b	1.00fg
	SST 843	11.75c	16.08dc	17.56cd	9.75b	1.25ef
NSN	Duzi	20.58b	19.33bc	21.11bc	10.00b	1.58de
	Steenbras	20.75b	20.08b	21.93b	10.08b	1.17efg
	SST 843	20.03b	20.89b	22.81b	9.83b	0.67g
NNS	Duzi	24.50a	22.25b	24.30b	13.17ab	2.25ab
	Steenbras	19.50b	21.75b	23.75b	11.42ab	2.08bcd
	SST 843	20.25b	23.00ab	25.11ab	11.33ab	1.67cde
NNN	Duzi	25.00a	22.92ab	25.02ab	15.33a	2.33ab
	Steenbras	20.42b	22.00b	24.02b	12.92ab	2.17bc
	SST 843	20.83b	26.25a	28.66a	15.00a	2.75a

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

Number of leaves were reduced by 41% in the SNN treatment, compared with the NNN control treatment at 87 DAP (Figure 4.7a). During the flowering stage (87 and 95 DAP) the mean of the SNN treatment was not different from the NSN treatment but was significantly lower than the NNN and NNS treatments. Furthermore, in the grain-filling stage the number of leaves of the SNN treatment was still lower than the NNN treatment. This shows that the number of leaves of SNN treatment did not attain full recovery after stress was terminated. The results are in agreement with the findings of Vurayai *et al*. (2011), who reported that the number of leaves of Bambara groundnuts that were stressed in the vegetative stages failed to recover at the flowering and pod-filling stages when compared with the well-irrigated treatment.

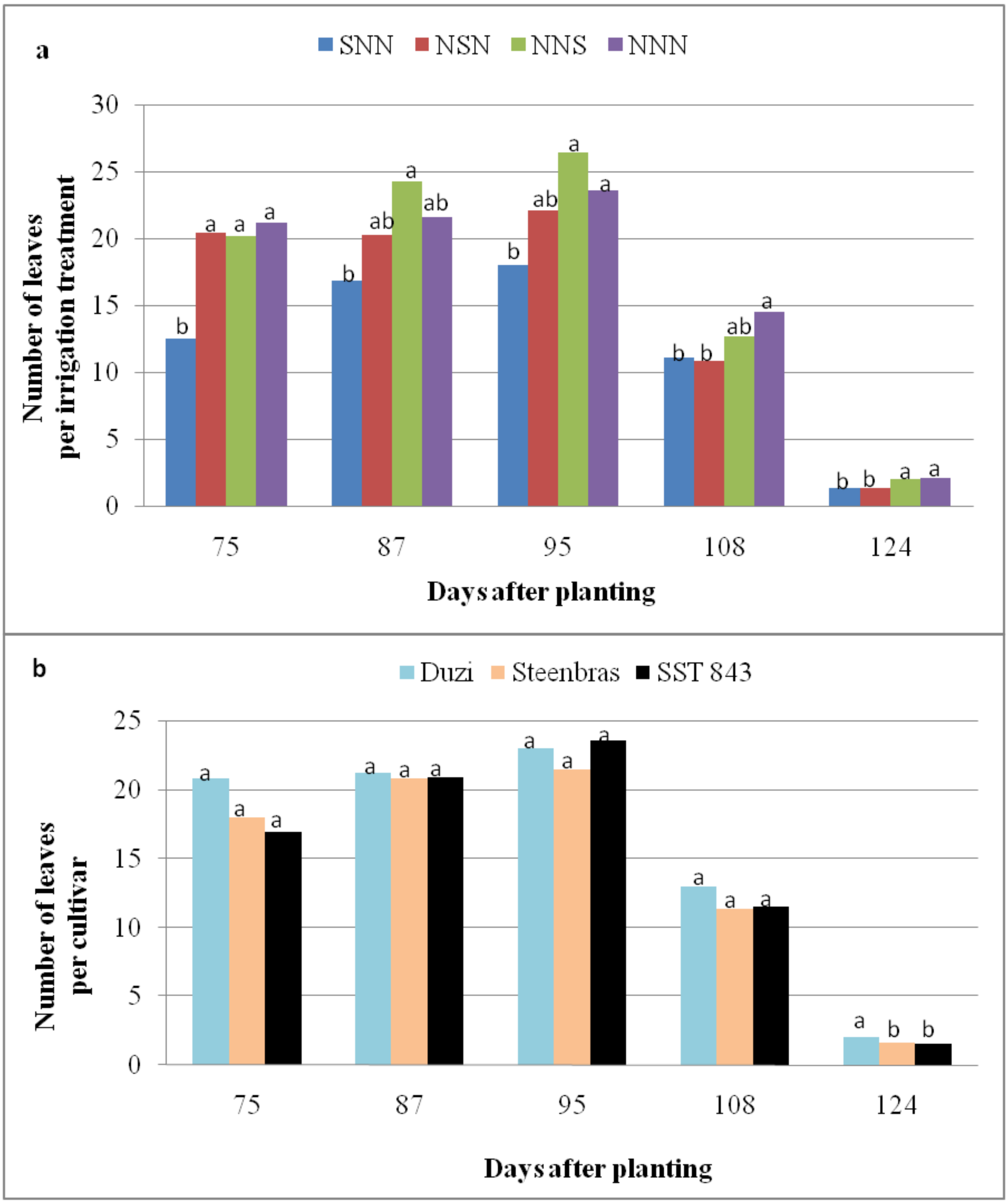

Figure 4.7 Effects water stress on average number of leaves per irrigation treatment and cultivar measured at various days after planting in 2011 season. *Bars with the same letter per day are not significantly different at p≤0.01; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

It was observed that the cultivar SST 843 had longer and broader leaves than the other cultivars, which resulted in a relatively higher LAI (Figure 4.6b) with few leaves (Figure

4.7b). Furthermore, the SST 843 had a higher number of leaves for the NNN treatment (Table 4.9), which corresponded with higher LAI (Figure 4.7b). This result agrees with reports of several authors (Zhang *et al.*, 1998; Abayomi & Wright, 1999), who found that reduced leaf size and development under water stress negatively affected LAI compared with optimal conditions. Zhang *et al.* (1998) found that reduction in LAI due to water stress was attributed to significant reduction in flag leaf width and length compared to the well-irrigated treatment. Generally water stress imposed at any growth stage in the present study reduced number of leaves significantly as compared to the control treatment (Figure 4.7a). Reduction in number of leaves due to water stress decreases the source strength which ultimately leads to reduced dry matter partitioning (Anjum *et al.*, 2011). Gupta *et al.* (2001) found that number of leaves was positively correlated with dry matter production during booting and anthesis stages, therefore reduction in number of leaves in those stages significantly reduced grain yield. Furthermore Ji *et al.* (2010), found that water stress in the flowering stage reduce sink size and starch reserves for grain-filling stage. In the present study water stress in the flowering stage (NSN) reduced number of leaves for a longer duration, during the most critical period. The number of leaves for NSN was significantly reduced by 25% and 36% at 108 and 124 DAP respectively. That was during grain-filling period and according to Slafer and Rawson (1994) this period is characterised by endosperm cell developed which serve as the main sinks for the accumulation of assimilates. Therefore, reduction of any source, mostly leaves, due to water stress in the flowering stage limit availability of assimilates in the grain-filling stage, which consequently reduced yield (Gupta *et al*., 2001).

4.3.3.3 Plant height

Plant height is a major agronomic character used in the selection of cultivars for performance and adaptability (Jatoi *et al*., 2011). Araus *et al*. (2008) reported that the aim of plant breeders in reducing plant height to the threshold of 70 cm to 100 cm was to encourage partitioning of biomass more efficiently to the grain (HI). Several authors reported reduction in plant height due to water stress in wheat (Abayomi & Wright, 1999; Gupta *et al*., 2001; Jatoi *et al*., 2011). The anava results on plant height are summarised in Table B.3 (Appendix B.3). In the present study during the 2010 season, plant height at harvest was not significantly ($p \leq 0.05$) influenced by water stress and cultivar effects (Table 4.10). Owing to the absence of significant differences at harvest in the first season, in 2011 plant height was measured at an interval of every seven to ten days. This was done mainly to determine whether the absence of differences in the first season was because of recovery after the termination of the stress periods (Table 4.11 and Figure 4.8). The results reveal that water stress imposed at any development stage reduced plant height, since the control treatment (NNN) of all cultivars had the highest height, compared with the SNN, NSN and NNS treatments (Figure 4.8). Comparable results were found by Abayomi and Wright (1999), who reported a reduction of plant height owing to water stress in the tillering, booting and flowering stages of wheat cultivars compared with the non-stressed treatment. Furthermore, similar results were recorded by Vurayai *et al*. (2011), who found that water stress imposed in the vegetative, flowering and pod-filling stages reduced the plant height of Bambara groundnuts compared with the well-watered treatment.

Table 4.10 Irrigation and cultivar effects on plant height at harvesting in the 2010 and 2011 cropping seasons

Final plant height (cm)			
		Cropping season	
Main factors		2010	2011
Irrigation	SNN	80.81a	101.00b
	NSN	81.85a	87.11c
	NNS	85.25a	105.67b
	NNN	86.64a	111.11a
Cultivars	Duzi	84.29a	101.75a
	Steenbras	84.54a	101.58a
	SST 843	82.08a	100.33a
Grand mean		83.64	101.22

Means in a column followed by the same letter are not significantly different at p≤0.05; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

Generally, at harvest cultivars were not significantly different from one another in both seasons, whereas irrigation treatments significantly affected plant height in 2011 only. In the 2011 season, plants exposed to water stress in the stem elongation period (SNN) had significantly reduced plant height (between 46 and 87 DAP) compared with other treatments (NSN, NNS and NNN) (Table 4.11 and Figure 4.8). These results are in agreement with the findings of Abayomi and Wright (1999). These authors concluded that water stress imposed on wheat before the flowering stage significantly impaired plant height. Plant height showed good recovery for all cultivars when water stress imposed during the stem elongation stage (SNN) was relieved (at 108 DAP, 30 days after stress termination). Though the plant height of the SNN treatment recovered, it never exceeded the plant height of the NNN treatment (Figure 4.8).

Table 4.11 Water stress effects on plant height of wheat cultivars stressed at various growth stages in 2011 season

		Plant height (cm)						
Interaction effect		**Days after planting (DAP)**						
Irrigation	***Cultivars***	62	75	87	95	108	112	165
SNN	Duzi	31.2d	35.8e	65.3d	81.7bcd	94.6bcd	94.7ed	103.7dc
	Steenbras	33.9cd	38.8de	66.8cd	76.7ed	86.2e	83.3f	97.3ed
	SST 843	36.3c	41.6d	70.9bcd	80.4cd	95.3bcd	95.3cde	102.0dc
NSN	Duzi	45.8ab	52.4abc	70.6bcd	71.7ef	95.0bcd	98.0bcd	91.0ef
	Steenbras	47.7ab	54.7ab	72.8ad	69.6f	85.3e	85.7f	88.3f
	SST 843	47.1ab	54.0abc	80.5ab	72.2ef	85.3e	90.7ef	91.7ef
NNS	Duzi	44.4bc	50.9bc	79.3abc	81.0dc	89.0ed	100.7bc	102.7dc
	Steenbras	45.7ab	52.6bc	78.9abc	83.8abc	90.7cde	90.7ef	106.3abc
	SST 843	49.2a	56.3a	82.58ab	85.1abc	97.7bc	97.7bcd	108.0abc
NNN	Duzi	44.0b	50.9c	80.5ab	88.5a	102.0ab	102.0ab	112.3a
	Steenbras	44.9b	51.38bc	79.7ab	86.4abc	100.0ab	100.0bcd	109.7abc
	SST 843	47.2ab	54.0abc	85.1a	87.7ab	106.2a	106.3a	111.3ab

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; plant height recorded at 62 and 71 DAP represent the stem elongation stage SNN; 87 and 95 DAP was during the flowering stage NSN; from 108 to 165 DAP represents plant height taken during the grain-filling stage (NNN); and NNN refers to the control treatment

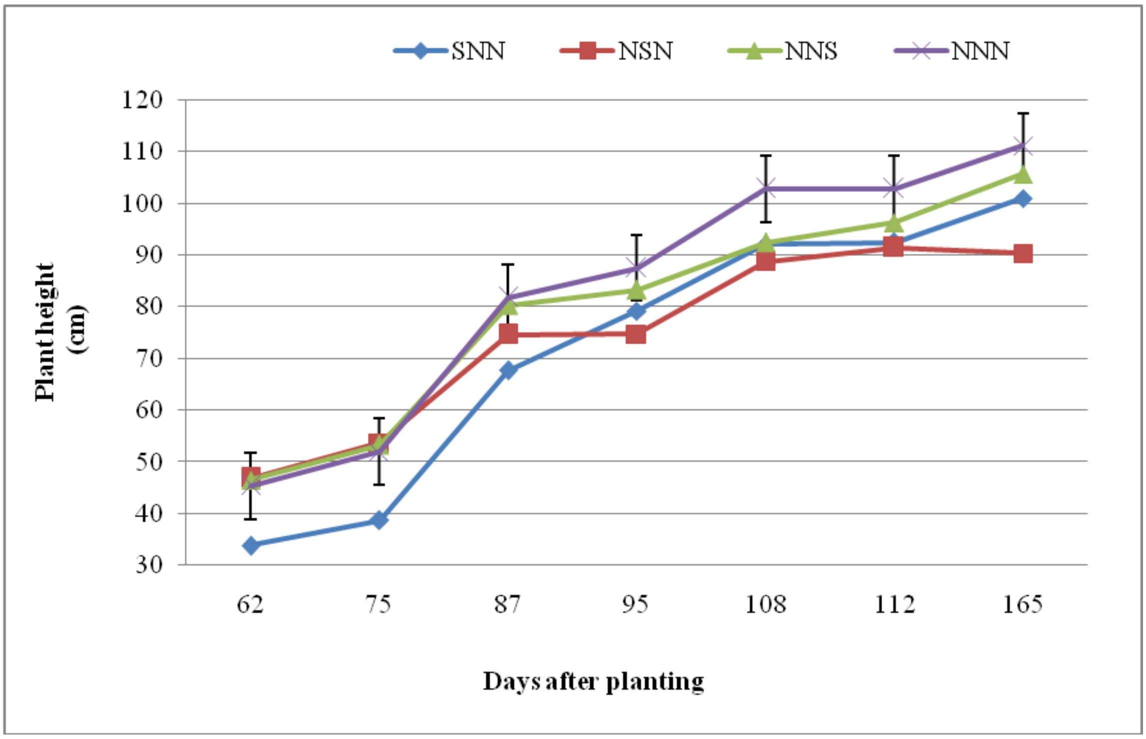

Figure 4.8 Effect of water stress on plant height of wheat measured at various days after planting in the 2011 cropping season. *Error bars indicate the least significant difference at p≤0.05; means of plant height recorded at 62 and 71 DAP represent the stem elongation stage (SNN); 87 and 95 DAP was during the flowering stage NSN; plant height taken from 108 to 165 DAP represents the grain-filling stage (NNS); and NNN refers to the control treatment*

The interaction effect shows that plant height amongst cultivars differed significantly on 108 and 112 DAP due to the water stress treatment SNN (Table 4.10). The SNN treatment of the cultivar Steenbras significantly reduced plant height by 17% on 112 DAP (grain-filling stage) compared with 16% and 9% for SST 843 and Duzi, respectively, but final height at 165 DAP was not significantly different (Table 4.10). The treatment stressed during the flowering stage (NSN) significantly decreased plant height from 87 DAP up to maturity, compared with the control treatment (NNN) (Figure 4.8), but the treatment combination was different only at 108 DAP (Table 4.11). Comparable results were found by Jatoi *et al*. (2011), who discovered that water stress in the flowering stage reduced plant height of wheat by 5%, compared with a well-irrigated treatment. On average water stress treatment NSN reduced plant height by 14% compared to 11% reduction of both SNN and NNS treatments on 108 DAP (Figure 4.8). Reduction in plant height by the NSN treatment in the grain-filling stage corresponds with a 59% reduction of TDM at that stage. These results are well supported by Gupta *et al*. (2001), who found that plant height was positively correlated to dry matter yield when stress was imposed in the flowering stage of wheat. Water stress imposed from grain filling to maturity (NNS) in all cultivars decreased plant height significantly at around 108 DAP, compared with the NNN treatment (Table 4.11 and Figure 4.8). However, the mean of the final plant height was not significantly different from the NNN treatment (Figure 4.8). This is in conformity to the report of Doorenbos and Kassam (1979), who noted that water stress in the grain filling and drying off period had slight or no effect on growth and yield components. Final plant height in 2011 was significantly higher than in the 2010 season (Table 4.10).

The variances in final plant height (between seasons) could also be attributed to late planting in the 2010 season (which resulted in shorter plants) and not to recovery of height after the termination of the stress period. Late planting in the 2010 season consequently shortened the vegetative period and the growing season (Table 3.1). The vegetative stage has been reported to be a period of active growth (Acevedo *et al.*, 2002). Therefore the vegetative growth period was reduced by 12 days in the 2010 season, as flowering was reached on 65 DAP in 2010 season compared to 82 DAP in 2011. After flowering, stem height growth ceases (Slafer & Rawson, 1994). However, awns, peduncles and spikes continue to grow (Acevedo *et al.*, 2002). Therefore the reduction in final height in the 2010 season could be ascribed to earlier completion of stem growth. Non-significant differences in final plant height in 2010 could also be attributed to a shorter stem elongation stage (SNN) period, which resulted in a short growing season (Table 3.1). This brought about a reduction in all plant growth parameters and yield components in 2010, and consequently lower grain yield and water use (Chapter 5) compared with the 2011 cropping season.

4.3.3.4 Dry matter production

Dry matter production during the growing season is a good indicator of plant growth, and potential grain yield (Wu & Bao, 2011). The anova table on variables that influenced dry matter production are summarised in Table B.4 (Appendix B). Table 4.12 present the effects of water stress on wheat cultivars stressed at various growth stages in the 2011 season and dry matter production of wheat per irrigation treatment are summarised by Figure 4.9.

Table 4.12 Water stress effects on dry matter production of wheat cultivars stressed at various growth stages in the 2011 season

Dry matter production (t ha^{-1})				
Interaction effect		**Growth stages**		
Irrigation	***Cultivars***	Stem elongation	Flowering	Grain filling
SNN	Duzi	2.77c	9.84ef	14.90c
	Steenbras	2.45c	10.63d	19.10ab
	SST 843	3.56bc	14.62c	17.60bc
NSN	Duzi	6.52a	8.65f	14.20d
	Steenbras	5.90a	8.91ef	17.9bc
	SST 843	6.51a	8.95ef	18.50b
NNS	Duzi	7.30a	17.01ab	17.10bcd
	Steenbras	5.53ab	17.96ab	19.10ab
	SST 843	5.52ab	17.40ab	18.40b
NNN	Duzi	7.04a	18.61a	18.90ab
	Steenbras	6.52a	18.56ab	22.10a
	SST 843	6.75a	17.96ab	20.3ab

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

The effect of water stress on dry matter production was not significantly influenced by cultivar during stem elongation, which implies that the cultivars responded similarly to water stress at that stage (Table 4.12). Though there were no significant differences between cultivars due to water stress imposed in the stem elongation stage (SNN), the cultivar SST 843 exhibited a 47% reduction in dry matter production and for the cultivars Duzi and Steenbras a 62% reduction in dry matter production was observed. The SNN treatment significantly influenced the dry matter production of cultivars in the flowering stage (Table 4.12). In this stage, the SNN treatment of cultivar SST 843 had a reduction in dry matter yield of 19%, compared with 47% and 43% for Duzi and Steenbras, respectively. Therefore, after the SNN treatment, dry matter production in SST 843 recovered quickly compared with other cultivars, even though they were not different at the grain-filling stage. Higher dry matter production of SST 843 was attributed to higher Pn as compared to other cultivars (Figure 4.2b). These results are in agreement of the research findings of several authors (Changhai *et al*., 2010; Wu & Bao, 2011) who found that the cultivars with higher photosynthetic rate under different water depletion levels also produced higher above-ground dry matter yield compared to the cultivars with lower photosynthetic rate.

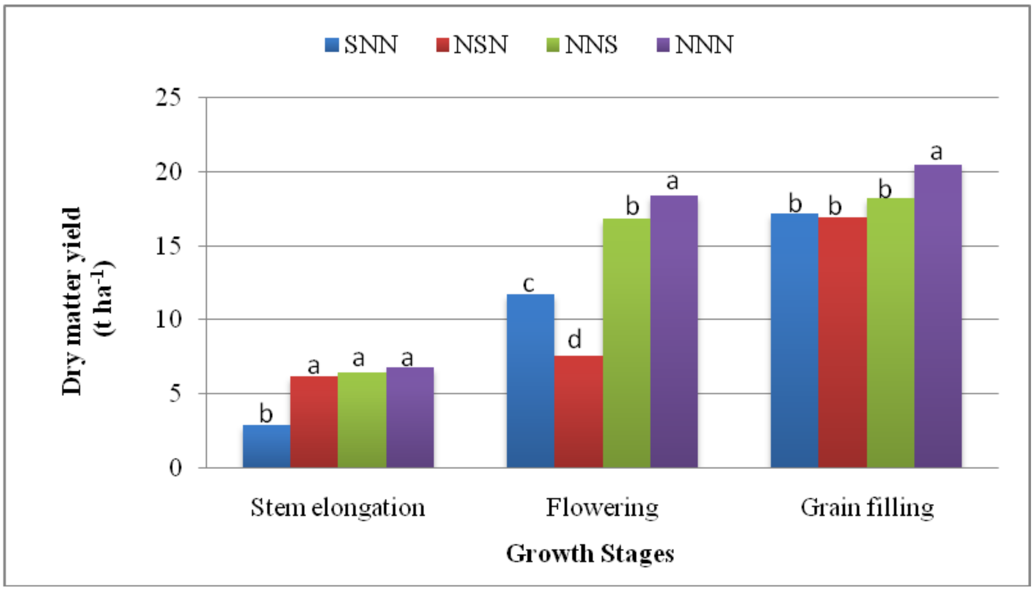

Figure 4.9 Water stress effect on dry matter production of wheat stressed at various growth stages in 2011 cropping season. *Bars with the same letter per growth stage are not significantly different at p≤0.01; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

Dry matter production of the NSN treatment was not significantly influenced by cultivars during the stress period (flowering). However, when water stress of the NSN treatment was terminated, cultivars differed in dry matter production during the grain-filling stage. Duzi proved to be the most susceptible cultivar to water stress in the flowering stage (NSN) as dry matter production measured in the grain-filling stage was reduced by 40%, compared with 26% and 22% for SST 843 and Steenbras, respectively (Table 4.12).

Generally, water stress imposed at any growth stage significantly reduced dry matter yield. Dry matter production was reduced by 57% owing to water stress in the stem elongation stage (SNN), whereas water stress in the flowering stage (NSN) and grain filling (NNS) reduced dry matter yield by 59% and 11%, respectively (Figure 4.9). Bogale and Tesfaye (2011) reported that the severity of dry matter reduction due to water stress depends on the growth stage at which water stress occurs. In the present study water stress imposed in the flowering stage (NSN) reduced dry matter yield most, compared with water stress in other growth stages. Several authors reported that reduced dry matter production due to water stress in the flowering stage is mainly attributed to reduced source and sink size (Ji *et al*., 2010; Anjum *et al*., 2011). The most reduced source that consequently inhibits dry matter partitioning is through reduced leaf expansion and development, resulting in reduced LAI (Anjum *et al*., 2011). In the present study the NSN treatment reduced dry mater production by 29%, compared with 13% and 8% of SNN and NNS treatments in the grain-filling stage (NNS), irrespective of the absence of significant differences (Figure 4.9). This confirms that water stress in the grain-filling stage had little effect on dry matter production as reported by Doorenbos and Kassam (1979). However, reduction in dry matter during grain filling could be attributed to a significant decrease in the number of leaves owing to accelerated senescence, which then reduced LAI (Table 4.12 and 4.9), thus triggering a drop in the grain-filling duration and rate, which negatively affected the kernel weight (Bogale & Tesfaye, 2011). Therefore, water stress imposed in the flowering stage (NSN) reduced dry matter for a longer duration, which consequently lowered grain yield and harvest index (Table 5.8 and 5.7 in Chapter 5 of this dissertation).

4.4 Conclusions

In the present study, water stress imposed at any developmental stage of wheat cultivars reduced the functioning of vital physiological components such as stomatal conductance, photosynthesis and the transpiration rate. Photosynthesis is related to growth and yield, therefore a reduction in photosynthesis affects leaf growth and formation, which diminishes the duration of the green LAI and dry matter production. Lower transpiration and photosynthesis under water stress at various growth stages were the result of lower stomatal conductance. Stomatal conductance was reduced most due to water stress imposed in the flowering stage (NSN), which induced a reduction in intercellular CO_2 concentration, photosynthesis and transpiration rate, and consequently raised leaf temperature and iWUE.

These physiological components (discussed above) were influenced by a cultivar effect in the flowering and grain-filling stages only. The cultivar SST 843 had higher stomatal conductance, which corresponded with higher photosynthesis and transpiration rates. Reduction in physiological functions under water stress was due to lower LWP, which affected the formation and enlargement of leaves (Zhang *et al.*, 1998). In the present study the number of leaves was reduced by water stress imposed at any growth stage, which significantly affected LAI and DM production. Reduction in the number of leaves reduced the duration of the green LAI. The NSN and NNS treatments reduced LAI most towards the end of the season in the grain-filling stage (131 DAP). This could have been due to the accelerated death of leaves, as the highest number of leaves and LAI were recorded in the flowering stage (95 DAP). The LAI was influenced by cultivars during the flowering and grain-filling stages only (87 DAP to 131 DAP). From the flowering stage, the cultivar SST 843 had higher LAI than the others. Plant height was not different among cultivars used in the present study. However, water stress at any growth stage reduced plant height. The plant height of the treatment stressed in the stem elongation stage (NSN) was reduced by 25%. However, it recovered through irrigation at flowering and grain filling. The treatment stressed in the flowering stage (NSN) had lower final plant height, which shows that the NSN failed to recover due to re-watering in the grain-filling stage. In the grain filling stage (165 DAP (harvest), the NSN treatment reduced plant height by 19% compared with 9% and 5% reduction for SNN and NNS treatments, respectively. Water stress in the stem elongation phase reduced dry matter production by 57%. However, the treatment showed great recovery after resumption of irrigation, showing a 36% and 16% reduction in the flowering and grain-filling stages, respectively. Stress in the flowering stage (NSN) reduced dry matter production most, and failed to recover when irrigated again in the grain-filling stage. The NSN treatment reduced dry-matter production by 59% in the flowering stage and in the grain-filling stage reduced dry matter by 18%, which was higher than the 11% reduction in dry matter observed for the treatment stressed in that stage (NNS). Generally, the NSN treatment reduced physiological measurements and growth components most compared with SNN and NNS treatment, whereas it increased leaf temperature and iWUE most. A reduction in stomatal conductance limited leaf gaseous exchange, which consequently resulted in increased leaf temperature (Deng *et al.*, 2000), whereas higher iWUE indicates that water stress reduced E more than Pn (Bogale *et al.*, 2011).

The discussion above proves that both hypotheses were accepted:

$H_0$1: Water stress induced stomatal closure, which restricted water loss, resulting in reduction of internal leaf CO_2 concentration, photosynthesis and transpiration rate;

$H_0$2: Photosynthesis of different wheat cultivars responded differently to water stress imposed at various growth stages.

In conclusion, significant reduction in physiological functions and growth components due to stress in the flowering stage (NSN) suggests that supplemental irrigation is most critical at this stage.

CHAPTER 5: EFFECTS OF WATER STRESS ON WATER USE, YIELD AND QUALITY OF WHEAT CULTIVARS STRESSED AT VARIOUS DEVELOPMENTAL STAGES

Abstract

Most wheat production areas are vulnerable to water stress during the growing season in both the summer and the winter rainfall areas of South Africa. Water stress reduces wheat productivity, depending on the growth stages at which stress occurs. Supplemental irrigation is the main strategy for adaptation and stabilisation of yield under water stress conditions. Therefore, understanding the effects of water stress on yield and quality is essential for good irrigation management so that water use efficiency (WUE) can be improved without reducing yield and quality significantly under water limited condition. Experiments were conducted under a rain shelter at the Hatfield Experimental Farm, University of Pretoria, in the 2010 and 2011 winter seasons. The aim of the study was to determine the growth stage at which limited water supply would improve water use efficiency without significant reduction in grain yield and quality of certain wheat cultivars, namely; Duzi, Steenbras and SST 843. Water stress (S) was imposed in the stem elongation (SNN); flowering (NSN) and grain-filling (NNS) stages and were compared to a well-watered control (NNN). Water use, grain yield and quality of all cultivars were influenced by water stress imposed at various stages. The total crop water use for the well-watered control treatment (NNN) ranged between 475 mm and 623 mm per season. Water stress in the stem elongation stage (SNN) and grain-filling stage (NNS) reduced water use by 27% and 17%, which translates to 173 mm and 105 mm less water used in each growth stage respectively, compared to the control (NNN) treatment in the 2011 season. In 2011 the cultivar SST 843 had higher WUE compared to other cultivars. The irrigation treatment exposed to water stress from flag leaf to end of flowering (NSN) reduced grain yield most by 33% and 35% in the 2010 and 2011 seasons, respectively. The cultivar Steenbras proved to the most drought tolerant cultivar because of lower yield reduction under water stress. In the 2011 season the NSN treatment (water stress in the flowering stage) of cultivar Steenbras reduced grain yield by 30%, compared with 34% and 40% yield reduction for Duzi and SST 843 respectively. Significant reduction in grain yield for the NSN treatment was due to a lower number of ears per unit area, fewer kernels per ear, shorter ear length and lower total dry matter production. On average, the NSN treatment reduced the number of ears per unit area by 26% compared with the control treatment (NNN). Total dry matter yield was reduced by 17% due to water stress in the NSN treatment, compared with the 16% and 10% reduction for the SNN and NNS treatments, respectively, in the 2011 season. The treatment exposed to water stress in the flowering (NSN) and grain-filling stages (NNS) both increased grain protein content (GPC) by 9% respectively, compared with the NNN treatment in 2011. The cultivar Duzi had lower GPC than the other cultivars. Hectolitre mass (HLM) was reduced by 3% and 5% in the 2010 and 2011 seasons, respectively, due to water stress imposed in the grain-filling stage (NNS), compared with the control treatment (NNN). Generally all quality parameters in the present study were acceptable for all irrigation treatments and cultivars. The hypothesis that water stress in the stem elongation and grain-filling stages will have little effect on yield and improve WUE was accepted. Therefore it can be recommended that supplemental irrigation should be applied from flag leaf to end of flowering (NSN) of wheat in order to minimise grain yield losses in the absence of rainfall.

Key words: grain quality, growth stages, water deficits, water use, water use efficiency, wheat cultivars, yield and yield components

5.1 Introduction

In South Africa wheat is the second most important grain crop after maize, which is consumed daily as bread, cakes, cookies, livestock feeds and as alcoholic beverages. Annual wheat production in South Africa over the past five years has ranged between1.4 million tons and 2.1 million tons, with an average yield of 2 to 3.1 t ha^{-1} under dryland and about 5 to 7 t ha^{-1} under irrigation (ARC-SGI, 2009; DAFF, 2010). South Africa is a net importer of wheat, and imported roughly 2 million tons in the 2010 season, mainly from Argentina, the USA and Australia (DAFF, 2012). Locally, wheat is produced in both the summer and winter rainfall regions. It is grown as a dryland crop mostly in winter rainfall regions, and under both irrigation and dryland conditions in summer production regions (ARC-SGI, 2009).

South Africa receives an annual average rainfall of 495 mm, which is far below the world’s average of 860 mm per year (Gbetibouo & Hassan, 2005). Furthermore, the rain is distributed unevenly across the country, with sub-tropical conditions in the east and dry desert conditions in the west (Blignaut *et al*., 2009). Consequently, water stress is one of the most serious environmental stresses, limiting yield of major staple cereal grains, including wheat. Therefore, there is a need to improve water use efficiency (WUE) in crop production, since agriculture uses more than 60% of total available water in South Africa (Gbetibouo & Hassan, 2005).

The solution is to optimise water application in any specific growth stage in order to save water, but minimise loss of yield from water stress (Zhang & Oweis, 1999). It is important to increase our knowledge of the interaction between crop development, grain yield and water use in order to face the climate change-driven increase in global aridity (Gbetibouo & Hassan, 2005; Blignaut *et al*., 2009). In agricultural production, supplemental irrigation has been proposed as a strategy to conserve water under limited water supply conditions (Shamsi *et al*., 2010). Many researchers have concluded that supplemental irrigation is an economically viable option under conditions of limited water supply (Oweis & Hachum, 2006; Zhang & Oweis, 1999; Shamsi *et al*., 2010). It is a suitable method of saving water while achieving acceptable yield under water shortage conditions (Ali *et al*., 2007), but it requires regular monitoring of soil water content in order to schedule irrigation (Zhang & Oweis, 1999).

Growth and yield responses to soil water availability differ, depending on the intensity of stress and developmental stage at which it occurs (Bogale & Tesfaye, 2011). Water stress during certain growth stages may have less effect on grain yield and quality than a similar stress in other growth stages (Ozturk & Aydin, 2004). For example, water stress in the vegetative stage may have little effect on grain yield if sufficient rain or irrigation occurs at later stages (Doorenbos & Kassam, 1979). Therefore it is important to understand the consequences of water stress at each developmental stage in relation to growth and yield potential for better irrigation management (Zhang & Oweis, 1999).

Several authors have found that water stress that is terminated before the booting stage of wheat resulted in the development of late tillers, which increased the number of ears per unit area, and consequently improved yield and WUE (Mogensen *et al*., 1985; Abayomi & Wright, 1999). Ji *et al*. (2010) indicated that water stress at the reproductive stage of wheat leads to spikelet sterility, which significantly decreases the number of grains per spike (Mirzaei *et al*., 2011). Water stress during grain-filling does not affect the number of fertile tillers; however, grain mass is reduced owing to a shortening of the grain-filling period because of accelerated senescence (Bogale & Tesfaye, 2011).

In South Africa, wheat grain with protein content above 12% , minimum falling number (FN) of 220 seconds, and hectolitre mass (HLM) of more than 77 kg hl^{-1} are considered as first grade in the bread industry (ARC, 2009; DAFF, 2010). The quality of wheat is influenced mainly by genotype (cultivar), environmental factors, and the interaction between genotype and environment (Agenbag & De Villiers, 1995). Water stress is one of the most important environmental factors that may influence end-use quality of wheat (Saint Pierre *et al*., 2008). Little research has been done on the effects of water stress on the quality of wheat in South Africa; therefore there is a need to conduct further research to elucidate the effects of water stress on quality components of wheat (Agenbag & De Villiers, 1995). Doorenbos and Kassam (1979) report that yield and quality under limited water supply are not linearly related. Several authors have indicated that there is an increase in grain protein content (GPC) under drought stress (Ozturk & Aydin, 2004; Saint Pierre *et al*., 2008). The positive effect on GPC takes place through the reduction of synthesis and storage of carbohydrates, which allows a higher concentration of nitrogen per unit starch to accumulate in the grain (Saint Pierre *et al*., 2008). Therefore the specific aim of this study was to identify the growth stages in which limited water supply will improve WUE, but have minimal effects on yield and quality of wheat cultivars with the hypotheses that:

> **$H_0$1**: Water stress during stem elongation will have a minimal effect on wheat grain yield, leading to higher water use efficiency
>
> **$H_0$2**: Water stress imposed in the grain-filling stage will improve grain protein quality, but have little effect on yield and water use efficiency

5.2 Materials and methods

General methodology was discussed in chapter 3 of this dissertation.

5.3 Results and discussion

The anova on water use, yield, and quality parameters are presented in Appendix C (Table C.1); whereas the correlations of grain yield and yield components, water use and quality parameters are presented in Appendix C (Table C.2). The first section presents the water depletion patterns in the root zone of wheat cultivars in the 2010 and 2011 seasons. Thereafter, water stress effects on water use and WUE, grain yield components and quality components during two consecutive seasons are discussed. Lastly conclusions are drawn from all these sections.

5.3.1 Water depletion patterns in the root zone

Average soil water contents per treatment as measured with a neutron water meter for the 2010 and 2011 cropping seasons are presented in Figure 5.1 and Appendix D. Figure 5.1 summarises the water depletion patterns per treatment in the two consecutive seasons, whereas Appendix D presents the water depletion patterns per cultivar. The cultivars extracted water similarly in both seasons (Appendix D). Water stress induced extraction of water from deeper soil layers, compared with the control treatment (NNN), in both seasons (Figure 5.1 and Appendix D). Comparable results were recorded by several authors (Zhang *et al*., 1998; Ali *et al*., 2007) who found that the well-watered treatment extracted water mainly from the top soil layers. Higher soil water deficit due to limited irrigation is associated with lower plant available water (PAW) in the root zone, which consequently reduced stomatal conductance, leaf area index and grain yield (Ahmed *et al*., 2012). In the present study profile soil deficits followed similar trends as the LAI data, i.e. higher deficits resulted in smaller LAIs (Figure 4.6 in Chapter 4). Comparable results were found by Zhang *et al.* (1998), who found that lower soil water content of the stressed treatment significantly reduced LAI, compared with the well irrigated treatment. On average the control treatment (NNN) maintained a deficit of 13 mm (30% of PAW) from 25 to 77 DAP in the 2011 season, whereas in 2010 season all the treatments were stressed in the beginning of the season (37 to 43 DAP).

In the 2010 season all treatments, including the control (NNN) depleted about 22 mm (50% of PAW) from 37 to 43 DAP. That had negative effects on overall yield, especially for treatments stressed during the stem elongation stage (SNN), which had higher deficits in the soil profile before exposed to planned water stress. In contrast, during the 2011 season, all treatments were well watered before being exposed to planned water stress. In South Africa the dry season or drought may occur in the vegetative stages in summer rainfall regions. On average, the highest deficit of the SNN treatment was up to 24 mm, whereas NSN and NNS depleted 62 and 66 mm respectively in the 2011 season. The average deficit was calculated by summation of deficits between the stress periods demarcated by dotted lines in Figure 5.1. Generally for SNN lower deficits (55% depletion of PAW) were experienced during the total stress period, compared to 78 and 83% depletion of PAW for the NSN and NNS treatments, respectively in 2011.

The wheat stressed in the grain-filling stage (NNS) extracted water from the profile in a similar pattern as the control treatment (NNN) in the beginning of the season. The NNS treatment was stressed from 105 DAP up to physiological maturity in 2011. Unlike other water-stress treatment (SNN and NSN) the NNS treatment was not irrigated after terminating stress until harvesting in both seasons. On average the NNS treatment depleted 83 and 60% of PAW at physiological maturity in the 2011 and 2010 seasons, respectively. That was on 95 and 125 DAP in 2010 and 2011 respectively. This means that the dry-off period was 30 days in 2010 and 40 days in 2011. As result of that, all treatments used more water (ET) in 2011 due to a longer growing season, which consequently affected the water use efficiency (Table 5.1).

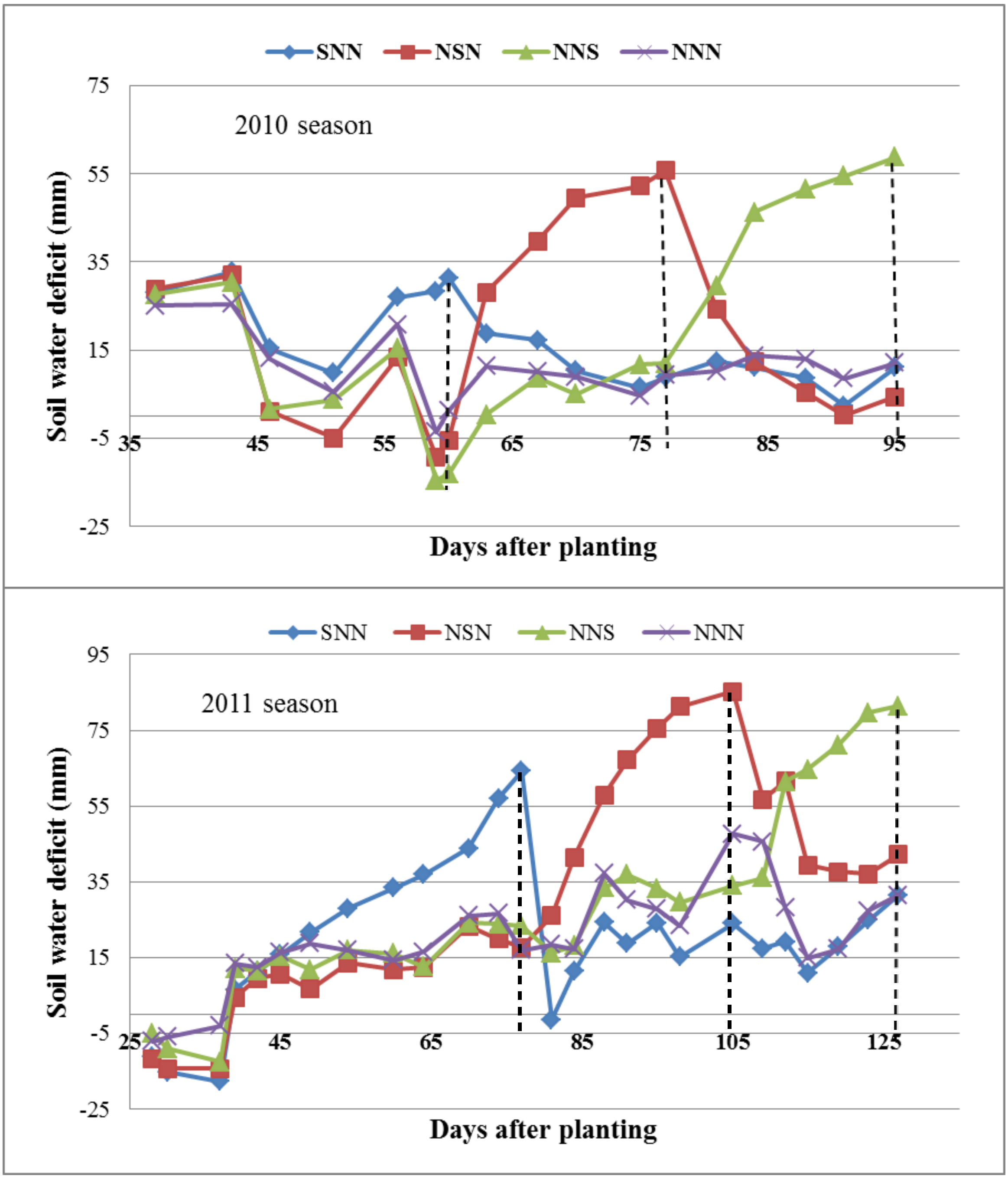

Figure 5.1 Average profile soil water deficits during the 2010 and 2011 cropping seasons at different days after planting. *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment. The dotted lines indicated the time of stress termination.*

The highest water deficit of the NNN treatment was recorded at the early grain-filling period (105 DAP). Generally higher deficits were recorded in the flowering (NSN) and grain-filling

(NNS) stages compared to deficits in the stem elongation stage in both seasons. Higher depletion of water from the profile during flowering and grain-filling stages was due to increased atmospheric demand, which induced higher loss of water from the soil. Zhang and Oweis (1999) indicated that a gradual increase in water depletion towards the end of the season is due mainly to higher temperatures and increased evaporative demand, mostly because growth of the root system is complete (Doorenbos & Kassam, 1979). Similar results were found in the current study, as temperature and solar radiation also increased towards the end of the season (Table 4.1 in Chapter 4). Therefore, the results agree with those of Zhang and Oweis (1999). Reports indicate that plants experience water stress whenever absorption of water by the crop is lower than the evaporative demand of the atmosphere, especially when 50% of available water is depleted (Simpson, 1981, Blum, 1996). In the present study all treatments exceeded more than 50% depletion of PAW at the end of the stress periods (dotted lines in Figure 5.1) in both seasons, which means that the plants suffered due to water stress as intended. However, the severity of stress was more in the 2011 season in all treatments, compared to the 2010 season. That can also be attributed to differences in the duration of stress days in the two seasons (Table 3.1 and 3.2 in chapter 3), which resulted in differences in soil water depletion patterns in the root zone (Figure 5.1), which contributed to the differences in total water use per season and WUE per season per cultivar (Section 5.3.2.1), grain yield (Table 5.1 and Table 5.8) and growth parameters (Chapter 4).

5.3.2 Water stress effects on water use and water use efficiency

5.3.2.1 Water use

Total evapotranspiration (ET), grain yield and water use efficiency (WUE) data per irrigation treatment and cultivar for the two cropping seasons are summarised in Table 5.1. Total ET was not significantly influenced by cultivar in the 2010 season, whereas in 2011, cultivars differed significantly in water use per season (Table 5.1). Figure 5.2 shows the relationship between total water used per season and grain yield. The results reveal that water use was not significantly different between cultivars in the 2010 season, whereas in 2011 both irrigation and cultivars significantly influenced water use.

Table 5.1 Total water use, grain yield and water-use efficiency of three wheat cultivars exposed to water stress at different growth stages in the 2010 and 2011 seasons

Parameters		**Water use (mm)**		**Grain yield (kg ha^{-1})**		**Water-use efficiency (kg mm^{-1} ha^{-1})**	
Source of variation	**Seasons**	2010	2011	2010	2011	2010	2011
Irrigation	SNN	419c	451c	5311b	6737b	12.8b	14.9a
	NSN	447b	426d	4189d	5471d	9.4c	12.8b
	NNS	381d	518b	4967c	6693c	13.1ab	12.9b
	NNN	475a	623a	6289a	8460a	13.2a	13.6b
Cultivars	Duzi	430a	491c	5383a	6660b	12.6a	13.6ab
	Steenbras	430a	514a	5100b	6652b	11.9b	13.0b
	SST 843	430a	509b	5083b	7210a	11.8b	14.2a
Irrigation	**Cultivars**						
SNN	Duzi	419c	446i	5467c	6293cd	13.1bcd	14.1bc
	Steenbras	419c	471g	5200d	6627c	12.5d	14.1bc
	SST 843	419c	436k	5267cd	7293b	12.6d	16.7a
NSN	Duzi	447b	390l	4433e	5403de	9.9f	14.1bc
	Steenbras	447b	450h	3933f	5560de	8.8g	12.4d
	SST 843	447b	439j	4200e	5360c	9.4fg	12.2d
NNS	Duzi	381d	495f	5300cd	6293cd	13.9a	12.7cd
	Steenbras	381d	523e	5200d	6493c	13.7ab	12.4d
	SST 843	381d	537d	4400e	7293b	11.6e	13.6bcd
NNN	Duzi	475a	635a	6333a	8560ab	13.3abc	13.5bcd
	Steenbras	475a	610c	6067b	7927b	12.8cd	13.0bcd
	SST 843	475a	625b	6467a	8893a	13.6ab	14.2b
	Overall mean	**430**	**505**	**5189**	**6841**	**12**	**14**

Means in a column followed by the same letter are not significantly different at p≤0.01; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

The absence of significant differences between cultivars in water use in the first season was due to simultaneous irrigation of all plots of the same treatment, regardless of cultivar (from the same valve and water meter, for example all NNN treatments were irrigated together). However, during the second season (2011), each treatment of each cultivar had its own valve and water meter. The total crop water use for the NNN treatment ranged between 475 mm and 623 mm per season (Table 5.1). The total water used by the NNN treatment in this study was within the typical water requirements of wheat, reported by several authors (Zhang & Oweis, 1999; Sun *et al*., 2006). Sun *et al*. (2006) found that optimal water consumption by wheat was about 453 mm, whereas the highest yield was produced with 680 mm per season in China. Water stress highly significantly influenced ET per growing season in the present study (Table 5.1). The differences in total ET was also influenced by the length of the cropping season (Table 3.1). Doorenbos and Kassam (1979) also indicated that water use depends on the length of the growing season and climatic conditions.

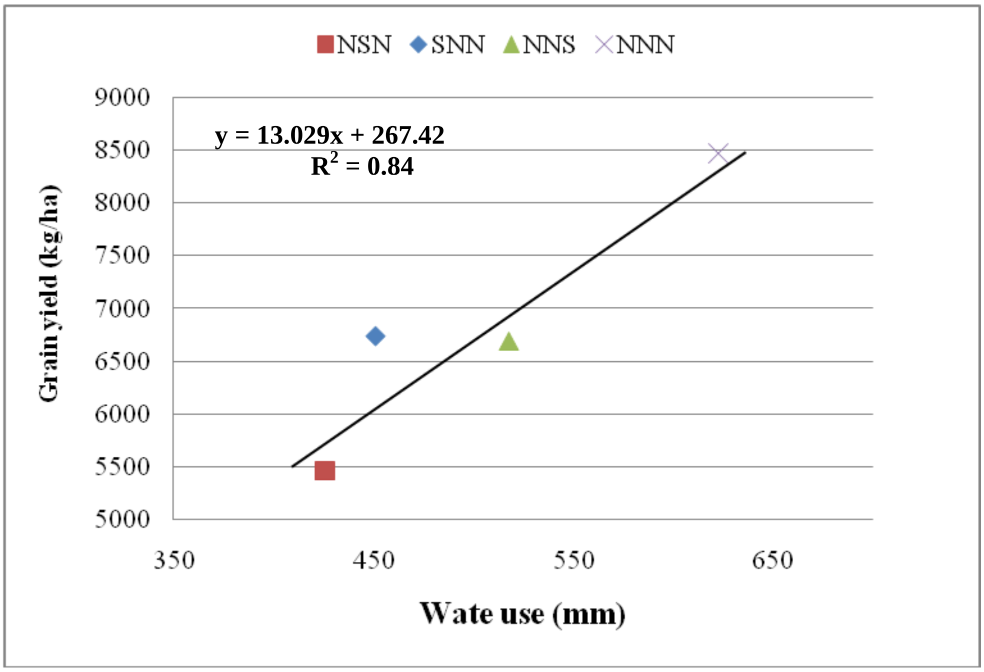

Figure 5.2 Relationship between grain yield and water use in 2011 cropping seasons at different days after planting. *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain-filling stage; and NNN refers to the control treatment*

Generally all treatments used less water in the 2010 season compared with 2011, and this was due mainly to delayed planting in the first seasons, which consequently resulted in lower total water use, but also lower yields. The results in the present study confirm those of Blum (1996), who reported that shorter seasons reduce total solar radiation interception, which consequently reduces seasonal assimilation, leading to lower yields. The control treatment (NNN) had significantly higher ET ($p \leq 0.01$) in both seasons, compared with all stressed treatments (SNN, NSN and NNS). The higher water use per season of the NNN treatment corresponded with higher yields in both seasons.

Generally water use was linearly correlated (0.84**) to grain yield (Figure 5.2). Comparable results were reported by several authors (Zhang and Owes, 1999; Sun *et al*., 2006) who report that grain yield increases linearly with an increase in total water use over the duration of the season. Generally SNN and NNS reduced ET by 27% and 17% relative to NNN treatment, which translates to 173 mm and 105 mm of water saved in each growth stage, respectively, in the 2011 season. Comparable results were reported by Ali *et al* (2007), who found that withholding irrigation in the crown root initiation and soft dough stages of wheat can save water, compared to a well irrigated treatment.

5.3.3.2 Water use efficiency

Water use efficiency (WUE) was calculated as the ratio of grain yield over total water used per treatment (in kg ha^{-1} mm^{-1}) for both seasons (Table 5.1). In the 2010 season, withholding irrigation in the grain-filling stage (NNS) resulted in the highest WUE for the stress treatments. This was due to less total water use by this treatment in 2010 due to lower irrigation in the beginning of the season, between 35 and 45 DAP (Figure 5.1). The NNS treatment depleted an average of 25 mm between 37 at 43 DAP (about 57% of PAW depleted) before onset of the planned water stress period in 2010. It means that some water was saved in this period without significantly reducing yield. These results are comparable to those of Ali *et al*. (2007), who found that withholding irrigation in the jointing and soft dough stages of wheat improved water use efficiency due to lower total water use per season. However, in 2011 the treatment that was stressed in the stem elongation stage (SNN) had the highest WUE, compared with other irrigation treatments ($P \leq 0.01$). The SNN treatment improved WUE by 11% compared to the control (NNN), which translates to 173 mm of water saved without reducing yield significantly in 2011, whereas NSN reduced WUE the most of all treatments. The NSN treatment reduced WUE by 29% and 6% in 2010 and 2011 respectively. Inconsistencies in WUE achieved per treatment could be ascribed to differences in the duration of the seasons, due to late planting in 2010. This is well explained by Doorenbos and Kassam (1979), who reported that water requirements of wheat depend on the duration of the growth season and climatic conditions. However, this depends on water availability in the soil profile before stress periods (Sun *et al*., 2006). In the present study, seasonal variation in WUE was also attributed to differences in water availability in the soil profile (Figure 5.1). Higher water deficits in the soil profile at the beginning of the first season (37 to 43 DAP) led to a lower yield of the SNN treatment compared with the wetter profile (28 to 39 DAP) in 2011 (Figure 5.1), which corresponded to higher yield and higher WUE (Table 5.1).

Water stress imposed in the flowering stage (NSN) had the lowest WUE in both seasons (Table 5.1). These results were analogous with the findings of Seghatoleslami *et al*. (2008), who found that stress in ear emergence reduced WUE more than stress in other growth stages. Therefore, the effects of WUE depend on the developmental stage at which water stress occurred (Bogale *et al*., 2011). Furthermore WUE depends on water use per season, and the duration of the season, as well as the time of termination of the last irrigation (Doorenbos & Kassam, 1979).

In the 2011 season, although the control treatment (NNN) had higher yield, it had significantly lower WUE compared with the SNN treatment. Lower WUE of the NNN treatment in 2011 could be ascribed to delayed termination of the last irrigation, as reported by Doorenbos and Kassam (1979). Late termination of irrigation in 2011 led to unproductive water loss through evaporation from the soil surface. Comparable results were found by Sun *et al*. (2006), who found that the treatments stressed in stem elongation and grain-filling improved WUE, compared with well-irrigated wheat. Water-use efficiency is important component that is widely used to assess grain yield sensitivity to water stress at different growth stage (Seghatoleslami *et al*., 2008; Shamsi *et al*., 2010). In this study, water stress had little effect on grain yield when stress imposed from tillering to the flag-leaf stage (SNN) and grain-filling stages (NNS), compared with stress imposed from flag-leaf to the end of flowering (NSN) and that gave higher WUE. Comparable results were found by Mirzaei *et al.* (2011). Grain yield response to water treatments is fully discussed in section 5.3.3.7.

Water use efficiency was significantly influenced by both irrigation treatments and cultivars in both seasons (Table 5.1). However, the WUE trend among cultivars was not consistent in subsequent seasons. The cultivar Duzi and SST 843 used water more efficiently in the 2010 and 2011 season respectively. Furthermore the interaction effect between irrigation and cultivars was only significant in the 2011 season. The absence of significant differences of cultivars in all irrigation treatments in WUE during 2010 was probably due to the fact that cultivars were irrigated simultaneously, which resulted in similar ET values (discussed in 5.3.2.1). In the 2011 season, WUE of cultivars differed significantly due to differences in water use and yield (Table 5.1). The cultivar Steenbras used more water than the other cultivars for the SNN and NSN treatments, which consequently maintain good grain yield in those stages (stem elongation and flowering stages), though that was not significantly different to other cultivars. However on average, the cultivar Steenbras had a lower WUE due to higher ET and lower average grain yield. On the other hand the cultivar SST 843 had a higher WUE (on average across irrigation treatments) due to a significantly ($p \leq 0.01$) higher grain yield (Table 5.1), especially for the treatments stressed in the stem elongation and grain-filling stages. Comparable results were also found by several authors elsewhere (Seghatoleslami *et al.*, 2008; Shamsi *et al.*, 2010), who noted that cultivars with higher yield potential got relatively higher WUE. Therefore, results in the current study agree with those of Shamsi *et al.* (2010) on wheat and Seghatoleslami *et al*. (2008) on millet.

5.3.3 Water stress effects on yield components

5.3.3.1 Number of ears

The results showed that the number of ears per metre square (NEM) was significantly ($p \leq 0.01$) influenced by the treatment (interaction of cultivar and irrigation). However, the effect was not consistent between seasons. Water stress treatments significantly ($p \leq 0.05$) reduced NEM in the 2011 season only (Table 5.2). The NSN treatment significantly reduced the number of ears per metre square most, compared with other treatments. On average, the NSN treatment reduced NEM by 26% compared with the control treatment (NNN). The cultivar effect also significantly influenced the NEM, but the trends were not consistent over the seasons (Table 5.2). In the first season the number of ears was significantly lower than the second season. That could be due to late planting which shortened the duration of the growth season in 2010, compared to the 2011 season (Table 3.1 in chapter 3).

Table 5.2 Water stress effects on number of ears of wheat cultivars stressed at various growth stages

Treatments		**Number of ears(m^2)**	
		Cropping seasons	
Source of variation		2010	2011
Irrigation	SNN	543a	734a
	NSN	485a	555b
	NNS	542a	738a
	NNN	509a	747a
Cultivars	Duzi	452b	622b
	Steenbras	502b	876a
	SST 843	606a	583b
Irrigation	**Cultivars**		
SNN	Duzi	465bc	726b
	Steenbras	523abc	903a
	SST 843	641a	572cd
NSN	Duzi	434bc	490d
	Steenbras	448bc	697bc
	SST 843	575ab	478d
NNS	Duzi	489bc	600bcd
	Steenbras	572ab	976a
	SST 843	566ab	638bc
NNN	Duzi	420c	672bc
	Steenbras	465bc	926a
	SST 843	641a	643bc

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage, NNS refers to water stress in the grain-filling stage, and NNN refers to the control treatment

Blum (1996) reported that the NEM is an important parameter that partly determines the final grain yield. According to Abayomi & Wright (1999) limited soil water affects the NEM, depending on the growth stage at which stress occurs, which will negatively affect the wheat grain yield. In the present study, the NEM was significantly reduced by water stress imposed in the flowering stage (NSN) in 2011 season. These results are in agreement with the findings of Abayomi and Wright (1999), who reported that water stress in the booting to flowering stage reduced the number of ears per metre square more than stress in other stages. The number of ears per metre square was not significantly reduced due to water stress in the stem elongation (SNN) and grain-filling stage (NNS), compared with the control (NNN) treatment (Table 5.2). The absence of significant differences in the NEM due to stress during stem elongation (SNN), when compared with the NNN treatment, could be attributed to additional ears that developed from late tillers after the resumption of irrigation. Abayomi and Wright (1999) found that development of late tillers led to an increase in the number of ears per metre square when stress was terminated in the booting stage. New ears from new late tillers can therefore contribute to the final grain yield (Mogensen *et al*., 1985). However, ears produced by late tillers are usually small, with relatively small grain seeds (Abayomi & Wright, 1999). The seeds formed from late tillers also require a longer period to dry, which consequently delays harvesting. That may cause other yield losses through lodging and bird damage (Doorenbos & Kassam, 1979). The ear formation takes place in the mid vegetative stage (jointing) and development occurs from that time onwards (Slafer &Whitechurch, 2001). Therefore, the absence of significant differences in the NEM due to water stress imposed during grain-filling stage (NNS) in this study could be because grain filling occurs when ears are completely formed. Similar results were reported by several authors, and they concluded that water stress at grain filling has little effect on the NEM compared with stress at earlier stages (Bogale & Tesfaye, 2011; Mirzaei *et al*., 2011; Shamsi *et al*., 2011).

5.3.3.2 Number of kernels per ear

The number of kernels per ear (NKE) determines the sink capacity and weight of grain that contribute to the final yield (Qadir *et al*., 1999). In the 2010 cropping season the NKE was not significantly influenced by irrigation treatments ($p \leq 0.05$). However, in 2011 water stress significantly ($p \leq 0.05$) lowered NKE in the flowering and grain-filling stages (Table 5.3). The number of kernelsper ear was also significantly ($p \leq 0.01$) influenced by the cultivar and the interaction effect (irrigation × cultivars) in both seasons (Table 5.3).

The cultivar SST 843 had significantly higher NKE at each irrigation treatment compared with other cultivars in both cropping seasons. The results are in agreement with the findings of Qadir *et al*. (1999), who also reported that the NKE under water stress was influenced by cultivar. The higher NKE of SST 843 was due to significantly longer ears in both seasons.

Table 5.3 Water stress effects on number of kernels per ear of wheat cultivars stressed at various growth stages

Treatments		**Number of kernels per ear**	
		Cropping seasons	
Source of variation		2010	2011
Irrigation	SNN	27a	46a
	NSN	30a	36c
	NNS	29a	42b
	NNN	32a	47a
Cultivars	Duzi	28b	40b
	Steenbras	25b	37b
	SST 843	39a	52a
Irrigation	**Cultivars**		
SNN	Duzi	27b	45bc
	Steenbras	21b	39cd
	SST 843	39a	53ab
NSN	Duzi	27b	37cde
	Steenbras	24b	28e
	SST 843	39a	43cd
NNS	Duzi	27b	34de
	Steenbras	26b	37cde
	SST 843	35a	55a
NNN	Duzi	27b	43cd
	Steenbras	25b	44bc
	SST 843	42a	56a

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage, NNS refers to water stress in the grain-filling stage, and NNN refers to the control treatment

Furthermore, the NKE is also determined by soil water availability at various growth stages (Bogale & Tesfaye, 2011). In the present study, water stress imposed in the flowering stage (NSN) reduced the NKE most, followed by stress during the grain-filling stage (NNS), compared with the SNN and NNN treatments (Table 5.3). On average, the NSN treatment reduced NKE by 26%, whereas NNS and SNN reduced NKE by 12% and 4%, respectively, compared with the NNN treatment. A significant reduction in NKE due to stress from flag leaf to the end of flowering could be due to reduction in the growth rate of ears. This is well supported by Slafer and Whitechurch (2001), who reported that growth stages after flag-leaf initiation is characterised by active growth of stems and spikes, and this stage or period may be the most sensitive to limited resources.

Generally the control treatment (NNN) had the highest NKE compared with stressed treatments in both seasons in all cultivars. Therefore, water stress at any growth stage negatively affects NEM, but the flowering stage seems to be the most sensitive to stress. This is in agreement with the results of Mirzaei *et al*. (2011), who found that NEM was reduced most due to stress in the flowering stage rather than in the stem elongation and grain-filling stages.

5.3.3.3 Ear length

The ear length determines the NKE, which is influenced by the cultivar and water availability at various growth stages (Bogale &Tesfaye, 2011). The results in the present study revealed that both irrigation and cultivar significantly ($p \leq 0.05$) influenced ear length in the 2011 season only, whereas cultivars differed significantly ($p \leq 0.01$) in both seasons (Table 5.4). The cultivar SST 843 consistently had longer ears than the other two cultivars in both seasons.

Generally all stressed treatments reduced ear length compared with the control treatment. Comparable results were recorded by Bogale and Tesfaye (2011), who found that water stress imposed during tillering, flowering and grain filling reduced ear length compared with the well-irrigated treatment. In the present study the treatment stressed in the flowering stage (NSN) had significantly shorter ear length than other treatments. On average the NSN treatment reduced ear length by 25% and SNN and NNS reduced it by 16% and 11%, respectively. The results are in agreement with the reports of Slafer and Whitechurch (2001), who described the stages from heading to early grain filling as characterised by active growth of ears (spikes). Therefore, any limited resource during those stages ultimately affects ear length. Significant reduction in ear length owing to water stress in the flowering stage (NSN) suggests that supplemental irrigation at that stage is more critical compared with water stress during the stem elongation (SNN) and grain-filling stages (NNS).

Table 5.4 Water stress effects on ear length of wheat cultivars stressed at various growth stages

Treatments		Ear length (cm)	
		Cropping seasons	
Source of variation		2010	2011
Irrigation	SNN	14a	14bc
	NSN	14a	13c
	NNS	12a	15ab
	NNN	14a	17a
Cultivars	Duzi	11b	12b
	Steenbras	13b	13b
	SST 843	18a	17a
Irrigation	**Cultivars**		
SNN	Duzi	10c	11c
	Steenbras	14abc	12bc
	SST 843	17abc	15abc
NSN	Duzi	11bc	13abc
	Steenbras	13bc	14abc
	SST 843	21a	16abc
NNS	Duzi	10c	12bc
	Steenbras	11bc	14abc
	SST 843	15abc	18a
NNN	Duzi	11bc	15bc
	Steenbras	14abc	17ab
	SST 843	18ab	18a

Means in a column followed by the same letter are not significantly different at p≤0.05; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage, NNS refers to water stress in the grain-filling stage, and NNN refers to the control treatment

5.3.3.4 Thousand kernel mass

Thousand kernel mass (TKM) is one of the yield components that are influenced by cultivar response to available soil water at various stages of wheat development (Qadir *et al*., 1999). Table 5.5 indicates the effect of water stress on wheat cultivars stressed at various developmental stages in the 2010 and 2011 seasons. Both water stress treatment and cultivar significantly (p≤0.01) influenced TKM in both seasons. Thousand kernel mass was higher in 2011compared with the 2010 season. Furthermore, the interaction between irrigation and cultivars significantly influenced TKM in both seasons (Table 5.5). Higher TKM in 2011 was due to early establishment of the trial which resulted in longer growth duration compared to 2010 (Table 3.1 in chapter 3).

Table 5.5 Water stress effects on thousand kernel mass of wheat cultivars stressed at various growth stages

Treatments		***TKM (g)***	
		Cropping seasons	
Source of variation		2010	2011
Irrigation	SNN	40b	50b
	NSN	36d	52a
	NNS	33c	41c
	NNN	44a	52a
Cultivars	Duzi	40a	54a
	Steenbras	39ab	40c
	SST 843	36b	49b
Irrigation	**Cultivars**		
SNN	Duzi	44b	56b
	Steenbras	37c	42e
	SST 843	37c	51c
NSN	Duzi	38c	51c
	Steenbras	38c	42e
	SST 843	38c	51c
NNS	Duzi	32de	45d
	Steenbras	34d	35f
	SST 843	31e	42e
NNN	Duzi	45b	63a
	Steenbras	48a	43de
	SST 843	38c	51c

Means in a column followed by the same letter are not significantly different at $p \leq 0.05$; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

The interaction results in the 2011 season showed that Duzi and Steenbras had the highest and lowest TKM respectively for all irrigation treatments. All cultivars had significantly ($P \leq 0.01$) lower TKM due to water stress in the grain-filling stage (NNS) in both years (Table 5.5). On average, NNS reduced TKM by 19% in 2011, and NSN and SNN lowered TKM by 7% and 5%, respectively. Similar results were found by several authors (Abayomi & Wright, 1999; Bogale & Tesfaye, 2011; Mirzaei *et al*., 2011). They concluded that reduction of TKM due to water stress in the grain-filling stage is attributed mainly to the shorter grain-filling period through accelerated senescence, which consequently reduces the grain-filling rate per day (Bogale & Tesfaye, 2011). Further reduction in TKM during the grain-filling stage is also accelerated by dry conditions caused by high temperatures (heat), coupled with high water deficits (Doorenbos & Kassam, 1979). That leads to shrivelled, malformed, broken, small kernels, which results in a reduction in HLM (Table 5.9), and grain and biomass yield (Barnard *et al*., 2002; ARC-SGI, 2009). In the present study, temperatures also increased in the grain-filling stage, thus in October and November (Table 4.1), resulting in lower HLM in this stage (Table 5.9).

5.3.3.5 Total dry matter yield

Total dry matter (TDM) yield is positively correlated with other yield components such as grain yield and harvest index under water stress conditions (Shamsi *et al*., 2010). Water stress treatment and cultivar effect significantly influenced TDM at harvesting (Table 5.6). The cultivar effect was not consistent between seasons. However, water stress imposed in the flowering stage (NSN) and the control treatment (NNN) produced the lowest and highest TDM yields, respectively, in both years. Cumulative dry matter production over time during the 2011 growing season was discussed in chapter 4of this dissertation (Table 4.12 and Figure 4.9).

Generally the interaction effect was not significant in the 2010 season, whereas in 2011 the cultivar Duzi reduced TDM most owing to water stress in the stem elongation (SNN) and flowering (NSN) stages. The SNN treatment of cultivar Duzi reduced TDM by 21%, which was higher than the 13% for both Steenbras and SST 843. On average, the NSN treatment of Duzi significantly reduced TDM by 24%, compared with the 20% and 8% for Steenbras and SST 843, respectively, in the 2011 season (Table 5.6). Reduction in total dry matter production under water stress is attributed amongst others, to a decrease in the number of leaves, which lowers the LAI (Abayomi & Wright, 1999; Vurayai *et al*., 2011). The NSN treatment reduced the number of leaves (Table 4.9) and LAI (Table 4.8) most and failed to recover fully when the stress period was terminated. In the present study the treatment stressed in flowering reduced TDM most by 16% and 17% in 2010 and 2011 seasons respectively. Comparable results were reported by Gupta *et al*. (2001), who found that TDM was reduced most because of stress in the flowering stage compared with stress in the boot stage and the well-watered treatment. Higher reduction of the TDM owing to water stress in the flowering (NSN) stage corresponded with higher grain yield reduction at that stage (Table 5.8 and Figure 5.4), which proves that TDM yield was correlated to grain yield (0.58**) in 2011 (Appendix C, Table C 2). These results are in agreement with the findings of Shamsi *et al*. (2010), who concluded that TDM yield was positively correlated with grain yield. Therefore, the cultivar Duzi was more susceptible to water stress in the stem elongation and flowering stages in the 2011 season; whereas for Steenbras TDM was most reduced by water stress in the grain-filling stage.

Table 5.6 Water stress effects on total dry matter yield of wheat cultivars stressed at various growth stages in the 2010 and 2011 seasons

Treatments		***TDM (t ha^{-1})***	
		Cropping seasons	
Source of variation		2010	2011
Irrigation	SNN	13.07ab	17.20b
	NSN	11.64b	16.87b
	NNS	13.09ab	18.22b
	NNN	13.84a	20.44a
Cultivars	Duzi	12.90a	16.28b
	Steenbras	12.73a	19.57a
	SST 843	13.10a	18.70a
Irrigation	**Cultivars**		
SNN	Duzi	12.8ab	14.9d
	Steenbras	12.5ab	19.labc
	SST 843	13.9a	17.6bcd
NSN	Duzi	12.3ab	14.2e
	Steenbras	11.1b	17.9bc
	SST 843	11.5ab	18.5bc
NNS	Duzi	13.1ab	17.1cde
	Steenbras	13.5ab	19.1ab
	SST 843	12.6ab	18.4bc
NNN	Duzi	13.7ab	18.9bc
	Steenbras	13.9a	22.1a
	SST 843	14.0a	20.3ab

Means in a column followed by the same letter are not significantly different at p≤0.05; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

On average water stress imposed in any growth stage reduced the TDM yield in 2011 season. The NSN, SNN and NNS treatment reduced TDM by 17%, 16% and 10% respectively when compared to the NNN treatment in the 2011 season. Comparable results were reported by Mirzaei *et al.* (2011), who also found that water stress imposed in the stem elongation; flowering and grain-filling stages also lowered TDM of wheat compared with the well-watered treatment.

5.3.3.6 Harvest index

Harvest index refers to the fraction of total dry matter harvested as yield, and is mostly expressed in terms of above-ground biomass, excluding roots (Araus *et al*., 2002). Table 5.7 indicates the effects of water stress on harvest index, and Figure 5.3 summarises the mean harvest index per irrigation treatment in both seasons. The results revealed that harvest index was not significantly influenced by the interaction effect in both season (Table 5.7), whereas the cultivars significantly differed in the 2011 season (Appendix C, Table C.1). The absence of significant differences in harvest index among the treatment combinations indicates that cultivars used in the present study responded similarly to water stress imposed to any growth stage (Table 5.7). Comparable results were recorded by Abayomi and Wright (1999), who also found that genotypes of spring wheat had similar harvest indices in the vegetative and reproductive stages.

Qadir *et al.* (1999) reported that harvest index indicates how dry matter partitioning is distributed among plant parts. However, it is influenced by the availability of soil water. In the present study, limited soil water in the flowering stage (NSN) and the control treatment (NNN) had significantly ($p \leq 0.05$) lower and higher harvest indices in both seasons (Figure 5.3).The NSN treatment reduced harvest index by 21% in both seasons. Generally, water stress imposed in the stem elongation, flowering and grain-filling stages (SNN, NSN, and NNS) reduced harvest index, compared with the control (NNN) treatment in both years, although all differences were not significant (Figure 5.3). The results in the present study are in agreement of those of Mirzaei *et al.* (2011), who found that harvest index was reduced due to water stress imposed in the stem elongation, flowering and grain-filling stages, though they were not significantly different to each other. Higher and lower harvest indices of the NNN treatment and NSN treatment correspond with higher and lower grain yield, respectively. Higher harvest index for the NNN treatment was also attributed to the significantly higher

TKM and TDM recorded. Comparable results were found by Qadir *et al*. (1999) who proved that water stress imposed at vegetative and reproductive stages of wheat reduced harvest index, which consequently reduced grain yield (Mirzaei *et al*., 2011). Furthermore like water use and total dry matter yield, HI was positively correlated to grain yield (R= 0.58** in 2011 and R=0.51** in 2010) (Appendix C, Table C 2). These results agree with those of Shamsi *et al*. (2010), who also found positive correlations between HI and grain yield.

Table 5.7 Water stress effects on harvest index of wheat cultivars stressed at various growth stages in the 2010 and 2011 seasons

Treatments		***Harvest index (%)***	
		Cropping seasons	
Irrigation	***Cultivars***	2010	2011
SNN	Duzi	43abc	42abc
	Steenbras	42abc	37abcde
	SST 843	38bc	42abc
NSN	Duzi	37bc	39abcd
	Steenbras	36bc	32de
	SST 843	37bc	29e
NNS	Duzi	40abc	37abcde
	Steenbras	39abc	34cde
	SST 843	35c	40abcd
NNN	Duzi	47a	45a
	Steenbras	44.4ab	36bcde
	SST 843	47a	44ab

Means in a column followed by the same letter are not significantly different at p≤0.05; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

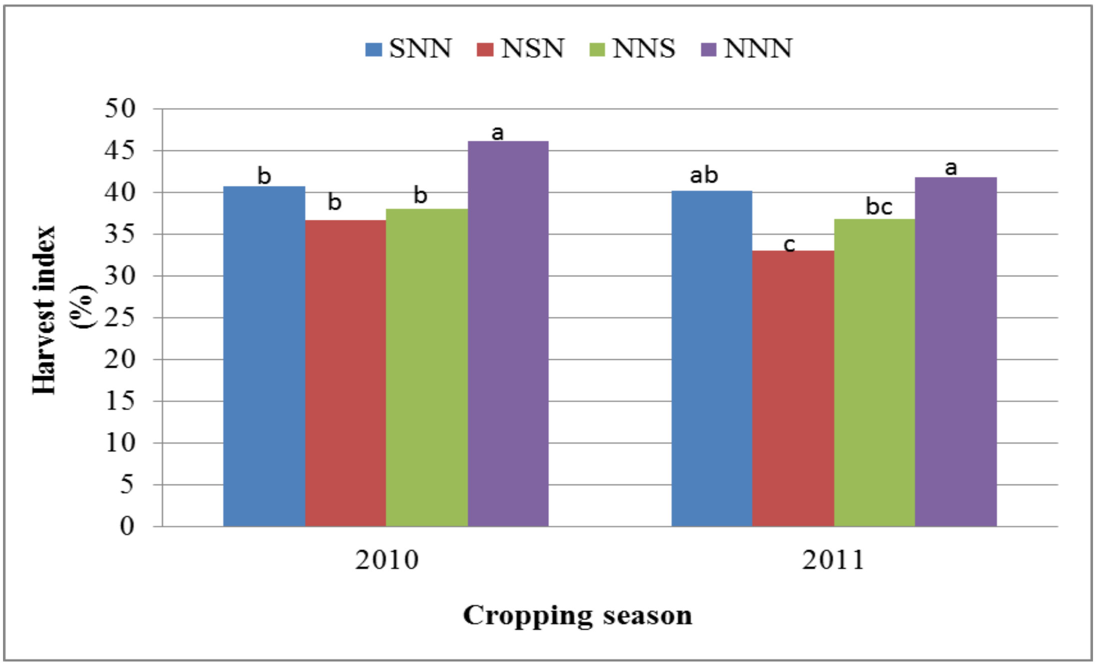

Figure 5.3 Water stress effects on harvest index of wheat stressed at various growth stages in the 2010 and 2011 seasons. Bars with the same letter per season are not significantly different at p≤0.01; *SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

5.3.3.7 Grain yield, yield stability index and stress tolerance

Grain yield is influenced by stability, tolerance and potential yield of a specific cultivar under stress (GYs) and optimal conditions (GYp) (Khan & Naqvi, 2011). Table 5.8 summarises the effects of water stress on grain yield, stability, and tolerance of wheat cultivars and the mean grain yield per irrigation treatment is presented in Figure 5.4. The correlations between grain yield, yield components and quality parameters are summarised in Table C 2 (Appendix C). The results revealed that grain yields of wheat cultivars were influenced by the water stress. However, the trend was not consistent in both seasons (Table 5.8). The inconsistency in grain yield could be due to late planting in the 2010 season, which affected grain yield components (Table 5.2 to 5.7). Generally, late planting shortens the duration of the season, whereas variations in response to the planting date could be due to genetic variability and adaptive mechanisms to drought stress in these cultivars. All the cultivars had significantly lower yields in 2010 due to late planting, which consequently reduced the growth or season duration, and that had a negative effect on the yield potential of the cultivars (Table 5.8).

Table 5.8 Water stress effects on grain yield of wheat cultivars stressed at various growth stages in the 2010 and 2011 seasons

Treatments		***Cropping seasons***							
		2010				2011			
Irrigation	***Cultivars***	GY (t ha^{-1})	YR (%)	YSI	TOL	GY t ha^{-1})	YR (%)	YSI	TOL
SNN	Duzi	5.46c	14d	0.86b	0.87d	6.23cd	27c	0.74bc	2.27bcd
	Steenbras	5.20d	14d	0.87b	0.87d	6.49c	18d	0.84b	1.30d
	SST 843	5.26cd	19c	0.81c	1.21c	7.29b	18d	0.82b	1.60c
NSN	Duzi	4.43e	30b	0.70d	1.90b	5.66de	34ab	0.65cd	3.07ab
	Steenbras	3.93f	35a	0.65e	2.14ab	5.56de	30bc	0.70cd	2.37bc
	SST 843	4.20e	35a	0.65e	2.27a	5.36e	40a	0.60d	3.53a
NNS	Duzi	5.30cd	16cd	0.84bc	1.03cd	6.29cd	27c	0.74bc	2.27bcd
	Steenbras	5.20d	14d	0.86b	0.87d	6.49c	18d	0.82b	1.43cd
	SST 843	4.40e	32ab	0.68e	2.07ab	7.29b	18d	0.82b	1.60cd
NNN	Duzi	6.33a	0e	1a	0e	8.56ab	0e	1a	0e
	Steenbras	6.07b	0e	1a	0e	7.93b	0e	1a	0e
	SST 843	6.47a	0e	1a	0e	8.89a	0e	1a	0e

Means in a column followed by the same letter are not significantly different at p≤0.05; GY refers to grain yield; YR and YSI refers to yield reduction and yield stability index respectively; whereas TOL refers to stress tolerance; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment

Araus *et al*. (2008) indicated that shifting the planting dates can be an adaptive mechanism under drought conditions. However, late planting affects the duration of the growth season. A shorter duration season reduces the total intercepted solar radiation per season (Table 4.1 in chaper 4 of this dissertation), which leads to lower total dry matter and grain yield production (Table 5.6 and 5.8). Grain yield was significantly and positively correlated to total dry matter (0.58**), harvest index (0.68**) and water use (0.84**) in 2011 season. Similar relationships were found by Shamsi *et al.* (2010) on wheat. Therefore water stress certainly reduce grain yield and other related yield components, which ultimately affect the water-use efficiency.

In the present study water stress treatments imposed at any developmental stage (SNN, NSN and NNS) significantly ($p \leq 0.01$) decreased grain yields compared with the control (NNN) treatment in both years (Figure 5.4). Zhang and Oweis (1999) indicated that the impact of drought stress on grain yield depends on the developmental stage at which stress occurs. In the present study it was found that water stress imposed in the flowering stage (NSN) gave the lowest grain yield, followed by the treatment stressed during the grain-filling stage (NNS), and stem elongation (SNN), respectively, in 2011 season. In the 2011 season the NSN treatment reduced yield by 35%, which was significantly higher than the 22% and 21% reduction of the NNS and SNN treatments (Figure 5.4).

The cultivar Steenbras had a lower percentage yield reduction, a lower yield stability index (YSI) and higher stress tolerance (TOL) due to stress in stem elongation (SNN) and grain-filling (NNS) stages in the 2010 season. Similar results were obtained from the same cultivar in the 2011 season, although differences were not statistically different (Table 5.8). On average, for Steenbras yield was reduced by 17% compared with the 27% and 18% for Duzi and SST 834, respectively, in 2011. In 2010 the cultivars Duzi and Steenbras had a significantly lower yield reduction of 15% compared with the 22% yield reduction for SST 843. Therefore, Steenbras was more resistant to water stress, especially in the 2010 season, due to a lower percentage yield reduction, whereas the control treatment (NNN) of SST 843 and Duzi obtained higher yields (Table 5.8). These results agree with those of Abayomi and Wright (1999), who also found that some of the cultivars that had higher yield under well-watered conditions, showed highest yield reduction under stress conditions in the vegetative and reproductive stages. Lower yield reduction of the cultivar Steenbras under stress corresponds with higher TOL, and YSI (yield stability index) (Table 5.8). Golabadi *et al*.

(2006) reported that a higher value of TOL indicates more susceptibility to stress, which implies higher loss of yield under stress (GYs) compared with well watered (GYp). Furthermore, Khan and Naqvi (2011) found that the cultivars with the highest YSI exhibited the lowest yield under non-stress conditions. Similar results were found in the present study since the cultivar Steenbras had higher YSI due to lower yield for the control treatment (NNN) although it was not significantly different from other cultivars in the 2011 season (Table 5.8).

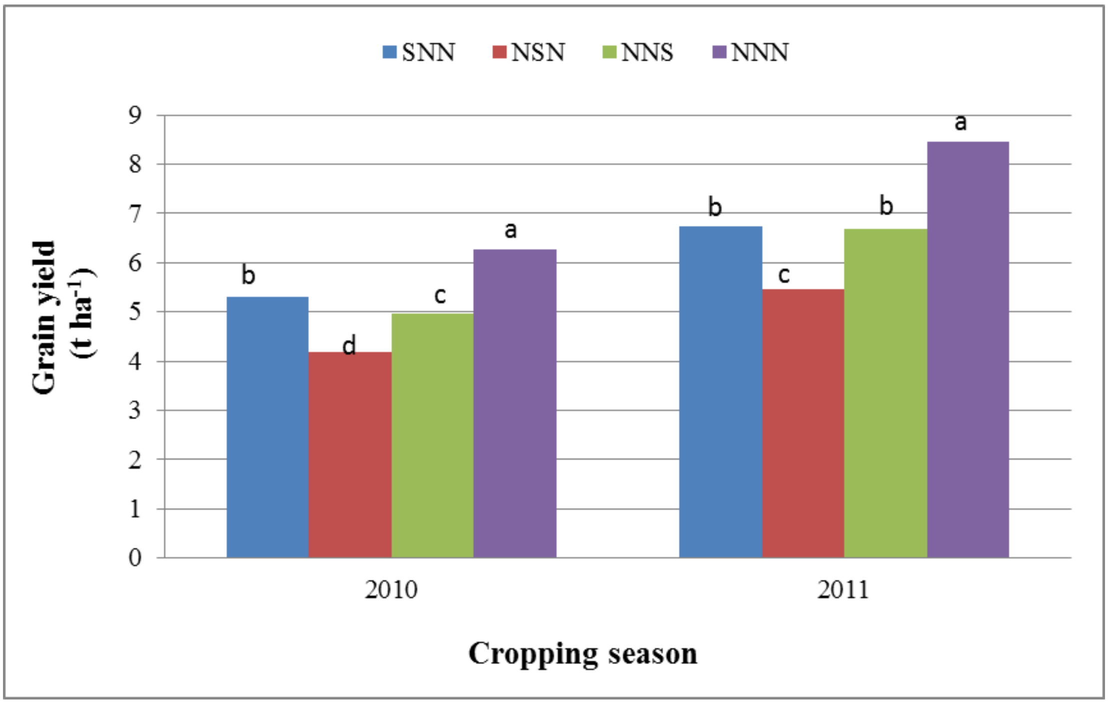

Figure 5.4 Water stress effects on grain yield of wheat stressed at various growth stages in the 2010 and 2011 seasons. *Bar means followed by the same letter are not significantly different at p≤0.01; SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stress in the grain-filling stage; and NNN refers to the control treatment*

For the cultivar Steenbras water stress in the flowering stage reduced grain yield by 30%, compared with 40% and 34% yield reduction for SST 843 and Duzi, respectively in 2011 (Table 4.9). On average water stress treatment NSN significantly reduced grain yield by 33% and 35% in 2010 and 2011, respectively, compared with the NNN treatment (Table 5.8 and Figure 5.4). Abayomi and Wright (1999) concluded that water stress before the flowering stage in wheat reduces the number of ears per fertile tiller, compared with stress in the vegetative and grain-filling stages. Similarly, in the present study, lower yield due to water stress during the flowering stage (NSN) was because of a reduction in the NEM (Table 5.2), as well as reduced NKE and ear length (Table 5.3 and 5.4). There was strong correlation between grain yield, ear length (0.46**) and number of kernels per ear (0.58**) in the 2011 season (Appendix C, Table C 2). Therefore, lower yield due to water stress during the flowering stage (NSN) was because of a reduction in the kernel number per ear (Table 5.3) and ear length (Table 5.4), consequently reduced sink size. Furthermore, Doorenbos and Kassam (1979) also reported that water stress in the flowering stage affects yield formation, and re-watering at later stages may not lead to yield recovery.

Grain yield for the treatment stressed during stem elongation (SNN) showed great recovery after re-watering in the present study (Figure 5.4). Although grain yield of the SNN treatment of all cultivars recovered, it was still significantly lower than the NNN treatment (Table 5.8 and Figure 5.4). These results are analogous with those of Abayomi and Wright (1999) for spring wheat and those of Vurayai *et al.* (2011) for Bambara groundnuts. Doorenbos and Kassam (1979) reported that the yield of wheat can recover from water stress during the vegetative stage, if good rains or irrigation occur at later stages. Several authors reported that wheat stressed in the vegetative stage and then irrigated at advanced stages has the ability to develop new tillers, which form new ears that can improve grain yield and WUE at the end of the season (Mogensen *et al*., 1985; Blum, 1996; Abayomi & Wright, 1999). Therefore, recovery of grain yield, and other yield components for the treatment stressed during stem elongation (SNN) in the present study could be due to development of additional tillers. Unfortunately, the number of tillers at the end of the season was not recorded. The recovery of grain yield for the treatment stressed from tillering to flag leaf (SNN) agrees with the suggestion of Abayomi and Wright (1999), who proposed that screening for drought tolerance due to recovery from stress may be best done at the tillering stage.

5.3.4 Water stress effects on grain-quality parameters

5.3.4.1 Grain protein content

Appendix C (Table C.1) present the anova of grain protein content (GPC) as affected by irrigation treatments, cultivars and the interaction effect of both irrigation and cultivars in 2010 and 2011 seasons. The results reveals that grain protein content (GPC) was not significantly influenced by irrigation and cultivar effects in the 2010 cropping season ($p \leq 0.05$). However, in the 2011 season, both irrigation and cultivar significantly ($p \leq 0.01$) influenced GPC, whereas the interaction effect of irrigation treatment and cultivars was not significant in both seasons (Table 5.9). Water stress imposed in the stem elongation stage (SNN) reduced GPC most in the 2011 season, followed by the control treatment (NNN), whereas the treatment imposed to water stress in the flowering (NSN) and grain-filling stages (NNS) had higher GPC than other treatments (Table 5.9). Generally both NSN and NNS increased GPC by 9% respectively, compared with the NNN treatment in 2011. The results are comparable with those of several researchers (Agenbag & De Villiers, 1995; Zhao *et al.*, 2005; Mirzaei *et al.*, 2011). Agenbag and De Villiers (1995) found that total protein during the milk stage (21 days after anthesis) was increased compared with unstressed treatment. The results of this study proved that grain yield was negatively correlated to grain protein content in both years (Appendix C, Table C 2). Comparable results were reported by Ozturk and Aydin (2004), who found that higher protein content under water stress was associated mainly with lower yield, and decreased kernel weight. In this study lower grain yield was found for treatment stressed in the flowering stage (NSN), whereas lower kernel mass or TKM was reduced most due to water stress imposed in the grain-filling stage (NNS). These results are supported by Zhao *et al.* (2005), who explained that water stress can result in small pinched kernels that are high in protein and low in flour yield.

The positive effect on GPC under water stress is mainly through reduction of synthesis and storage of carbohydrate, which allows more concentration of nitrogen (N) per unit starch accumulated in the grain (Saint Pierre *et al.*, 2008). Therefore, lower GPC for the SNN and NNN treatments could be due to a reduction in the concentration of N per grain. Doorenbos and Kassam (1979) explained that the effect of nitrogen on GPC is reduced more under moderate or optimal water supply compared with water-limited conditions. Duzi had significantly lower GPC than Steenbras and SST 843, whereas the GPC for Steenbras and SST 843 was not significantly different (Table 5.9). Generally, GPCs in this study were acceptable (>12%) for all irrigation treatments and cultivars as prescribed by the ARC-SGI (2009) and DAFF (2010).

Table 5.9 Water stress effect on quality components of wheat cultivars stressed at various growth stages in the 2010 and 2011 seasons

Quality components		***Grain protein content (%)***		***Hectolitre mass (kg hl^{-1})***		***Falling number (seconds)***	
Source of variation	**Seasons**	2010	2011	2010	2011	2010	2011
Irrigation	SNN	15a	14c	86a	82ab	412b	421a
	NSN	15a	16a	85a	84a	415ab	422a
	NNS	15a	16a	83b	76c	414ab	421a
	NNN	14a	15b	86a	80b	420a	423a
Cultivars	Duzi	14a	15b	85a	81b	418a	423a
	Steenbras	14a	16a	85a	79c	416a	422a
	SST 843	14a	16a	85a	83a	413a	421a
Irrigation	**Cultivars**						
SNN	Duzi	16a	13e	85bc	81acb	413a	427a
	Steenbras	14ab	14de	86b	82ab	414ab	417a
	SST 843	14ab	15cd	89a	84a	408b	420a
NSN	Duzi	15ab	15cd	85bc	83ab	424a	419a
	Steenbras	14ab	17ab	86b	83ab	413ab	425a
	SST 843	15ab	18a	85bc	84a	410b	421a
NNS	Duzi	13b	16bc	85bc	76d	413ab	425a
	Steenbras	14ab	17ab	83cd	72e	415ab	422a
	SST 843	13b	17ab	82d	80bc	413ab	416a
NNN	Duzi	14ab	14de	86b	81abc	421ab	422a
	Steenbras	13b	16bc	86b	78c	420ab	422a
	SST 843	14ab	16bc	86b	82ab	418ab	426a

Means in a column followed by the same letter are not significantly different at $p \leq 0.01$: SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain-filling stage; and whereas NNN refers to the control treatment

5.3.4.2 Hectolitre mass

Hectolitre mass (HLM) gives a direct indication of the potential flour extraction of the grain sample. Flour extraction is a critical parameter for the miller as it largely influences his profitability. Grains with a HLM higher than 77 kg hl^{-1} are preferred most according to the bread wheat grading system in South Africa (ARC-SGI, 2009). The results revealed that HLM was significantly ($p \leq 0.01$) influenced by irrigation treatments in both seasons (Table 5.9). Water stress imposed during grain-filling (NNS) reduced HLM more than other treatments. Water-stress treatment NNS had a significantly lower HML of 76 kg hl^{-1} compared with 80 kg hl^{-1}, 82 kg hl^{-1} and 84 kg hl^{-1} of the NNN, SNN and NSN treatments, respectively (Table 5.9). This result agrees with the reports of the ARC-SGI (2009). Hectolitre mass is associated with the genetic characteristics of a particular cultivar and interaction with environmental conditions during grain-filling (Barnard *et al*., 2002; ARC, 2009). Several authors confirmed that HLM is influenced by extreme soil water and heat stress, mostly at grain filling (ARC-SGI, 2009; DAFF, 2010). Reduction of HLM with stress at grain filling is mainly due to the percentage of small malformed and broken kernels, which results in a reduction in TKM (Mirzaei *et al*., 2011). The cultivar SST 843 had the highest HLM and Steenbras the lowest ($p \leq 0.05$) in the 2011 season. Lower HLM of Steenbras corresponds with lower TKM and grain yield. The HLM of all cultivars and irrigation treatments in this study was acceptable according to the South African grading system (ARC-SGI, 2009).

5.3.4.3 Falling number

Falling number (FN) is a grain-quality characteristic that indicates which form of carbohydrate (starch or sugar) outweighs the other (Barnard *et al*., 2002). Biddulph *et al*. (2008) reported that lower falling number usually occurs as a result of rainfall after the maturity of the crop, which causes sprouting and consequently a reduction in quality due to conversion of starch to sugars (ARC-SGI, 2009). Grains with a falling number higher than 220 seconds are preferred for first grade, according to the South African wheat grading system. Falling number in the present study was not significantly ($p \geq 0.05$) influenced by cultivars in both seasons. In the 2010 season the SNN and NNN treatments had significantly lowest and highest FN respectively, however both these treatments were not different from NSN and NNS (Table 5.9). Generally the control treatment (NNN) had the highest mean falling number in both seasons. The lowest mean falling number was associated with the SNN and NNS treatment in 2011, although they were not significantly different from the other treatments (NSN, and NNN). The non-significance of water stress on falling number in this study could generally be attributed to the absence of rain or irrigation water on the ears, mainly because of the use of a rain shelter and a drip irrigation system. The falling number for all irrigation treatments and cultivars in this study was acceptable according to the South African wheat grading system (ARC-SGI, 2009).

5.4 Summary and conclusions

The stressed treatments extracted substantial amounts of water from deeper soil layers compared with the control treatment (NNN) in both seasons. However, the peak depletion period for the control treatment (NNN) in the 2011 season was at the end of the flowering period (NSN). This shows that highest demand for water by the wheat crop is from flag leaf to early grain filling. Higher extraction of water from the soil profile from the flowering stage onwards was due to a larger canopy, increased temperatures and higher evaporative demand. The 2010 season was generally drier and shorter, compared with 2011, which consequently reduced the yield potential of the cultivars. The total crop water use for the well-watered/control treatment (NNN) ranged between 475 mm and 623 mm per season. Generally all treatments used less water in the 2010 season compared with 2011. This was due mainly to delayed planting in the first season. The control treatment (NNN) had the significantly highest ET and yield in both seasons compared with all stressed treatments (SNN, NSN and NNS). Yield generally increased linearly with increase in ET and duration of the season. The treatment that was stressed in the stem elongation stage (SNN) and grain-filling stage(NNS) reduced ET by 27% and 17%, which translated to 173 mm and 105 mm of water saved in each growth stage, respectively (in 2011). Since water stress in the stem elongation and grain filling stages reduced ET, but had little effect on yield, it improved WUE. In the 2010 season, withholding irrigation in the grain-filling stage resulted in the highest WUE. Higher WUE due to water stress in the SNN treatment in 2010 was because of lower LAI, which is related to lower transpiration per unit leaf area compared with the control treatment (NNN). In the 2011 season, higher WUE of SST 843 corresponded with significantly higher grain yield of 7210 kg ha^{-1}and higher ET of 509 mm.

The irrigation treatment subjected to water stress from flag leaf to the end of flowering (NSN) significantly reduced grain yield by 33% and 35% in the 2010 and 2011 seasons, respectively, when compared with the control treatment (NNN). In the 2011 season the NSN treatment reduced grain yield of cultivar Steenbras by 30%, compared with 40% and 34% yield reduction for SST 843 and Duzi, respectively. Significant reduction of grain yield due to stress from the flag-leaf stage to the end of flowering was because of the lower number of ears per unit area (NEM), lower NKE, shorter ear length and lower total dry matter production. On average the NSN treatment reduced NEM by 26% when compared with the NNN. The NKE determines the sink capacity and weight of grain, which contributes to the final yield. The cultivar SST 843 had a significantly higher number of seeds per ear for each irrigation treatment compared with other cultivars in both cropping seasons. The higher NKE of SST 843 was due to significantly longer ear length in both seasons.

In 2011 water stress in the stem elongation (SNN) and flowering (NSN) stages reduced TDM of the cultivar Duzi most. Water stress treatment SNN reduced TDM of the cultivar Duzi by 21% compared with a 13% reduction for both Steenbras and SST 843. The NSN treatment of Duzi reduced TDM by 24%, which was significantly higher than the 20% and 8% of Steenbras and SST 843. During grain-filling water stress (NNS) reduced TDM of Steenbras by 13%, compared with 9% for both Steenbras and SST 843, respectively. Higher TDM reduction for the cultivar Duzi due to water stress in the stem elongation (SNN) and flowering (NSN) stages corresponded with higher grain yield reduction, which proved that Duzi was more susceptible to water stress in those stages than the other cultivars (in 2011). Generally water stress imposed in any growth stage (SNN, NSN, and NNS) reduced TDM yield in the 2011 season compared with the well-watered control treatment (NNN).On average the NSN treatment reduced TDM by 17% compared with 16% and 10% for the NNS and SNN treatments respectively in the 2011 season.

The NSN treatment reduced the harvest index by 21% in both seasons, whereas the control treatment (NNN) gave higher harvest index. Higher harvest index for the NNN treatment was attributed to significantly higher TKM and TDM, which corresponded with higher grain yield. Grain yield for the treatment stressed during stem elongation (SNN) showed great recovery after resumption of irrigation in the present study.

Water stress imposed in the stem elongation stage (SNN) reduced GPC most, followed by the control treatment (NNN), whereas the treatment exposed to water stress in the flowering (NSN) and grain-filling stages (NNS) had higher GPC than the other treatments. Generally NSN and NNS increased GPC by 9% respectively, compared with the NNN treatment in 2011. The positive effect on GPC under water stress is mainly through reduction of synthesis and storage of carbohydrates, which allows more concentration of nitrogen (N) per unit starch accumulated in the grain (Saint Pierre *et al*., 2008). The cultivar Duzi had significantly lower GPC than Steenbras and SST 843. HLM was reduced by 3% and 5% in the 2010 and 2011 seasons, respectively, owing to water stress imposed in the grain-filling stage (NNS), compared with the control treatment (NNN). Reduction of HLM at grain filling is due mainly to an increase in the percentage of small, malformed and broken kernels, which resulted in a decrease of TKM (Mirzaei *et al*., 2011). Falling number was not affected by water stress imposed at any growth stage in both seasons. This was because of the absence of rain or irrigation water on the ears, mainly due to the use of the rain shelter and drip irrigation system. Biddulph *et al*. (2008) reported that lower falling number usually occurs as a result of rainfall after the maturity of the crop, which causes sprouting, and consequently reduction of quality and yield. Generally all quality parameters in the present study were acceptable for all irrigation treatment and cultivars, as prescribed by the ARC-SGI (2009) and DAFF (2010).

CHAPTER 6: GENERAL DISCUSSION, CONCLUSIONS AND RECOMMENDATIONS

6.1 Discussion and conclusions

Crop production is attributed mainly to the leaf photosynthesis of plants (Shan *et al*., 2012). Therefore future productivity will be determined mostly by the ability of the plant to maintain the rate of carbon assimilation under various environmental stresses (Anjum *et al*., 2011). The CO_2 assimilation rate in plants is controlled by stomatal conductance. Water stress imposed at any growth stage (stem elongation (SNN), flowering (NSN), and grain filling (NNS)) significantly decreased net CO_2 assimilation, transpiration rate and stomatal conductance ($p \leq 0.01$) compared with the control treatment (NNN). These results are well supported by the findings of Bogale *et al*. (2011) and Shan *et al*. (2012). Siddique *et al*. (2000) also found that the photosynthetic rate and stomatal conductance was reduced by water stress in the vegetative and anthesis stages, compared to a well-irrigated treatment. Water stress due to limited irrigation results in a decrease in water absorption (increased depletion) at root level, thus reducing the transpiration rate (Zhang *et al*., 1998). The results of the present study indicate a significant decrease (of about 84% on average) in stomatal conductance due to limited irrigation for the treatment stressed from the flag leaf stage to the end of flowering (NSN), compared with the control treatment (NNN), which could be attributed to the partial closure of stomata under water-limited conditions. Reduction in stomatal conductance limit CO_2 intake into the leaf, thereby reducing the photosynthetic rate. Stomatal conductance responds mainly to soil water availability, although it is influenced by many enviromental factors, such as vapour pressure deficit, air temperature, and crop factors, such as leaf water potential (LWP), leaf temperature and canopy closure (Anjum *et al*., 2011).

In this study LWP decreased due to water stress compared with the control treatment. Zhang *et al*. (1998) found that reduction of LWP due to water stress induce an increase in leaf temperature. In the present study, leaf temperature increased in any growth stage exposed to stress, which ultimately affects photosynthesis. These results are in agreement with those of Zhang *et al*. (1998) and Deng *et al*. (2000), who found that reduction of LWP due to water stress at various growth stages, leads to higher leaf temperature and partial closure of stomata, resulting in lower net CO_2 assimilation. Reduction in LWP due to water stress furthermore affects the formation and enlargement of leaves, which consequently lower leaf area index and biomass yield (Zhang *et al.*, 1998). In the present study the number of leaves was reduced by water stress imposed at any growth stage, which significantly affected LAI and DM production. The NSN and NNS treatments reduced LAI most towards the end of the season in the grain-filling stage. That could due to the accelerated death of leaves in the grain-filling stage. This is well supported by Bogale and Tesfaye (2011), who noted that water stress in the grain-filling stage accelerated leaf senescence.

The physiological and growth parameters discussed above affect grain yield formation and water use. Water use efficiency (WUE) indicates the performance of a crop growing under any environmental conditions. Plant biomass production and grain yield depend on the amount of water used for the growth season (Zhang & Oweis, 1999). At crop level, WUE is calculated as the ratio of grain yield (kg ha^{-1}) to the amount of total water used in mm (Ali *et al.*, 2007). Water stress treatments and cultivar effect significantly influenced yield, water use, WUE and quality components, depending in the growth stage in which stress was imposed (Gupta *et al.*, 2001; Shamsi *et al.*, 2010). Grain yield showed to be tolerant to water stress during the stem elongation and grain-filling stages in this study, compared with stress imposed at flowering stage. Comparable results were found by Mirzaei *et al.* (2011). In this study water stress imposed in the flowering stage (NSN) reduced grain yield and yield components significantly more than water stress during other growth stages. On average, water stress in the flowering stage reduced yield by 33% and 35% in the 2010 and 2011 season respectively. These results agree with the findings of several authors (Seghatoleslami *et al.*, 2008; Khan & Naqvi, 2011). Khan and Naqvi (2011) reported that water stress in the flowering stage reduced yield by 65% compared with the well-irrigated treatment, whereas Seghatoleslami *et al.* (2008) found that water stress at ear emergence reduced yield more than stress in the vegetative and grain-filling stages of millet cultivars. In the current study the sensitivity of grain yield to water stress in the flowering stage was due mainly to the significant reductions in the number of ears per unit area, ear length and number of seeds per ear. These findings are well supported by the research of Ji *et al.* (2010), who reported that grain number decreases sharply when water stress occurs during the spike growth period, due mainly to decreased kernels per ear of fertile tillers. Anjum *et al.* (2011), reported that reduced grain yield due to stress in the flowering stage is due to reduced source that can support the potential sink later in the grain-filling stages. The same author further explained that the most reduced source due to stress in the flowering stage is inhibition of leaf expansion and development, which consequently limit dry matter production. Water stress imposed in the stem elongation stage resulted in significantly lower GPC (grain protein content), followed by the control treatment, whereas the treatment exposed to water stress during flowering (NSN) and grain-filling (NNS) stages had higher GPC. However, both treatments were not significantly different from the control (NNN) treatment. Water stress imposed in the grain-filling (NNS) stage significantly reduced hectolitre mass (HLM) compared with stress imposed in the stem elongation (SNN) and flowering stages (NSN) as well as the control treatment (NNN) in both seasons. The HLM of NNS was reduced by 5%, 8% and 9% compared with NNN, SNN and NSN treatments respectively in 2011. Reduction of HLM at grain-filling was due lower TKM (Mirzaei *et al*., 2011), as a result of shorter grain filling rate and duration (Bogale & Tesfaye, 2011).

The cultivar Steenbras had significant lower percentage yield reduction (YR) due to stress in stem elongation (SNN) and grain-filling (NNS) stages in 2010 season and the same trend was found in 2011 season. On average the cultivar Steenbras and Duzi had significantly lower YR of 15% compared to 22% redction for SST 843 in the 2010 season. In the 2011 season the same trend of yield reduction was found for Steenbras, though cultivars were not significantly different on grain yield. The cultivar Steenbras reduced yield by 17% compared to 19% and 22% YR of Duzi and SST 843 respectively in the 2011 season. Generally both Duzi and SST 843 produced higher grain yield than Steenbras under well-watered conditions (NNN). However, Steenbras had the lowest yield reduction under water stressed conditions. These results are comparable to those of Abayomi and Wright (1999), who also found that the cultivars that had higher yield under well-watered conditions, showed highest yield reduction under stress conditions. On average both SST 843 and Duzi got higher WUE efficiency in 2011 and 2010 respectively. The cultivar SST 843 had highest WUE of 14.2 kg ha^{-1} mm^{-1} which corresponded to higher grain yield in the 2011 season. The cultivar Duzi had significantly lower GPC as compared to other cultivars in 2011. It can be concluded that the three cultivars differ in their physiological, grain yield and protein response to water stress imposed at any growth stage.

The irrigation treatment exposed to water stress in the flowering stage (NSN) reduced grain yield most in both seasons, but maintained higher grain protein content. Water stress treatment NSN reduced grain yield by 35% and improved protein content by 9% in the 2011 season. Higher reduction of grain yield due to stress in the flowering stages was due to lower TDM, and HI, due to reduction in other yield components such as ears per metre square, kernels per ear and ear length. Comparable results were found by other researchers elsewhere (Qadir *et al*., 1999). Withholding irrigation in the grain-filling stage (NNS) maintained WUE and had little effect on both grain protein content and yield. Water stress treatment NNS reduced grain yield by 21% and improved protein content by 9% in the 2011 season. Withholding irrigation in the stem elongation stage (SNN) maintained good yield and improved water use efficiency, but reduced grain protein content most (although it was still acceptable). Water stress at the stem elongation stage had WUE of 14.9 kg ha^{-1} mm, which corresponded with total water use (ET) of 451 mm and grain yield of 6738 kg ha^{-1}.

Hectoliter mass was reduced by 3% and 5% in the 2010 and 2011 seasons, respectively, due to water stress imposed in the grain filling stage (NNS) as compared to the control treatment (NNN). Falling number was not affected by water stress imposed at any growth stage in both seasons. This was due to the absence of rain or irrigation water on the ears mainly due the use of a rain shelter and drip irrigation system. Generally all quality parameters in the present study were acceptable for all irrigation treatments and cultivars as prescribed by the ARC-SGI (2009) and DAFF (2010).

From the discussion above, the hypothesis that the three South African wheat cultivars will respond differently to water stress at various growth stages, was accepted. It is conclusive that the cultivar Steenbras was slightly more tolerant to water stress in the stem elongation and grain-filling stages, compared with other cultivars. However the cultivar SST 843 and Duzi seem to have higher grain yield potential under well-watered conditions. Secondly, the hypothesis that water stress during stem elongation will have a minimal effect on wheat grain yield, and therefore lead to higher water-use efficiency, was also accepted. Furthermore, the hypothesis that water stress imposed in the grain-filling stage will improve grain protein quality, but have little effect on yield and water use efficiency was accepted.

6.2 Recommendations

The current study shows that water stress imposed in the flowering stage significantly reduced grain yield most, which is the most important target of crop production. Therefore it can be recommended that if water is limited, supplemental irrigation should be applied from flag leaf to the end of flowering (NSN) of wheat in order to minimise grain yield losses. Withholding irrigation in the stem elongation stage (tillering to flag leaf stages) can maintain good yield and improve water use efficiency, and at the same time save water, which might reduce the cost of irrigation as well. This strategy could be more beneficial in winter production regions in South Africa, since they receive most of their rainfall at the beginning of the season, with highest risk of drought stress in the flowering stage.

Limiting irrigation in the grain filling stage has little effect on grain yield, improves grain protein content and maintains good WUE. This can be used for irrigation scheduling by irrigation farmers, who produce wheat mostly in the (warmer) summer production areas of South Africa. In most summer production regions, the first rain starts between October and November, which reduces the chance of grain-filling water stress. The hypothesis that water stress in the stem elongation and grain-filling stages will have little effect on yield and improve WUE was accepted. Further research could focus on extrapolation of the results to other production regions using crop models.

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APPENDIX A: WATER STRESS EFFECTS ON PHYSIOLOGICAL PARAMETERS DURING 2011 SEASON

Table A.1 Water stress and cultivar effects on photosynthesis and other physiological traits related to photosynthesis

2011 Cropping season						
Para-meters	*Pn* (µmol CO_2 m^{-2} s^{-1})	*E* (mmol H_2O m^{-2} s^{-1})	*gs* (mol H_2O m^{-2} s^{-1})	*Ci* µmol.mol^{-1}	*iWUE* (µmol m^{-2} s^{-1}. Mol m^{-2} s^{-})	*LT* (ºC)
Stem elongation stage (SNN)						
R-square	0.76	0.72	0.65	0.68	0.57	0.82
C.V	16.6	32.92	46.07	14.01	29.37	2.34
LSD^{I}	1.6**	0.71**	0.05**	28.27**	1.60**	0.47**
LSD^{C}	1.99**ns**	0.85 **ns**	0.06 **ns**	34.50 **ns**	1.95 **ns**	0.58*
LSD$^{I\times C}$	3.34 **ns**	1.41 **ns**	0.09 **ns**	50.11 **ns**	2.78 **ns**	0.98 **ns**
Flowering stage(NSN)						
R-square	0.65	0.83	0.73	0.84	0.68	0.88
C.V	27.94	20.92	30.39	6.24	15.06	1.89
LSD^{I}	2.92**	0.87**	0.075**	13.04**	0.29**	0.39**
LSD^{C}	2.53*	0.75**	0.06*	11.29**	0.25 **ns**	0.33**
LSD$^{I\times C}$	5.79ns	1.50*	0.13*	22.59**	0.51**	0.77**
Grain filling stage (NNS)						
R-square	0.65	0.83	0.82	0.48	0.43	0.80
C.V	24.85	22.08	28.26	7.87	24.24	2.61
LSD^{I}	2.45**	1.45**	0.07**	21.16**	0.36**	0.59**
LSD^{C}	1.03**	1.03**	0.05**	14.97 **ns**	0.25**	0.42**
LSD$^{I\times C}$	3.47 **ns**	2.05 **ns**	0.10 **ns**	29.93 **ns**	0.50 **ns**	0.83*

Pn: photosynthesis; E: transpiration; gs: stomatal conductance to water; Ci: intercellular carbon dioxide concentration; IWUE : instantaneous water use efficiency; and LT refers to leaf temperature. LSD^{I}, *LSD*^{C} *and LSD*$^{I\times C}$ *refer to least significant difference between irrigation treatment, cultivars and interaction respectively.* ***ns*** *means non-significant difference, and asterisks (*) and (**) mean significant difference at* $p\leq0.05$ *and* $p\leq0.01$*, respectively.*

APPENDIX B: WATER STRESS EFFECTS ON GROWTH PARARAMETERS RELATED TO PHOTOSYNTHESIS AND YIELD

Table B.1 Water stress effects on leaf area index measured at various growth stages in 2011 season

Leaf area index (m^{2} m-^{2})						
Days after planting	75	87	95	108	124	131
R-Square	0.89	0.96	0.95	0.98	0.97	0.99
C.V	12.29	8.90	7.64	5.05	13.02	1.59
LSD^{I}	0.53**	0.52**	0.54**	0.24**	0.37**	0.02**
LSD^{C}	0.46 **ns**	0.45**	0.47**	0.21**	0.32**	0.02**
$LSD^{I\times C}$	0.91 **ns**	0.89 **ns**	0.93**	0.42**	0.64**	0.04**

Table B.2 Water stress effects on number of leaves per plant measured at various growth stages in 2011 season

Number of leaves per plant					
Days after planting	75	87	95	108	124
R-Square	0.92	0.72	0.72	0.43	0.82
C.V	8.04	10.89	10.89	22.44	19.43
LSD^{I}	2**	2*	2*	3	0.3**
LSD^{C}	1**	2**ns**	2**ns**	2**ns**	0.28**
$LSD^{I\times C}$	3*	4**ns**	4 **ns**	5 **ns**	0.57**

ns: *non-significant difference; asterisks (*) and (**) mean significant difference at $p\leq0.05$ and $p\leq0.01$ respectively.*

Table B.3 Effect of water stress on plant height stressed at various growth stages in 2011 and 2010 seasons

Plant height (cm) at different days after planting in the 2011 season								***2010 season***
DAP	62	75	87	95	108	112	165 (harvest)	124 (harvest)
R-Square	0.92	0.92	0.50	0.81	0.73	0.84	0.87	0.2
C.V	4.76	4.76	9.94	4.56	0.54	3.40	4.74	7.4
LSD^{I}	2**	2**	8**	4**	5**	3**	5**	6 **ns**
LSD^{C}	2**	2**	6.37 **ns**	4 **ns**	4**	3**	4 **ns**	5 **ns**
$LSD^{I\times C}$	4**ns**	4**	13 **ns**	8 **ns**	8**ns**	6**ns**	8 **ns**	11 **ns**

***DAP** refers to days after planting whereas **ns** means non-significant difference; asterisks (*) and (**) mean significant difference at p≤0.05 and at p≤0.01 respectively.*

Table B.4 Water stress effects on dry matter production harvested at various growth stages in 2011 season

Dry matter production (t ha-^{1})			
Growth stages	Stem elongation	flowering	Grain-filling (Harvest)
R-Square	0.65	0.98	0.78
C.V	25.85	5.21	10.41
LSD^{I}	1.40*	0.69**	1.89**
LSD^{C}	1.22 **ns**	0.59**	1.63**
$LSD^{I\times C}$	2.43 **ns**	1.19**	3 **ns**

***ns** means non-significant difference; asterisks (*) and (**) mean significant difference at p≤0.05 and at p≤0.01 respectively.*

APPENDIX C: ANOVA AND CORRELATIONS OF YIELD AND QUALITY PARAMETERS IN 2010 AND 2011 SEASONS

Table C.1 Effects of irrigation treatments and cultivars on growth, yield and quality

2010 Cropping season													
Parameters	EL (cm)	TDM ($t\ ha^{-1}$)	HI (%)	GY ($t\ ha^{-1}$)	TOL ($t\ ha^{-1}$)	YSI ($t\ ha^{-1}$)	TKM (g)	NEM m^2	NKE	WUE ($kg\ mm^{-1}\ ha^{-1}$)	GPC (%)	FN (s)	HLM (kg/hl)
R-Square	0.44	0.33	0.47	0.98	0.98	0.98	0.92	0.53	0.76	0.98	0.33	0.31	0.53
C.V	34.61	12.8	12.95	2.96	14.45	2.95	4.32	15.38	16.61	2.99	8.77	1.91	1.73
LSD^I	4.62**ns**	1.55**ns**	5.09**	0.14**	0.15**	0.02**	1.62**	84**ns**	4.49**ns**	0.41**	1.21**ns**	7.72 **ns**	1.47**
LSD^C	4.00**	130**ns**	4.41**ns**	0.23**	0.12**	0.02**	1.40**	72.75**	3.88**	0.35**	1.04**ns**	6.68**ns**	1.28**ns**
$LSD^{I\times C}$	8.00**ns**	2.60**ns**	8.82**ns**	0.25**	0.27**	0.04**	2.81**	145.49**ns**	7.76**ns**	0.70 **ns**	2.09 **ns**	13.37**ns**	2.50 **ns**
2011 Cropping season													
R-Square	0.49	0.78	0.32	0.91	0.85	0.89	0.98	0.86	0.75	0.75	0.80	0.26**ns**	0.81
C.V	26.22	10.41	12.39	6.10	35.6	7.10	10.41	11.28	13.41	6.08	4.64	1.62	2.46
LSD^I	2**	1.89**	4.91*	0.42**	0.56**	0.06**	1.36**	55.45**	3.69**	0.83**	0.70**	6.78**ns**	1.93**
LSD^C	2**	1.63**	4.26*	0.36**	0.49**	0.04**ns**	1.18**	48.02**	3.20**	0.72**	0.61**	5.87**ns**	1.67**
$LSD^{I\times C}$	6 **ns**	3 **ns**	8.70**ns**	0.76**	0.97**ns**	0.09**ns**	2.57**	131.83*	9.64*	1.44**	1.22**ns**	11.74**ns**	3.34**ns**

Table C.2 Correlation coefficients between grain yield, yield components and quality parameters

Season	2010	2011
Parameters	Grain yield	
TDM	0.50**	058**
HI	0.64**	0.68**
EL	0.08 ns	0.46**
NEM	0.05 ns	0.20 ns
NKE	0.07ns	0.58**
PH	0.23 ns	0.78**
WUE	0.62**	0.42**
GPC	-0.03 **ns**	-0.26 **ns**
FN	0.05 **ns**	0.16 **ns**
HLM	0.28**ns**	-0.17**ns**

PH: plant height; TDM: total dry matter yield; HI: harvest index; TKM: thousand kernel mass; NKE: number of kernels per ear; NEM: number of ears per metre square; WUE: water use efficiency; GPC: grain protein content; FN: falling number; and HLM: hectolitre mass. ns means non-significant; one asterisk (*) means significant at p = 0.05; and two asterisks (**) mean significant difference at P =0.01. LSD^C *and* LSD^I *mean least significant differences for cultivars and irrigation respectively; and* $LSD^{I \times C}$ *refers to the least significant differences of interaction effect between irrigation and cultivars*

APPENDIX D: SOIL WATER DEFICITS PER CULTIVAR DURING 2010 AND 2011 SEASONS

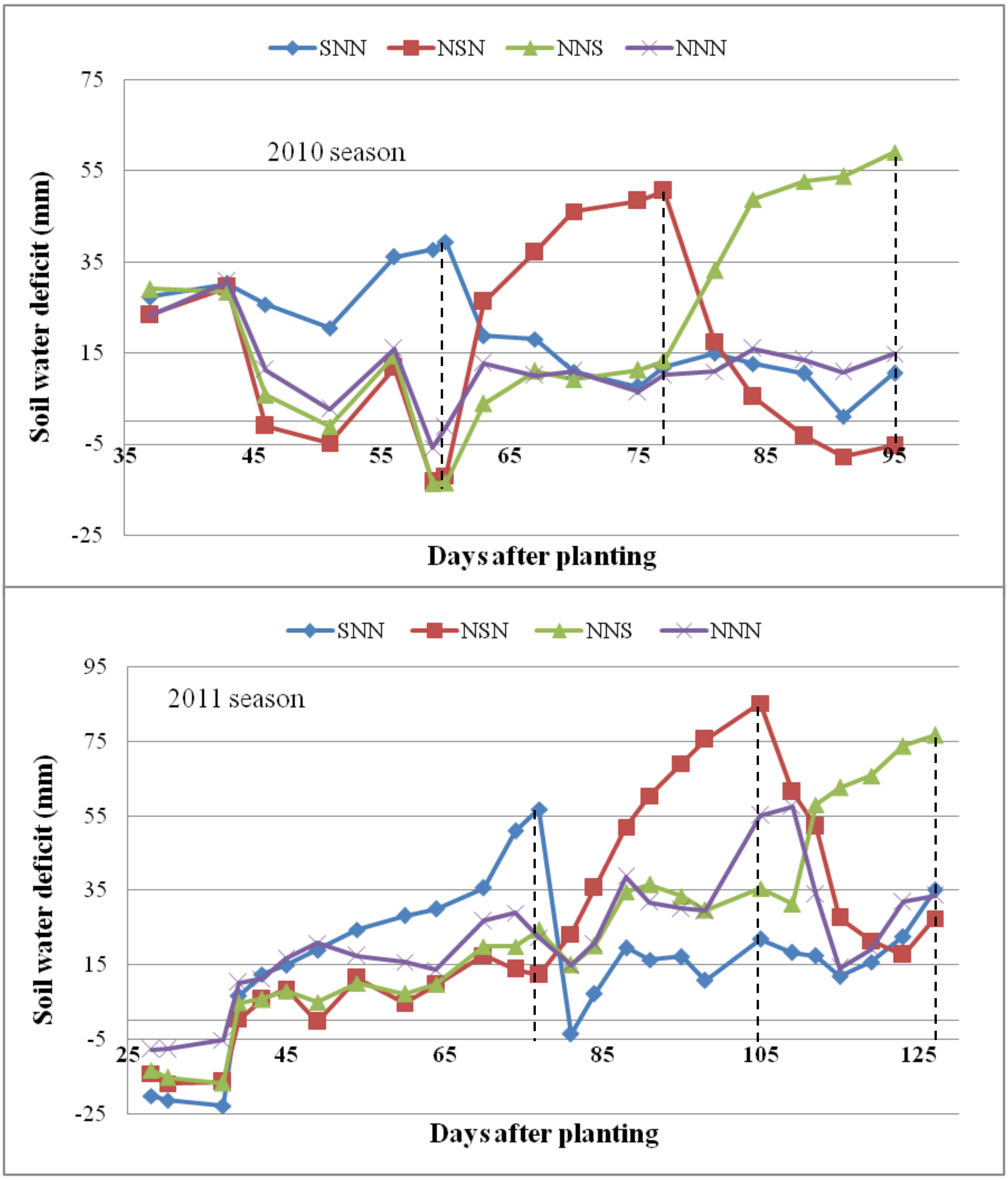

Figure D.1 Soil water profiles of Duzi during 2010 and 2011 cropping seasons at different days after planting

SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain filling stage; and NNN refers to the control treatment. The dotted lines indicated the time of stress termination.

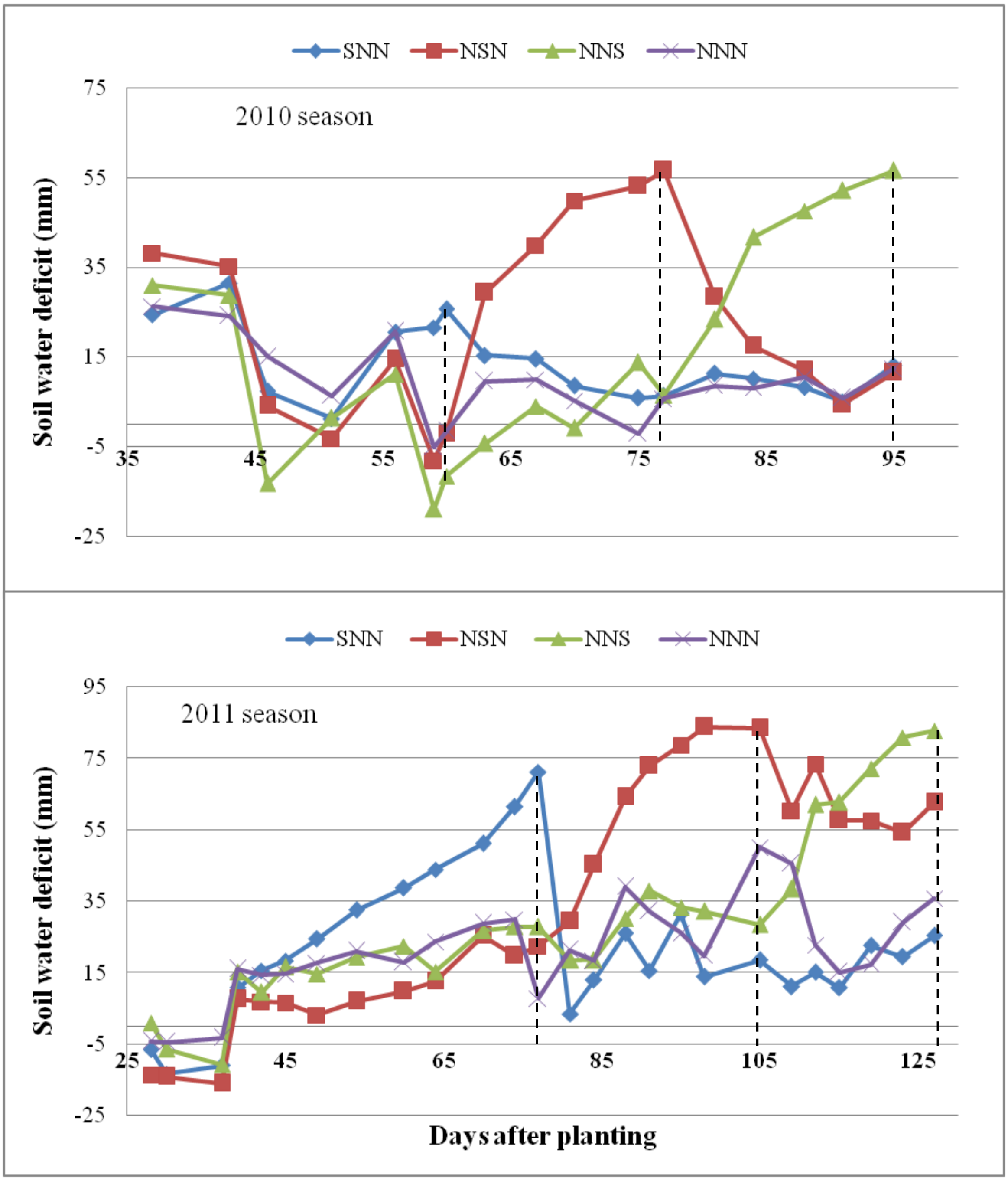

Figure D.2 Soil water profiles of SST 843 during 2011 and 2010 cropping seasons at different days after planting

SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain filling stage; and NNN refers to the control treatment. The dotted lines indicated the time of stress termination.

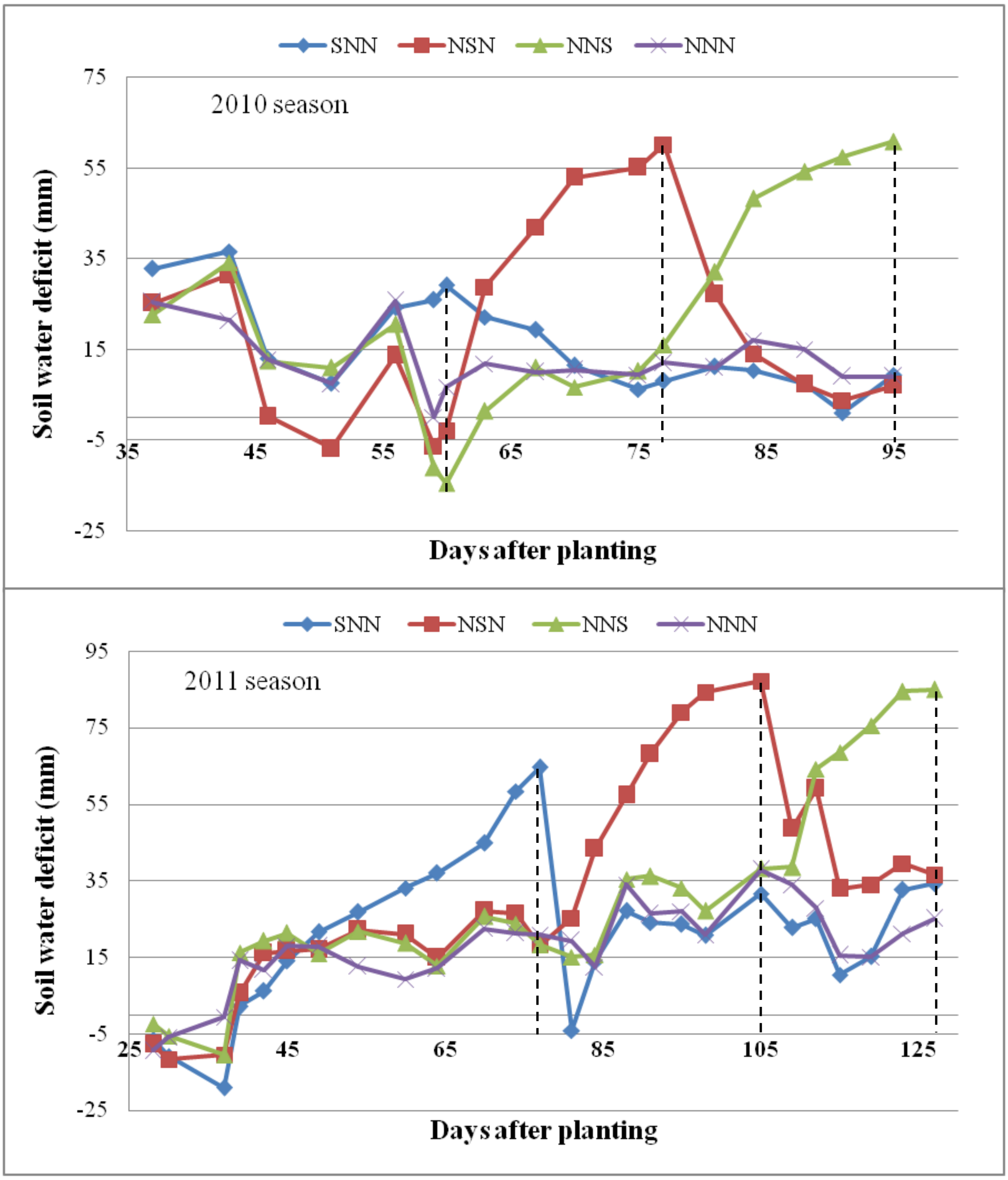

Figure D.3 Soil water profiles of Steenbras during 2011 and 2010 cropping seasons at different days after planting

SNN refers to water stress in the stem elongation stage; NSN refers to water stress in the flowering stage; NNS refers to water stressed in the grain filling stage; and NNN refers to the control treatment. The dotted lines indicated the time of stress termination.