

BREEDING FOR INCREASED WATER USE EFFICIENCY IN CHICKPEA

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Certificate of Originality

I certify to the best of my knowledge that all the content of this thesis is my own work and that it has not been submitted elsewhere for the purposes of obtaining a diploma or degree in any other University.

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ABSTRACT

Traditionally, chickpea is grown as a winter crop with in-crop rain or stored soil moisture, or as a spring crop using residual stored soil moisture. In the semi-arid tropics, it is grown when rainfall is tapering off in the late rainy season and utilises moisture stored in the soil profile. These growing conditions are characterised by a gradual decline in soil moisture towards the end of the growing season leading to terminal drought. Drought causes up to 50% yield losses in chickpea, however, depending on the genotype, environment, and type of drought experienced, seed yield losses can range from 30 – 100%. The effect of drought will be exacerbated by global warming which is projected to be responsible for a 20% increase in water shortages in drought prone areas.

Since 80% of the world's allocable water is consumed in irrigated agriculture, and water resources for agriculture are generally decreasing, it may not be feasible to grow chickpeas under irrigation to mitigate the effect of drought. Breeding cultivars with high water use efficiency (WUE) is a more practical and economical long-term approach to increasing yields in drought prone areas. WUE leads to moderate water uptake while maintaining increased yields under drought conditions making WUE an integral part of breeding programs. Any modifications above the soil surface have an effect on WUE since it impacts on the soil water balance via soil water evaporation and infiltration. This necessitates the incorporation of management practices, such as tillage, in studies analysing WUE.

Since WUE is a complex trait, secondary traits that are easy to measure and that have genetic variation, high heritability and are associated with yield under water-limited conditions make breeding for WUE easier. Little attention has been paid to the pattern of water use in legumes and the relationship between water used, WUE and seed yield. Despite evaluation of WUE in chickpea in various studies, little has been achieved as those studies focused on single factors affecting WUE, which caused variability in outcomes due to a failure to integrate other factors.

The central research question of this study was: *can chickpea yields be sustained by increased water use efficiency under drought conditions?* The aims of this thesis were to study the genetic variation underpinning WUE and grain yield in different tillage and irrigation regimes, as well as the basis of yield formation under water limited conditions.

Water use and WUE are important traits under water-limited conditions. It was hypothesised that genotypes with high WUE would produce high yields under water-limited conditions. For this hypothesis to be tested, a total of 36 entries were planted in the field at the IA Watson Plant

Breeding Institute, The University of Sydney in Narrabri, northwest New South Wales in Australia. Water use was monitored using a neutron probe moisture meter and WUE calculated using the soil water balance method. Grain yield was higher under irrigation (1722 kg ha^{-1}) than rainfed conditions (1478 kg ha^{-1}). No till plots resulted in an average yield of 1658 kg ha^{-1} which was 7.4% higher than in the till regime. There were no significant differences in water use; however, there were significant differences for WUE. WUE was higher under no till ($5.02 \text{ kg ha}^{-1} \text{ mm}^{-1}$) than under till ($4.87 \text{ kg ha}^{-1} \text{ mm}^{-1}$), and higher under irrigation ($5.05 \text{ kg ha}^{-1} \text{ mm}^{-1}$) than under rainfed conditions ($4.84 \text{ kg ha}^{-1} \text{ mm}^{-1}$). Sonali was the highest yielding genotype and also had the best WUE.

Identifying drought tolerant genotypes to be used as sources of tolerance in a breeding program is imperative. Traits that can confer drought tolerance under field conditions should be considered instead of yield alone. It was hypothesised that drought selection indices differ in their prediction accuracy and that some indices can be used to predict marker traits that can confer tolerance to drought in the field. To test this hypothesis, phenological, morphological, physiological and yield component data were analysed from the experiments performed in Narrabri. Drought indices were calculated and multiple linear regression was used to identify the most important traits that explained variation in yield. The stress tolerance index, mean relative performance and relative efficiency index were highly and positively associated with yield. These three traits were identified as the most effective indices for use in chickpea using principal component analysis compared with drought resistance index, yield index and yield stability index, which were not as suitable. Sonali, ICCV 96853 and PBA Slasher were identified as drought tolerant genotypes whereas Amethyst and Genesis 079 were identified as susceptible to drought. A total of 21 traits (Agyeman et al., 2015) out of 40 were identified as important in drought tolerance. The indices identified normalised difference vegetation index (NDVI) at early podding and late podding, as well as chlorophyll content at late podding, as useful marker traits to identify genotypes with potentially high yield and high drought tolerance.

Sustaining yield under different environments is important for the grower as well as the plant breeder. Genotype by environment interaction affects varietal ability to sustain yields across environments. It was hypothesised that there would be a significant genotype by environment interaction and hence, yield would not be stable across environments. To test this, 36 genotypes were sown using a two factorial experimental design in two seasons under no till, with and without irrigation, and till, with and without irrigation, in Narrabri making a total of eight

environments. The data were analysed using restricted maximum likelihood (REML) to check for genotype by environment interaction as well as genotype and genotype by environment interaction (Staggenborg and Vanderlip) biplot analysis to identify stable and high yielding genotypes. There was a significant genotype by environment interaction and genotype performance varied with environment. Generally, the yields in 2014 were higher than those in 2015 with 58% of the variation in yield accounted for by the year (season) effect. No till with irrigation in 2014 resulted in the highest average yield and till rainfed in 2015 resulted in the lowest mean yield. Some genotypes were more stable and high yielding than others. PBA Slasher and ICCV 96853 were high yielding and stable, whereas Genesis 079 was high yielding and very unstable. Sonali and Amethyst had moderate stability.

The plant ideotype approach is an alternative strategy to empirical breeding and allows the breeder to predict the ideal genotype in the target environment. Each ideotype is designed to grow in a defined target environment, hence, it is important to characterise the environment. It was hypothesised that selecting for key plant traits can confer drought tolerance and that abiotic stress sensitivity varies across plant phenophases. To test these hypotheses, data generated from the Narrabri field experiment was used. The key phenological, morphological and physiological traits were determined for ideotype targeting using multiple linear regression and ideotype values assigned depending on trait relationship with yield and other traits. The ideotype was then tested against selected commercial varieties (Sonali, PBA Hattrick, Kyabra, Tyson and Amethyst) *in silico* in the Australian grain belt using the APSIM crop model. The constructed chickpea ideotype showed 76% resemblance to Sonali which performed well under water-limited conditions. Simulated yield ranged from 760 to 3902 kg ha⁻¹ across the Australian grain belt, with consistently higher yield in the ideotype compared with the commercial cultivars. The growing environments were grouped into three major clusters using the soil water deficit method with varying water stress levels. Grain filling is the most critical stage where soil moisture deficit caused chickpea yield loss. By incorporating key target traits and targeting the right environment, chickpea yields can be sustained.

This study shows that there is genetic variation for WUE and it is a major component of drought tolerance. By identifying drought tolerant genotypes which are high yielding and stable, yields may be sustained under water limited conditions. By targeting a chickpea ideotype for specific environments, plant breeders can have a more focused strategy and hence, faster delivery of technologies to develop cultivars that are suitable for the target environment

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List of Abbreviations

ATP	Adenosine triphosphate
APSIM	Agricultural Production Systems Simulator
CGIAR	Consultative Group on International Agricultural Research
CID	Carbon isotope discrimination
CO ₂	Carbon dioxide
DI	Drought resistance index
ECV	Environmental coefficient of variation
GA	Genetic advance
GCV	Genotypic coefficient of variation
GEI	Genotype by environment interaction
GGE	Genotype plus genotype by environment interaction
GLM	Generalised linear models
ICARDA	International Centre for Research in to Dry Areas
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
LAI	Leaf area index
MET	Multi-environment trials
MRP	Mean relative performance
NDVI	Normalised difference vegetation index
NIR	Near infrared
NVT	National variety trials
PAR	Photosynthetic active radiation
PC	Principal component
PCV	Phenotypic coefficient of variation
REI	Relative efficiency index
REML	Restricted maximum likelihood
STI	Stress tolerance index
USDA	United States Department of Agriculture
VPD	Vapour pressure deficit
WS	Water stress
WUE	Water use efficiency
WW	Well watered
YI	Yield Index

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1.0 GENERAL INTRODUCTION

Chickpea (*Cicer arietinum* L.), a grain legume, has been a focus crop in recent times with renewed interest in its cultivation due to its high protein content and soil amelioration capabilities. The average annual area under cultivation between 2010 – 2012 was 12.4 million ha (FAOSTAT, 2012), which was spread across 52 countries in the Indian sub-continent, Mediterranean basin, Australia, East Africa and the Americas. These areas lie under the tropics, subtropics with winter rainfall and subtropics with summer rainfall as described by Kassam (1981). Being a cool season crop, chickpea cultivation has been traditionally restricted to cool climates. This implies that they grow well under cool temperatures during their vegetative stage and as they change to reproductive phase, temperatures start to increase. However, during the flowering phase, temperatures lower than 14°C to 16°C cause flower abortion (Berger et al., 2004). As a result of breeding efforts coupled with its agronomic benefits, the growing area has since expanded to include the semi-arid tropics, where it has become a main food security (staple) crop in the drought prone areas. In these areas, they are cultivated such that the vegetative phase coincides with cool temperatures.

Drought is the most limiting abiotic factor during various chickpea growth phases (Gunes et al., 2008, Boyer, 1982). It can be either intermittent and occasioned by a break in the normal rainfall pattern during the growing season, resulting in insufficient rainfall overall, or terminal drought resulting from continued moisture decline from the soil profile towards the end of the growing season (Canci and Toker, 2009). In all environments where chickpea is grown, terminal drought is almost certain (Turner, 2003) accounting for up to 50% of chickpea production losses (Varshney et al., 2013b). However, seed yield losses vary depending on the genotype, the type of drought experienced, and the environment, and can range from 30% to 100% (Leport et al., 1999). This situation is expected to be exacerbated by climate change, where it has been predicted that there will be more frequent drought events due to a general reduction in the amount of rainfall in the arid and semi-arid areas (IPCC, 2007).

Chickpea morphology, phenology and physiology are affected by drought in various ways. The most sensitive growth stage to water deficit is at flowering and early podding (Khanna-Chopra and Sinha, 1987). Early transient water deficit has been shown to reduce flower production by almost 50%, increase flower abortion and reduce pod abortion compared with well-watered

controls in two chickpea cultivars, Rupali, a desi-type and Almaz, a kabuli type (Fang et al., 2011). Terminal drought caused 33-63% flower reduction, 37-56% flower abortion and 54-73% pod abortion, in the same cultivars (Fang et al., 2010).

Behboudian et al. (2001) reported that pod formation was greatly reduced after moisture stress was induced, although if induced at late flowering, it had minimal effect on pod production. The total number of pods was reduced by 66-75% in plants exposed to early podding moisture stress compared with the well-watered control (Leport et al., 2006). Pods formed before water stress was imposed were not affected in terms of dry mass, whereas those formed later had their final dry mass reduced (Behboudian et al., 2001). Although pod abortion was increased under increased moisture stress, seed abortion and individual seed mass were not (Behboudian et al., 2001).

Davies et al. (1999) reported that chickpeas exposed to terminal drought under field conditions had a shorter seed filling duration and seed filling rate, resulting in smaller final seed size. Terminal drought reduced seed yield by 58-95% compared with the irrigated controls (Leport, 1999; Leport 2006 in Fang 2011). However, early transient water deficit in a pot study increased the rate of seed filling and final seed size at maturity compared with the well-watered control (Fang et al., 2011). Moisture stress at early podding reduced the number of seeds per pod from two to one in kabuli whereas desi-types were not affected (Leport et al., 2006). Fewer seeds per pod and smaller seed size caused a decrease in seed yield (Leport et al., 1999, Fang et al., 2010). Moisture stress induced at early podding caused a reduction in seed size and seed yield by 28% and 90%, respectively, although moisture stress at late podding did not reduce the seed size (Leport et al., 2006). Reduction in seed yield under the early transient water deficit was lower compared with terminal yield losses (Fang et al., 2011).

Drought tolerance research has been very difficult (Tuberosa and Salvi, 2006) primarily due to a lack of proper understanding of the physiological basis of yield under drought conditions, as well as its quantitative inheritance nature (Sinclair, 2011). One of the key steps for a breakthrough in drought tolerance research is an understanding of the physiological basis of drought, which will in turn, open new frontiers in molecular breeding strategies (Reyazul et al., 2012). The multifaceted nature of drought needs a more comprehensive approach and deeper understanding of all its components. It is, therefore, prudent to dissect yield under drought conditions, which in effect is a function of water uptake, water use efficiency and harvest index

(Passioura, 1977). Little attention has been paid to the pattern of water use in legumes and the relationship between water used and seed yield (Zhang et al., 2000b). Despite evaluation of water use efficiency (WUE) in chickpea in various studies, little progress has been achieved because those studies focused on single factors affecting WUE. This causes variability in results from different studies due to a failure to integrate the various factors responsible for WUE (Gan et al., 2010). The identification of key morphological, physiological and biochemical traits that are associated with stress tolerance is important in understanding plant responses to water deficit conditions (Araus et al., 2002, Poormohammad et al., 2007, Condon et al., 2004, Reynolds et al., 1999).

Once properly identified, these morphological, physiological and biochemical responses may be used as surrogates to select for WUE. This can be carried out in the framework of target trait based breeding, which has gained primacy in recent years as opposed to general breeding for increases in yield. Plant breeders are using easily measurable traits as surrogates for traits that were traditionally difficult to breed for. Drought tolerance is a very complex trait and WUE, which is one of the major components of drought adaptation, is complex as well. Hence, it is of prime importance to improve other traits that give an additive gene effect to eventually increase WUE and drought tolerance. Breeding cultivars with high WUE is a more practical and economical approach to improving yields in drought prone areas (Yong'an et al., 2010).

The genotype and crop management practices play a key role in plant-water interactions. Hence, the need to understand more about genotype by environment by management interactions. More recently, chickpea has increasingly been cultivated under zero or minimum tillage systems, coupled with retention of crop residues on the soil surface, to conform to the principles of conservation agriculture (Bimbraw, 2016, Hobbs, 2007). Any modifications above or on the soil surface have an effect on water use efficiency since it impacts on the soil water balance via soil water evaporation and infiltration. These soil management practices can influence WUE by bringing about changes in net radiation, soil heat flux, sensible heat flux and photosynthetic efficiency (Hatfield et al., 2001). Increased crop residue retention is beneficial in that it provides more substrates for soil microbes, consequently increasing soil microbial biomass (Doran et al., 1998). Increased organic matter quality, favourable soil temperatures, increased soil moisture and improved soil structure result in a greater diversity in soil microbes, especially bacterial and fungal populations (Lupwayi et al., 1998, Wang et al., 2010).

There is limited understanding of how various moisture and tillage regimes affect WUE in chickpea and how morphological, phenological and physiological traits are associated with WUE. There is also limited understanding of which morphological, phenological and physiological traits are best used as surrogates to breed for increased WUE. Hence, the key research question for this study was: is there genetic variation for WUE in chickpea, and can surrogates be used to improve it? The overall aim of this study was to better understand how chickpea can be bred for increased WUE using morphological, phenological and physiological traits; and the effect of genotype, environment and management interactions on WUE.

The specific objectives of this study were:

1. To identify genetic variation for WUE in chickpea under different moisture and tillage regimes
2. To investigate the effect of genotype by environment by management interaction on chickpea phenotypic stability
3. To understand the physiological basis of chickpea yield under water-limited conditions
4. To develop a model chickpea plant ideotype for semi-arid subtropical climates to assist plant breeding

2.0 LITERATURE REVIEW

2.1 Introduction

Chickpea (*C. arietinum* L.) is among the first grain crops grown by man dating back to 7500 – 6800 BC in the Middle Eastern archeological sites (Zohary and Hopf, 2000). Its cultivation has since spread to many parts of the world due to rising interest in its high protein content, nitrogen fixing capabilities and its ability to grow in harsh conditions where other legumes cannot do well. Although it was initially a cool season crop, breeding efforts have seen its growing area expand to include the semi-arid tropics, and it has become one of the main food security crops in areas which are prone to drought. Inasmuch as chickpea is drought tolerant, it often suffers from terminal drought because it is grown on receding soil moisture in many of the cropping systems.

Water is becoming increasingly scarce and development of plants that use water efficiently is one of the steps in conferring drought tolerance to plants. One of the challenges is that WUE is a complex trait. Hence, the need to explore other simple physiological traits for additive gene effects that can be used as surrogates to breed for improved WUE using both conventional and molecular techniques.

2.2 Origin and cytogenetics

Substantive evidence, including unearthed seeds dating back to 5450 BC (Helbaek, 1970) and the presence of the progenitor of chickpea, *Cicer reticulatum*, suggest that chickpea originated in the area of southeastern Turkey adjoining Syria (Van der Maesen, 1987). From Turkey, chickpea cultivation spread in two main directions; the western province of the region, where it is grown in spring and summer, and the eastern and southern parts, where it is grown in the cool dry season (Mallikarjuna et al., 2011). De Wet et al. (1982) suggested four secondary centres of diversity, namely: the Near East region (including the Fertile Crescent), Hindustani region (current India and East Pakistan), Central Asian region (Western Pakistan, Afghanistan, Iran and south of the former Union of Soviet Socialist Republics) and the Mediterranean region (Lebanon and Palestine).

Chickpea was later introduced to other parts of the world by the Portuguese and Spanish around the 1600s with kabuli types finding their way to India by the 1800s (van der Maesen, 1972). Indian immigrants imported desi chickpeas into Kenya in the 1800s (van der Maesen, 1972) and kabuli cultivars were introduced much later. Chickpea is a relatively new crop in Australia

with the first variety, Tyson, (a selection from C235, a northern India cultivar) released in 1978 (Berger et al., 2004).

2.3 Distribution, climate, area, production and uses of chickpea

Chickpea is the third most important food legume globally after dry beans and dry peas (Parthasarathy Rao et al., 2010). It is grown mainly in the Indian sub-continent, Mediterranean basin, Australia, East Africa and the Americas. Globally, it is currently grown across 13 Mha (Foyer et al., 2016) with Asia accounting for 89% of the total area, Africa 4.6%, Oceania 2%, North America 1.6%, Latin America 1% and Europe 1%. India, which is the largest producer of chickpea in the world, accounts for 72% of total area under chickpea cultivation in Asia (which is two thirds of the global area), and is closely followed by Pakistan and Iran accounting for 11% and 7% of Asia's chickpea cultivation area respectively (Parthasarathy Rao et al., 2010).

Chickpea is primarily grown under rainfed conditions under diverse moisture and temperatures conditions with rainfall ranging from 350 mm to 600 mm annually (Malhotra and Singh, 1991). These moisture conditions vary from location to location, for example, in Australia there is variation in rainfall within the growing season among locations (Figure 1). This variation has an implication on chickpea water use efficiency.

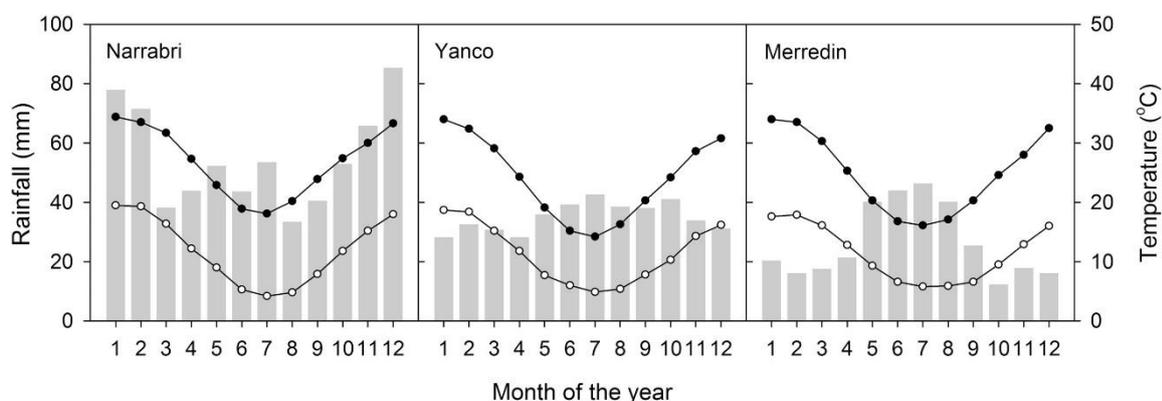


Figure 2.1: Climate data from 1981 to 2010 for chickpea growing areas in Australia adapted from Moeller and Rebetzke (2017). Closed circles indicate average maximum temperature and open circles indicate average minimum temperatures. Bars indicate mean monthly rainfall. 1 to 12 represent month of the year where 1 = January, 12 = December.

The total global chickpea production is 13 Mt with an average yield of 0.96 t ha⁻¹ (Foyer et al., 2016). Of the main chickpea producing countries in 2012, many had low yields due to various production constraints. Ethiopia produced the highest yields of 1.7 t ha⁻¹, followed by Australia at 1.5 t ha⁻¹, Turkey at 1.3 t ha⁻¹ and India at 0.9 t ha⁻¹ (FAOSTAT, 2012).

Chickpea is an important legume in farming systems since it avails nitrogen to non-legume crops through biological fixation, which subsequently increases their yield and quality. Furthermore, in most cases, you don't need to fertilise chickpea, hence it contributes to savings due to decreased use of nitrogen based fertilisers as well. Most of the positive responses expressed by cereals following legumes are primarily a result of nitrogen deposited by legumes in the previous season (Chalk, 1998). Chickpea can fix up to 140 kg N ha⁻¹ per season which meets up to 80% of its nitrogen requirements (Saraf et al., 1998, Serraj, 2004). Unkovich et al. (2010) has also shown that chickpea can fix a range of 85 to 194 kg N ha⁻¹. In addition, inclusion of chickpea in rotations acts as disease break and its crop residues help in maintenance of soil health and fertility through addition of organic matter, which ensures sustainability in the cropping systems.

Chickpea is a very good source of protein with mature grains having a protein content of 12-31%, which is among the highest in pulses (Parthasarathy Rao et al., 2010). It is also among the cheapest sources of protein (Byerlee and White, 2000), which makes it suitable for resource poor farmers, especially in developing countries. Chickpea is also a very good source of soluble and insoluble fibres, vitamins and minerals, and many other phytochemicals which are health-promoting (Geervani, 1991). Generally, chickpea has 64% total carbohydrate, 47% starch, 6% crude fibre, 6% soluble sugars, 3% ash, and 5% fat (William and Singh, 1987). Chickpea is deficient in sulfur containing amino acids like methionine and cysteine, but rich in the essential amino acid, lysine (Sarmah et al., 2012).

Chickpea is mainly used as human food and to a lesser extent as animal feed. Kabuli is mainly used as a whole grain, whereas desi can be used as whole grain or split (El-Hendawy et al.) (Sarmah et al., 2012). In some diets, chickpea seeds are eaten fresh as green vegetables, whereas in others they are parched, roasted, fried, or boiled. Chickpea can be eaten as a snack food, condiments or as stew. The seeds can be ground into flour which is used to make soup, *dhal*, bread, or served as a side dish (Saxena et al., 1990). Split chickpea, without its seed coat, is commonly known as *dhal*, which can be dried and cooked into a thick soup, or ground into flour for snacks and sweetmeats (Hulse, 1991). Gram husks, and green or dried stems and leaves are used for livestock feed. Whole seeds may be milled and used directly as feed.

2.4 Mode of reproduction and types of chickpea

Chickpea is a self-pollinated crop and cross-pollination is rare with only 0-1% reported (Smithson et al., 1985). Self-pollination is enforced by its cleistogamous flower, whereby pollen transfer takes place before the flower opens. This may lead to a narrow genetic base having an effect on the general genetic diversity in chickpea.

Chickpea is an annual diploid species divided into two types; kabuli and desi. Kabuli-types have white flowers, large, cream-coloured seeds and traditionally have been grown around the Mediterranean basin and central Asia. Desi-types have pink/purple flowers, small, dark, angular seeds and are mainly produced on the Indian subcontinent, in east Africa, central Asia and to a limited extent in the Mediterranean Basin (Cobos et al., 2007)

Chickpea has an indeterminate growth habit and it can grow continuously as long as the environmental conditions especially water availability are adequate. If adequate soil moisture is present during the vegetative phase, the crop continues to be vegetative and, thus becoming a competitive sink for pod and seed formation (Khanna-Chopra and Sinha, 1990). If the crop remains vegetative for a long time, its performance at the end of the season may be affected, especially in areas which are prone to terminal drought.

2.5 Chickpea genetic resources

Chickpea has three gene pools based on its crossability with the cultivated species *C. arietinum* (Mallikarjuna et al., 2011). The primary gene pool is comprised of cultivated species and landraces, the secondary gene pool is comprised of *C. reticulatum* and *C. echinospermum*, and the tertiary gene pool is comprised of all annual and perennial *Cicer* species that are not crossable with *C. arietinum* (Mallikarjuna et al., 2011). International Consultative Group on Agricultural Research (CGIAR) centres like the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and the International Centre for Agricultural Research in the Dry Areas (ICARDA), and other gene repositories like the United States Department of Agriculture (USDA), maintain huge collections of cultivated chickpea comprising the primary gene pool (Mallikarjuna et al., 2011). There are 76,221 chickpea accessions conserved *ex situ* around the world with ICRISAT and the National Bureau of Plant Genetic Resources (NBPGR), India, holding 27% and 19% of these accessions, respectively (Foyer et al., 2016).

Chickpea is a diploid with 16 chromosomes, thus; $2n = 2x = 16$ (Ahmad and Hymowitz, 1993) with a genome size of 738.09 Mb. The estimated number of genes is in excess of 28,000 with

close to 50% of the chickpea genome comprised of transposable elements and unclassified repeats (Varshney et al., 2013a). Generally, chickpea has low genetic diversity as is the case with most legumes (Foyer et al., 2016).

2.6 Chickpea production constraints

Chickpea production is affected by various production constraints; both biotic and abiotic, depending on the ecological region where it is grown. Drought resulting from water limited growing conditions is a period where soil moisture declines and can eventually lead to crop failure (Mishra and Singh, 2010). It is one of the abiotic production constraints limiting chickpea production and can either be intermittent drought occasioned by rainfall disruptions from the usual pattern of the growing season, hence leading to overall insufficient rainfall; or terminal drought occasioned by steady moisture depletion from the soil profile or less rainfall towards the end of the growing season (Canci and Toker, 2009). Drought alone causes up to 50% of chickpea production losses (Varshney et al., 2013b). However, depending on the genotype, the type of drought experienced and the environment, seed yield losses due to drought have been reported to range from 30% to 100% (Leport et al., 1999).

Besides drought, other important abiotic constraints for chickpea production in Australia include high temperatures, waterlogging, boron toxicity, salinity, cold and frost. Drought and heat are also important in Kenya. Heat stress remains a major constraint, especially for cool season crops like chickpeas, and more so when they are grown in transitional and warm climatic regions (Xu and Huang, 2001).

Biotic production constraints include pests like pod borers (*Helicoverpa armigera*, *Spodoptera exigua* and *Helicoverpa punctigera*), cutworms (*Agrotis* spp.), aphids (*Aphis craccivora*), leafminers (*Liriomyza cicerina*), bruchids (*Callosobruchus* spp.) and diseases like Ascochyta blight (*Ascochyta rabiei*), Fusarium wilt (*Fusarium oxysporum*), Phytophthora root rot (*Phytophthora medicaginis*), dry root rot (*Rhizocotonia bataticola*), collar rot (*Sclerotium rolfsii*) and black root rot (*Fusarium solani*) (Sarmah et al., 2012, Ghosh et al., 2013). The severity of pests and diseases differ from one region to another. In Australia, Ascochyta blight and Phytophthora root rot are major diseases, whereas in Kenya, Fusarium wilt and Ascochyta blight are serious diseases. In India, Fusarium wilt is the major disease affecting chickpea production but recently other diseases like dry root rot and collar rot are becoming important (Ghosh et al., 2013). Storage pests are also a major problem in India and east Africa. It is

estimated that 20% - 30% of stored chickpea is damaged by bruchids (*Callosobruchus* spp.) in South Asia (Sarmah et al., 2012). All in all, abiotic stresses cause more yield losses than biotic stresses (Sarmah et al., 2012).

2.7 Chickpea cropping systems and tillage practices

The crops grown in a field over a fixed period, under a particular management system, following a specific sequence, coupled with their interaction with the farm resources, denote the cropping system. Some of the most common cropping systems include crop rotation, monocropping, intercropping and succession cropping. Sustainable cropping systems should maintain and enhance soil fertility, enhance crop growth, minimise spread of disease, weed control, enhance soil cover, reduce risk of crop failure and ensure better utilisation of resources.

Highly productive and effective agricultural systems with minimal environmental damage are deemed to be important strategies for the future development of agriculture (Hanson et al., 2007). To attain these goals, there is a need to develop production systems which are diverse and intensely managed (Kirschenmann, 2007). These, coupled with ecologically based management principles employed in dynamic cropping systems in farmlands, leads to sustainability. This will ensure agricultural production based on a strategy of annual crop sequencing which optimises production, resource conservation and economic returns (Hanson et al., 2007).

Crop sequencing generally increases the WUE of a cropping system (Merrill et al., 2007) since the plants make maximum use of the available soil moisture. Legumes perform well in crop sequences and offer a great opportunity to sustain increased productivity because of their ability to adapt to different cropping patterns (Jeyabal and Kuppaswamy, 2001) and fix atmospheric nitrogen. They also help reduce soil erosion (Giller and Cadisch, 1995) and suppress weeds (Exner and Cruse, 1993) if included as an intercrop in a cropping system.

Chickpea fits into various cropping systems (which vary from region to region). They include sole crop, mixed or intercropped, however, it is mainly intercropped with barley, linseed, mustard, maize, peas, safflower, sorghum and coffee among others (Berrada et al., 2007). Chickpea is grown in rotation following wheat, barley or rice (van der Maessen L.J.G., 1972). Wheat-chickpea sequential cropping has been successfully used in Australia, Ethiopia and Spain, and rice-chickpea sequences in Nepal, Bangladesh and Eastern India (Garrido and Lopez-Bellido, 2001, López-Bellido et al., 1998, Zewdu, 2002, Harris et al., 2005, Felton et

al., 1998). A decline in arable land has led to the integration of chickpea into sequential cropping systems where it is grown under irrigation or receding soil moisture (Berrada et al., 2007). Sequential cropping is recommended in chickpea cultivation since growing chickpea in the same field repeatedly is highly discouraged due to the risk of diseases like *Ascochyta* (*P. rabiei*) (Berrada et al., 2007). Crop rotation helps lower pest and disease pressure in cropping systems by causing a break of suitable host for the pest or disease organisms. Cyst nematodes (*Heterodera cicero*) can be controlled by rotating chickpea with non-leguminous crops (Ahlwat and Shivakumar, 2003).

Intercropping reduces the incidence of pests and diseases in chickpea compared with a chickpea monocrop (Berrada et al., 2007). The incidence of crown rot in wheat is always lower when wheat is grown following chickpea compared with wheat grown consecutively in the same field (Felton et al., 1998). Rotations including pulse crops in wheat fields, especially in no till systems, minimise the damage caused by cereal root diseases as well as increase the population and activity of beneficial soil microorganisms (Krupinsky et al., 2002). Wheat yields increased by 810 kg ha⁻¹ and 1360 kg ha⁻¹ in 1989 and 1990, respectively, when wheat was grown after chickpea as opposed to after wheat at Warra in Queensland, Australia. Similarly, wheat grain protein content increased from 9.4% to 10.7% (Hossain et al., 1996). Wheat shoot dry biomass and nitrogen increased by an average of 0.85 t ha⁻¹ and 19.2 kg N ha⁻¹, respectively, when wheat was grown after chickpea in northern New South Wales, Australia (Felton et al., 1998).

Pulse crops, including chickpea, pose a soil erosion threat since they produce lower crop residues with lower carbon to nitrogen (C/N) ratios when compared to grain cereals (Berrada et al., 2007). In this regard, it is imperative to grow chickpea alongside cereal crops that produce large amounts of residues to ensure residue retention especially in conservation tillage.

2.8 Conservation agriculture and its implication on chickpea cultivation

Conservation agriculture is founded on three main principles; minimal soil disturbance, soil cover with crop residues and crop rotation. This broad system of management helps in the improvement of soil fertility, disease and weed control (Verhulst et al., 2010). The principle of minimal soil disturbance encompasses reduced tillage systems whereby at least 30% of the soil surface is covered by crop residue between harvesting and the next planting (Fowler and Rockstrom, 2001). Zero till is a form of conservation tillage which ensures no more than 20-25% of the soil surface is disturbed with seeding performed using narrow slits into untilled soils (Sayre and Govaerts, 2012). Zero till has been successfully implemented in over 96 Mha

of rainfed production systems in the USA, Brazil, Argentina, Canada and Australia (Derpsch, 2005).

The use of conservation tillage has increased since its inception in the 1960s, primarily due to its ability to lower farm resource requirements, soil erosion control and soil moisture conservation (Verhulst et al., 2010). It also increases soil aggregate stability (Chan and Mead, 1988, Li et al., 2007), improves soil structure (Page et al., 2013), increases water storage, especially in the semi-arid regions (Marley and Littler, 1989, Felton et al., 1995, Radford et al., 1995) due to increased infiltration rates and reduced evaporation. Increased infiltration rates occur due to the continuity of macropores created by plant roots from the previous crop and soil fauna, particularly earthworms. Macropores act as channels that help transport water into the lower soil horizons. Crop residues on the soil surface and increased aggregate stability prevent the formation of surface seals, which normally impede infiltration in soils (McGarry et al., 2000). The crop residues also lower soil temperature and reduce soil surface wind speeds, consequently reducing water loss through evapotranspiration (Jones et al., 1994, Hatfield et al., 2001).

Due to reduced levels of soil disturbance in conservation tillage, soil bulk density increases (Li et al., 2007). Consequently, soil porosity decreases (Mielke et al., 1986), and, if coupled with an increase in soil moisture, it leads to decreased air permeability and a reduced number of air-filled pores. This causes an increase in anaerobic processes such as denitrification in wet periods (Linn and Doran, 1984).

Several researchers (Muñoz-Romero et al., 2012, Jan et al., 2012, Gan et al., 2010) have looked into the productivity of chickpea under no till regimes. Jan et al. (2012) reported that chickpea planted under conventional tillage yielded more than the no till treatment. This may have been a result of higher plant density observed in conventional tillage systems as opposed to no till. In addition, Muñoz-Romero et al. (2012) reported that chickpea root length was higher in conventional tillage than no till systems. However, there was no significant difference in root biomass in the two tillage systems. Chickpea root length, root biomass and root nitrogen decreased with increasing soil depth under both conventional and no till systems (Muñoz-Romero et al., 2012). In wet years, root distribution was highest in the superficial soil layer as opposed to drier years where there was a higher distribution in the deeper soil layers (Muñoz-Romero et al., 2012). Chickpea roots have the ability to grow more than 1 m deep in the semi-arid regions, so they can scavenge for water in the deeper soil horizons (Gan et al., 2010). Chickpea water use has been demonstrated to be higher in tilled-fallow systems than no-till

systems and increased with increasing soil depth in Saskatchewan, Canada (Gan et al., 2010). Despite all these studies, the results have not been conclusive.

2.9 Drought resistance mechanisms in plants

Plants respond to water deficit conditions in various ways depending on the duration and intensity of the deficit, and the stage of plant development. The main defence mechanisms against drought include escape, avoidance and tolerance. Drought escape can either be through early flowering or early vigour. In most cases, early flowering genotypes mature early in the season to ‘escape’ terminal drought, especially in the semi-arid areas where this is the norm. An example of a very early flowering chickpea type includes ICCV 96029, and an early maturity type includes ICCV 2 (Gaur et al., 2008). The disadvantage with early maturing genotypes is that they tend to be smaller in stature and consequently have a lower photosynthetic area, and in most cases, have lower yield potential (Blum, 1988). That is why it is important to match genotypes with environment to take advantage of the maximum growing duration with least amount of stress for optimum yields. Early vigour is an equally important drought escape mechanism in grain legumes (Thomson and Siddique, 1997). Early plant vigour should also be matched with the right environment.

Dehydration avoidance is the ability of the plant to maintain turgor in its tissues and cells under water deficit conditions by maintaining water uptake and reducing water loss. Long roots allow access to water deep in the subsoil. ICC 4958 has large roots which develop quickly to rapidly extract water from the subsoil (Toker et al., 2007). Other mechanisms involved in maintaining water uptake and reducing water loss include osmotic adjustment, which maintains stomatal conductance and photosynthesis and, in effect, delays leaf senescence and death (Toker et al., 2007). Leaf characteristics like glandular droplets consisting of organic acids such as succinic, malic, citric and oxalic (Toker et al., 2004) help in lowering the leaf temperature, thereby protecting the plant from drought (Lauter and Munns, 1986).

Drought tolerance is the ability of the plant to tolerate water deficits with low tissue water potential and maintain metabolic function at low leaf water status. Some of the mechanisms that can be exploited to confer drought tolerance include an ability to remobilise stem reserves to fill grains, maintenance of cell membrane stability and accumulation of abscisic acid during water stress conditions. Others mechanisms include proline accumulation, presence of polyamines, brassinosteroids, jasmonates, phosphatidic and salicylic acids (Toker et al., 2007).

2.10 Effects of water deficit on chickpea growth and development

Chickpea is indeterminate crop, which has the habit of continuous vegetative growth if there is no water limitation. However, it can quickly change from vegetative to reproductive phase. The challenge is normally that chickpea is grown under receding soil moisture and there is a high probability that by the time the plant changes from vegetative to reproductive, there is insufficient soil moisture for the reproductive phase, hence leading to seed yield loss. Generally, water deficit causes a reduction in seed yield due to various factors as shown in previous studies. Seed yield, pods per plant and average seed size were all higher on primary branches than on secondary branches when moisture stress was induced at the early podding stage (Leport et al., 2006). Chickpeas exposed to terminal drought under field conditions had a shorter seed filling duration and seed filling rate and thus, had smaller final seed size (Davies et al., 1999). However, early transient water deficit increased the rate of seed filling and final seed size at maturity compared with well-watered controls (Fang et al., 2011). Moisture stress at the early podding stage reduces the number of seeds per pod to predominantly one in kabuli, whereas desi-types are not affected (Leport et al., 2006). Fewer seeds per pod and smaller seed size result in a decrease in seed yield (Leport et al., 1999, Fang et al., 2010), although at late podding, moisture stress does not reduce the seed size (Leport et al., 2006). Similar data were reported by Davies et al. (1999) who reported the average seed size of chickpea genotypes Tyson, ICCV 88201 and Kaniva were reduced by 19, 23 and 34%, respectively, under field conditions.

Reduction in seed yield under the early transient water deficit was lower compared with terminal drought yield losses (Fang et al., 2011), probably because of chickpea's indeterminate nature and ability to recover. Water stress reduced the total plant dry mass (Behboudian et al., 2001), particularly in kabuli types where there was greater pod number and yield reduction, than in desi-types (Leport et al., 1999). Terminal drought reduced seed yield by 58-95% compared with irrigated controls (Leport et al., 2006).

Chickpea is most sensitive to water deficit during the flowering and early podding stages (Khanna-Chopra and Sinha, 1987). A study by Fang et al. (2011) showed that early transient water deficit reduced flower production by almost 50% and increased flower abortion compared with the well-watered controls in two chickpea cultivars, Rupali, (a desi-type) and Almaz (a kabuli-type). Terminal drought caused a 33-63% reduction in flowering, and an increase of 37-56% in flower abortion and 54-73% in pod abortion (Fang et al., 2010). The rate of flower abortion was higher for flowers on secondary branches than on primary branches,

and for late produced flowers than those produced earlier in the season (Fang et al., 2010). When pre-dawn leaf water potential was below -1.2 MPa, flower abortion occurred as a result of low pollen viability and failure of pollen tubes to grow down the style resulting in no fertilisation. Water deficit impaired the function of both pollen and the stigma/style – pollen germination was low with fewer pollen tubes reaching the ovary (Fang et al., 2010), which is characteristic of angiosperms grown under stressed environments (Porch and Jahn, 2001).

Pod abortion is more sensitive to water stress in kabuli than desi types, and kabuli tends to yield less than desi under similar conditions (Leport et al., 2006). Pod formation is greatly reduced after moisture stress is induced (Behboudian et al., 2001) although if induced at late flowering, it has a minimal effect on pod production. Pod abortion is higher in pods borne on secondary branches compared with those borne on primary branches regardless of when the stress is induced (Leport et al., 2006). Leport et al. (2006) reported that the total number of pods was reduced by 66-75% in plants exposed to early podding moisture stress compared with well-watered controls

2.11 Chickpea physiological responses to water deficit

Many plant morphological and physiological processes are affected by water deficit conditions (Toker and Cagirgan, 1998). These include reduced water content and water potential, stomatal closure, turgor loss and cell enlargement and plant growth (Rahbarian et al., 2011).

Lower soil water potential in drying soils slows plant growth (Ohashi et al., 2000), reduces photosynthesis (Gren and Quist, 1985), affects hormonal balance (Munns and Cramer, 1996), reduces cell enlargement (Nonami et al., 1997) and slows cell division as a result of reduced cyclin-dependent kinase activity (Schuppler et al., 1998b).

Relative water content is a very good indicator of a plant's response to water deficit as it indicates the hydration status of leaves (Barrs and Weatherley, 1962). When chickpea plants were exposed to water deficit conditions in pots, the relative water content of the leaves decreased (Krouma, 2010). Matos et al. (2010) reported similar responses for two chickpea genotypes whereby the relative water content was lower under water stress compared with the well-watered control. Water deficit can reduce the relative water content of chickpea genotypes at seedling, flowering or podding stages (Rahbarian et al., 2011).

Leaf water potential, an indicator of plant water status has been reported to be lower in drought tolerant chickpea than drought sensitive genotypes under drought stress conditions (Rahbarian

et al., 2011). Similar data have been reported by Siddique et al. (2000) in wheat, although there are also contrasting reports for wheat and other crop species. The water potential measured in the leaves of three chickpea genotypes, Chetoui, Kesseb and Andoun, under water deficit decreased by 1.5, 1.6 and 2.1 fold, respectively over a 21 day period (Krouma, 2010). In general, Andoun was more drought tolerant than the other genotypes.

Among the first signals of water stress is stomatal closure, which consequently slows photosynthesis as a result of limited carbon dioxide availability to the mesophyll (Chaves, 1991). Several factors including leaf water deficit (Hsiao, 1973), soil water deficit and leaf to air water vapour pressure deficit (Schulze, 1986) can cause stomatal closure. Water stress reduced stomatal conductance by 28-70% compared with well-watered controls in three chickpea genotypes (Krouma, 2010).

Transpiration and transpiration efficiency was higher in well-watered chickpea plots compared with water stressed plots (Singh and Sri Rama, 1989). Krouma (2010) reported a decrease in transpiration of between 27-61% in three chickpea genotypes under water stress.

Photosynthesis is generally inhibited under water stress conditions due to stomatal closure and various factors including the imbalance between light capture and utilisation (Foyer and Noctor, 2000), a decrease in the internal carbon dioxide concentration, inhibition of ribulose-1,5-biphosphate carboxylase/oxygenase enzyme activity and ATP synthesis (Rahbarian et al., 2011). In three water stressed chickpea genotypes, net photosynthesis was decreased by 33-51% compared with the well-watered controls (Krouma, 2010). This decrease later translated into yield penalties, which was related to the strong positive correlation (0.965) between biomass and photosynthesis in water stressed plants compared with a moderate positive correlation (0.50) in the well-watered plants. A decrease in photosynthesis at the flowering and podding stages for chickpea genotypes exposed to water stress compared with well-watered controls was related to a decrease in internal CO₂ concentration (Rahbarian et al. (2011).

The down-regulation of photosynthesis causes an energy imbalance in photosystem II, which results in photoinhibition (Pastenes et al., 2005). Rahbarian et al. (2011) reported a decrease in photosystem II efficiency in chickpea genotypes under water stress. Photosystem efficiency (Fv/Fm) helps in the detection of any damage to photosystem II and its probable inhibition. Water stress affects photosystem efficiency and thus, decreases the electron transport rate and the effective quantum yield of photosystem II (Ahmed et al., 2002). Stomatal conductance, net photosynthetic rate and photosynthetic capacity were reduced in chickpea under water stress

conditions but recovered after rehydration (Matos et al., 2010). The recovery upon rehydration shows that, inasmuch as water stress slows down photosynthesis, it does not damage the photosynthetic apparatus (Zanella et al., 2004), though this largely depends on the level of water stress.

Water stress can reduce chlorophyll a and b levels, which in turn alters their light harvesting capabilities (Farooq et al., 2009). Sayed (2003) pointed out that water stress decreases chlorophyll a/b binding proteins and, in effect, impairs the synthesis of chlorophyll a/b, thus leading to a reduction in light harvesting pigment protein associated with photosystem II. The thylakoid membrane emits chlorophyll fluorescence and it can be used as a proxy for photosynthetic reaction in photosystem II (Ahmed et al., 2002). Damage to the light reaction systems in photosynthetic apparatus as a result of water stress can be detected by analysing chlorophyll fluorescence and photosynthetic efficiency (Rahbarian et al., 2011).

Membrane stabilisation is important under water stress conditions and it can be achieved through changes in lipid composition or preservation of membrane lipids (Thi et al., 1990). Under water stress conditions, cell membranes experience dysfunction, causing increased levels of ion permeability and leakage (Sayar et al., 2008). Changes in membrane stability are thus identified by measuring electrolyte leakage from leaf discs in solution (Blum and Ebercon, 1981). An increase in electrical conductivity of the solution indicates increased membrane damage. Rahbarian et al. (2011) and Matos et al. (2010) reported reduced membrane stability in chickpea genotypes under water stress compared with well-watered controls. Moreover, membrane injury was higher when the relative water content was $\leq 40\%$ compared with when the relative water content was 55-50% (Matos et al., 2010), demonstrating that chickpea cell membranes become less stable with increasing severity of the water stress.

2.12 Water use efficiency and associated breeding efforts

Water use efficiency has various meanings depending on the discipline of study (Passioura, 2006) and can also be interpreted at various scales including farm, field, plant and plant part levels (Morison et al., 2008). Water use efficiency in agriculture can be considered at the whole plant level (ratio of total dry matter produced to total water used), economic yield (ratio of crop grain per unit area to transpiration), and at the leaf level (ratio of instantaneous carbon dioxide assimilation rate to transpiration rate) during the growing season (Ali and Talukder, 2008). For the purposes of this thesis, future reference of water use efficiency from Chapter 4 onwards

will be to water use efficiency in agriculture (ratio of total dry matter produced to total water used).

At the crop level, water loss is a result of the difference in water vapour concentration between the crop canopy and the atmosphere, and it is least during the cool humid months of the year. At the leaf level, the rates of CO₂ assimilation (A) and transpiration (T) are a product of stomatal conductance (g_s) and also a concentration gradient between the inside and outside of the leaf for CO₂ and water vapour, respectively (Condon et al., 2002). Theoretically, intrinsic water use efficiency ($W_T = A/g_s$) can be improved by lowering the ratio between intracellular to atmospheric CO₂ concentration (C_i/C_a), although trade-offs are likely to occur (Condon et al., 2002). However, breeding efforts have been made to select for lower C_i/C_a values that are reflected as low stomatal conductance values, high photosynthetic capacity or a combination of both (Farquhar et al., 1989). There is substantial genetic variation for C_i/C_a determined through carbon isotope discrimination (CID), which is large enough to cause variation in A/T, and consequently, WUE for dry matter production (Farquhar and Richards, 1984). Rebetzke et al. (2002) showed that CID is a highly heritable trait for wheat, which can be manipulated through plant breeding. Thus, increasing the intrinsic WUE has been an attractive crop breeding target over the years (Fischer, 1981). By exploiting genetic variation associated with intrinsic earliness and response to photoperiod, breeders have developed genotypes that can grow in times of the year when the evaporative demand is low which in turn raises the ratio of A/T and increases yield (Condon et al., 2004).

Chickpea has a slow initial growth rate and low photosynthetic rate, hence low WUE (Singh et al., 1987). As the crop progresses, WUE at the biomass level increases from the vegetative stage and peaks at full flowering and thereafter, decreases again towards maturity (Singh et al., 1987). WUE varies depending on the environment grown. WUE for grain ranged from 7 to 20 kg ha⁻¹ mm⁻¹ in a tropical climate compared to 10 to 13 kg ha⁻¹ mm⁻¹ in a sub-humid temperate climate (Table 2.1).

Table 2.1: Water use efficiency (ratio of total dry matter produced to total water used) of chickpea genotypes across different environments

Site	Climate type	Plant part	WUE (kg ha ⁻¹ mm ⁻¹)	Reference(s)
Thohoyandou, Limpopo Province, South Africa	Tropical (summer crop)	Grain production	7 – 20.9	Ogola and Thangwana, 2013
		Above ground biomass production	12 – 41.1	
Canterbury, New Zealand	Sub-humid temperate	Grain production	10 - 13	Anwar et al., 2003
		Above ground biomass production	22 - 29	
Warra, Queensland, Australia	Humid Sub-tropical	Grain production	5.9	Dalal et al., 1997
		Above ground dry matter	14.2	
		Total dry matter	29.2	
Windridge, North Star, NSW, Australia	Humid Sub-tropical	Grain	8.8	Herridge et al., 1995
Glenhoma, North Star, NSW, Australia	Humid Sub-tropical	Grain	5.8	
Tel Hadya, Northern Syria	Mediterranean climate	Above ground biomass production	8.7	Zhang et al., 2000
		Grain	3.2	

2.13 Breeding for increased water use efficiency using surrogates

Target trait based breeding has gained primacy in recent years as opposed to breeding for increased yields generally. Plant breeders are selecting for physiological traits that are simple to work with as surrogates for traits that have been traditionally difficult to select for. Drought tolerance is a very complex trait and WUE, which is one of the major components of drought

adaptation, is complex too. Hence, it is of prime importance to improve related traits that give an additive gene effect to increase WUE and drought tolerance.

Some traits associated with WUE have been identified, which include CID, where low CID implies higher transpiration efficiency resulting from low stomatal conductance or high rates of CO₂ assimilation (Condon et al., 2002, Farquhar et al., 1989). Delayed leaf senescence in sorghum is related to higher WUE through greater biomass accumulation post-anthesis (Borrell et al., 2014) and spike photosynthesis improves WUE in cereals probably due to re-fixation of respiratory CO₂ and better maintenance of water status through osmotic adjustment (Araus and Tapia, 1987). These traits can be used as surrogates for WUE (Reynolds and Tuberosa, 2008)

2.14 Phenotyping target physiological traits in chickpea

Over the last century, breeders have made progress in improving drought tolerance by selecting constitutive traits that affect dehydration avoidance rather than drought responsive traits because of fewer yield penalties (Blum, 2006). Target traits in water-limited environments should be correlated with yield and should have higher heritability than yield (Monneveux and Ribaut, 2006). Phenotyping these traits should also be non-destructive, accurate, cheap and inexpensive (Tuberosa, 2011). The phenotypic performance needs to be associated with genotypic data to understand the genetic basis of these complex traits (Montes et al., 2007). For phenotyping to be successful and relevant, environmental characterisation (Tuberosa, 2011, Chenu et al., 2011) is vital so that genotype by environment interactions can be exploited (Trethowan, 2014).

Phenotyping of large plant populations for various traits in the field can be labour intensive and expensive. However, the emergence of high-throughput phenotyping platforms such as near infra-red spectroscopy and multi-spectral reflectance make it possible to phenotype some simple traits in large populations in multi-locations (Montes et al., 2007). Unmanned aerial platforms such as polycopters mounted with cameras further increase the data capture and resolution, hence, increasing the output of the system (Araus and Cairns, 2014).

Chickpea phenotyping for drought tolerance has focused on selection for early maturity to avoid drought, and root traits to confer improved WUE (Upadhyaya et al., 2011). Phenotyping for WUE in chickpea has mainly been conducted using gravimetric methods in a pot culture (Upadhyaya et al., 2011); however, these methods do not generally correlate well with field conditions.

Near infrared spectroscopy has been used to capture differences in dry matter, starch and crude protein of maize (Montes et al., 2007). Spectral reflectance allows monitoring of various dynamic complex traits using high temporal resolution without destroying the plant (Montes et al., 2007). It can be used to measure canopy architecture and nitrogen concentration (Montes et al., 2007). Other measurements can be made on individual plants including plant photosynthesis pigment composition and plant water status. (Peñuelas and Filella, 1998).

Examples of some of the data that can be captured for chickpea breeding programs include morphological, phenological, physiological data (Figure 2.2).

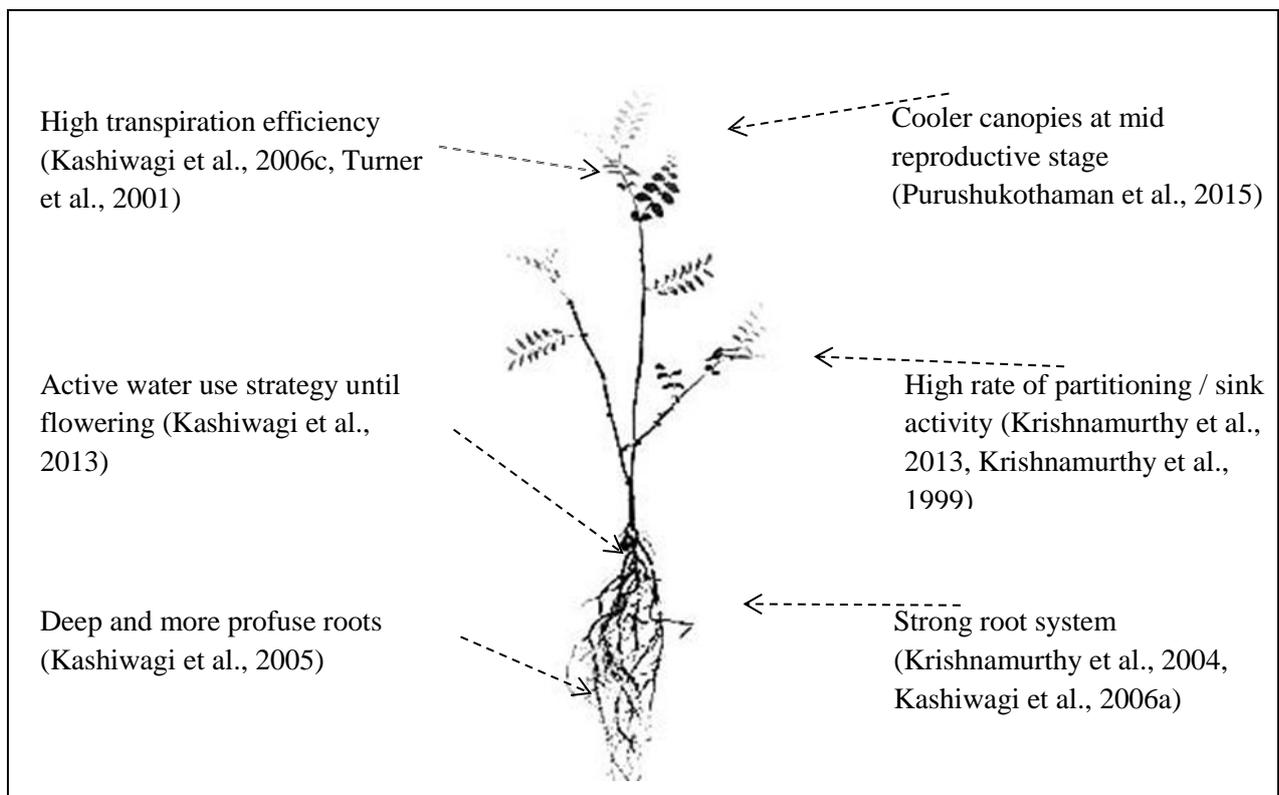


Figure 2.2: Some target traits for chickpea physiological breeding

2.14.1 Canopy temperature

Canopy temperature has been used as an indirect indicator of crop water status in cereals since water deficit results in partial stomatal closure, thus reducing transpiration and in effect causing sunlit leaves to become warmer than the ambient temperature (Jackson et al., 1977). Since transpiration has a cooling effect on canopies, cooler plant canopies can indicate higher transpiration rates, which is also a function of available soil water. Other factors that affect canopy temperature include morphological traits like leaf angle, canopy architecture, waxy deposits or other compounds that reflect heat (Pietragalla, 2012, Tuberosa, 2012), agronomic

traits like plant density and tillage (Yang et al., 2014) and atmospheric conditions like incident radiation, wind and relative humidity (Mariano et al., 2012). Under water limited conditions, cooler canopy temperatures are related to the capacity of plants to extract soil water from deep in the subsoil, whereas under well-watered conditions sink strength and photosynthetic capacity are more important (Pietragalla, 2012). The hand held canopy temperature gun is a simple and rapid method of determining canopy temperatures, however, in very large fields it may be limiting. Thermal imagery systems are more amenable to high throughput phenotyping for canopy temperature in large experiments (Kashiwagi et al., 2008) and these can be achieved by mounting the thermal imagery systems (e.g. cameras) on unmanned aerial platforms like drones, polycopters and airplanes. Canopy temperature is quite sensitive to environmental conditions and caution should be taken while taking the measurements. Good results are achieved when the conditions are ideal for high vapour pressure deficit (VPD), in conditions of warm air, generally above 15°C and relative humidity of less than 60% with clear sunny skies and low wind speeds (Pietragalla, 2012).

2.14.2 Plant vigour and plant green biomass

Over the years, remote sensing imagery has gained popularity because it is not limited by sampling interval or geostatistical interpolation (Moran et al., 1997), does not involve destructive sampling, and is amenable to high throughput. The premise for using optical remote sensing for crop assessment is that crop canopy multispectral reflectance and temperature is associated with photosynthesis and evaporation in which leaf area index (LAI) and crop development stages are central (Bauer, 1985).

Several indices have been developed which are used to analyse aerial imagery (Shanahan et al., 2001) including the normalised difference vegetation index (NDVI). The NDVI links reflectance in the red region and the near infra-red (NIR) to vegetation parameters such as canopy cover, leaf area index and the concentration of total chlorophyll (Shanahan et al., 2001). Korobov and Railyan (1993) concluded that the NIR and red areas of the spectrum correlated highly with plant parameters such as plant height, plant density and percent plant cover.

Initially, the NDVI was used for estimating green biomass (Tucker, 1979), however it has been subsequently used to assess crop health (Douglas Ramsey et al., 1995, Teillet, 1992). The use of NDVI in breeding has been made possible by the development of inexpensive equipment that is simple to use, affordable and accurate.

2.14.3 Photosynthetically active radiation (PAR)

The photosynthetic active radiation spectrum (PAR), which makes up 50% of the total global radiation (Bonhomme, 2000), lies in the wavelength 400 – 700 nm (Zhang et al., 2008). The crop canopy absorbs PAR, referred to as intercepted photosynthetically active radiation (IPAR) which is intercepted light used for photosynthesis and eventually producing plant biomass (Johnson et al., 2010). The radiation intercepted during the growing period is determined by the canopy radiation extinction coefficient (k) and is influenced by leaf orientation and the green leaf area (Thomson and Siddique, 1997). Research has shown that lower k values are associated with narrow and erect leaves compared to plant genotypes with more horizontal leaf arrangements (Kiniry et al., 2005). Lower k values allow more light to penetrate the canopy and illuminate more leaf area in conditions of low light intensity, thus increasing carbon exchange rates, and consequently, radiation use efficiency (Kiniry et al., 2005).

The fraction of intercepted photosynthetically active radiation can be used to estimate the leaf area index (LAI) through its relationship with the plant canopy (Johnson et al., 2010). This provides an easy and non-destructive way of estimating the leaf area index. IPAR can be accurately determined using a ceptometer, though care should be taken to avoid confounding factors such as the soil albedo, row spacing and lack of canopy uniformity (Andrade et al., 2002).

2.14.4 Chlorophyll content

There is a close relationship between chlorophyll concentration, leaf nitrogen content and crop yield (Cartelat et al., 2005). This relationship arises because the majority of leaf nitrogen is usually contained in chlorophyll (Cartelat et al., 2005). Since chlorophyll absorbs PAR, which aids in photosynthesis, it indicates the strength of the internal leaf apparatus during photosynthesis (Li et al., 2006).

Leaf chlorophyll content can be determined by extraction with organic solvents including acetone (Liu et al., 2008) and methanol (Cenkci et al., 2010) and subsequent quantification using a spectrometer; however this method is expensive and time consuming (Jangpromma et al., 2010). A higher throughput non-destructive method is the SPAD chlorophyll meter that allows rapid and inexpensive assessment of leaf greenness (Ahmed, 2011). SPAD measures leaf absorbance in the red (650 nm) and infrared (940 nm) regions (Markwell et al., 1995), and gives readings that have been correlated with chlorophyll content under different moisture regimes in many crops (Jangpromma et al., 2010).

2.15.5 Root traits

Plants extract water from the soil through the roots and the spatial distribution of the root system influences water and nutrient intake capacity (Lynch, 1995). Dense root systems are more efficient at extracting water from the top soil horizon whereas deeper rooting systems are better at extracting water from the lower soil horizons. These contrasting traits are important influencers on yield under water deficit conditions during the reproductive stage in many crops (Ludlow and Muchow, 1990). Kashiwagi et al. (2006a) showed that root architecture of chickpea affects transpiration by influencing soil moisture use and subsequent harvest index under terminal drought. However, the heritability of these root characteristics will determine their utility in plant breeding. Varshney et al. (2014) reported genetic variation for both root length density and root depth in chickpea and found heritabilities ranging from medium to low. Root hydraulic conductivity impacts the amount and efficiency of water uptake by the plant and is determined by the anatomy and morphology of the roots and their aquaporin activity (Bramley et al., 2009). In legumes, root hydraulic conductance is influenced by the total root length since water is absorbed along the full root (Bramley et al., 2009).

Root phenotyping is difficult and for this reason the literature on chickpea is not extensive. However, Kashiwagi et al. (2006a) and Zaman-Allah et al. (2011) used polyvinyl chloride (PVC) cylinders (lysimeters) to grow chickpeas for assessment. The soil was subsequently washed off sampled plants to measure total rooting depth. Image analysis software was then used to estimate the root length at various sections of the lysimeters and divided by the specific volume of that section to determine the root length density. With these advances in root phenotyping, many plants can be assessed.

2.15 Chickpea ideotype development

Plant breeders empirically select for yield in their breeding program. This selection is based on variation created through hybridisation or by introduction of various genotypes with varying responses to the trait of interest. Inasmuch as this method has led to yield increases over the years, it still poses a challenge in that little is known about the morphological, physiological and biochemical determinants of yield. Furthermore, yield is highly affected by the environment due to its polygenic nature and thus, affects the repeatability of the results over different seasons (Johnson and Gadelmann, 1989).

The ideotype approach is an alternative strategy to empirical breeding where a deliberate attempt is made to understand the factors that influence yield formation under different abiotic stresses. Donald (1968) defined an ideotype as a biological plant model that behaves in a known manner when exposed to a distinct environment. The idea behind the ideotype was to consolidate several important plant traits into one genotype, which would be ideal for growing in a specified environment. The definition of the plant type assists plant breeders to have more clear cut objectives (Rasmusson, 1987, Rasmusson, 1991) and thus, a blueprint for pyramiding traits (Mock and Pearce, 1975). This makes ideotype breeding more analytical than the traditional empirical selection and breeding methods used in the past.

Key steps in ideotype breeding include the identification of the target population of environments (Mock and Pearce, 1975, Trethowan, 2014). The ideotype should perform optimally in the defined target environment. The second step entails identification of the physiological and morphological traits that contribute to yield either directly or indirectly. These traits should have genetic diversity and be highly heritable to be incorporated into an ideotype breeding program (Rasmusson, 1987). The identification of both morphological and physiological traits can be done through physiological breeding (Figure 2.2).

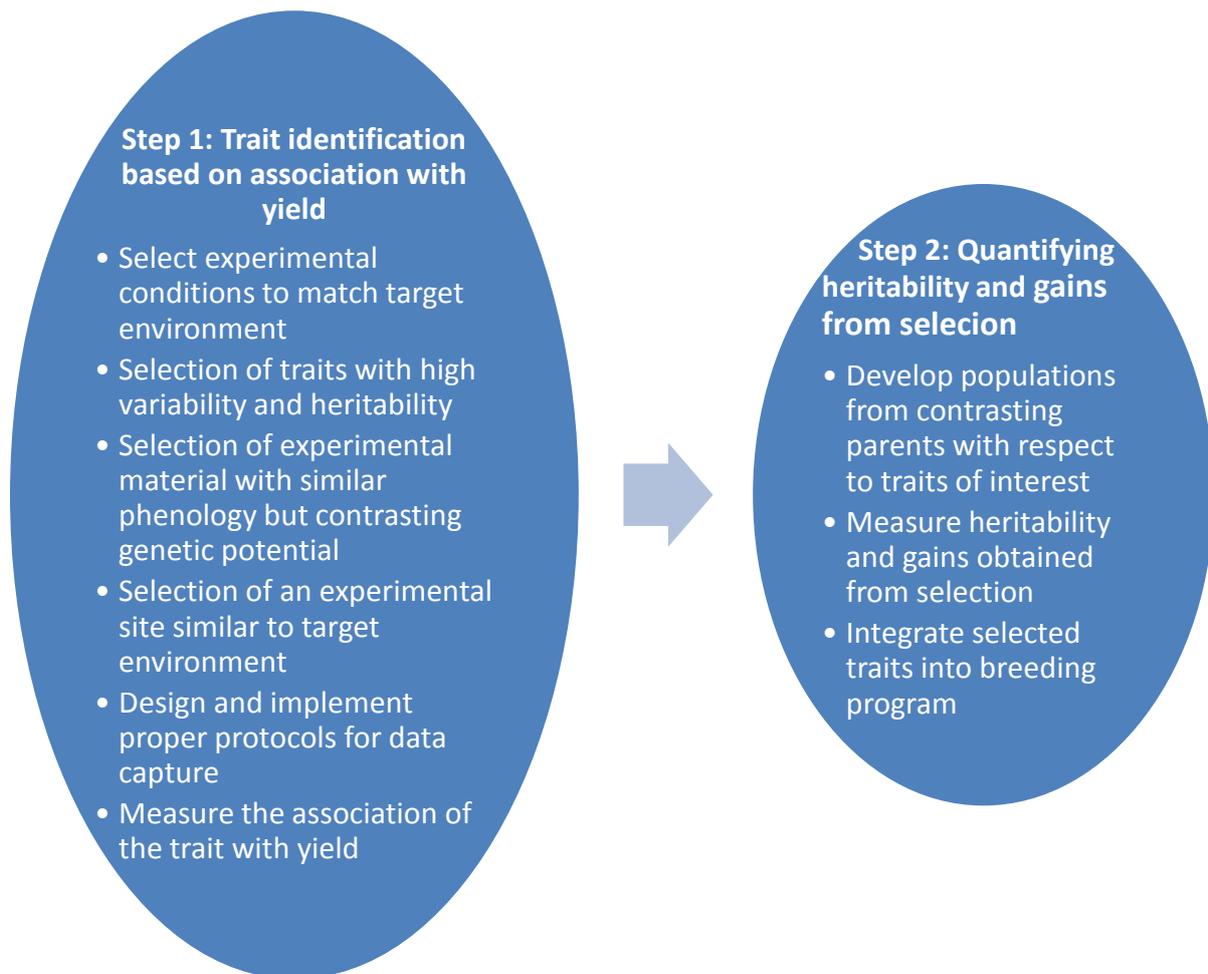


Figure 2.3: Schematic illustration of physiological breeding. Adapted from Reynolds et al. (2001).

2.16 Crop modelling and ideotype design

From a modelling perspective, crop ideotype is a set of defined crop parameters that drive growth and development in defined environmental conditions (Rotter et al., 2015). This entails the use of high quality, long-term data, for model calibration and the generation of accurate simulation results (Rotter et al., 2015). Data from multiple sites over many years can be produced without running actual field trials, thus creating a powerful tool for ideotype design and testing *in silico* (Semenov and Stratonovitch, 2013). This in turn saves a lot of time and money that would have been used to test the genotypes in a wide set of environments.

Agricultural Production Systems sIMulator (APSIM) is an important software package used in agricultural crop modelling. It simulates cropping systems using climate, soil, management and crop genetic coefficients to predict the economic yield of a crop species (Keating et al., 2003). The APSIM model mainly employs the supply and demand concept of important plant growth

resources (light, water, nitrogen and carbon) to create a plant phenotype (Hammer et al., 2001). This is mainly based on the input parameters which are therefore used to give the output of the plant trait being modelled.

2.17 Conclusion

Tillage systems may increase WUE, but the results to date are inconclusive. Hence, more research needs to be conducted to elucidate how tillage systems affect WUE in chickpea. Furthermore, the effect of genotype by environment by management in chickpea has not been extensively studied, hence the need to delve further in this area of study. A few surrogate traits, including carbon isotope discrimination, have been identified that can be used to select for drought tolerant genotypes. However, previous studies mostly identified one or two surrogates and in single environments. There is a need to identify multiple surrogates in different environments, to develop a chickpea ideotype that can perform well in a target environment because previous attempts to develop chickpea ideotypes have used only a few traits resulting in poor crop ideotypes. The proposed ideotype traits are either labeled as low, medium or high and this makes it difficult for the plant breeder to know what is high or low without figures. There should be an attempt to guide plant breeders with a quantitative trait range with values, e.g., low should be X_1 to X_2 within the available genepool.

CHAPTER 3: GENERAL MATERIALS AND METHODS

3.1 Introduction

This chapter covers the general materials and methods for the field experiment. Each chapter has more specific materials and methods including formulas.

3.2 Experimental site

The field experiment was carried out at the University of Sydney's Plant Breeding Institute at Narrabri (30.275616°S and 149.803547°E) in 2014 and 2015. This site has a summer dominant rainfall and in winter the rainfall is not sufficient for a successful crop. Hence, crops grown during winter, including chickpea, tend to experience terminal drought. On average, the long-term annual rainfall is 662 mm distributed throughout the year with a peak in December and January. The long-term mean annual maximum and minimum temperatures are 26.5°C and 11.7°C, respectively, with the coldest month being July. The soil at the site is characterised by deep Vertosols, which are black clays that shrink and expand with changes in soil moisture.

The planting window for chickpea in Narrabri is from the second week of May to the second week of June according to the annual winter crop sowing guide produced by New South Wales Department of Primary Industries (DPI).

3.3 Experimental design

The field experiment was planted under no till and till systems with each having irrigation splits such that there was no till, +/- irrigation and till, +/- irrigation (Figure 3.2) using an alpha lattice design replicated twice. The irrigated side which received two supplementary irrigations was considered to be the well-watered treatment and the rainfed side was considered to be the water stress treatment. There were 30 chickpea entries (25 desi and 5 kabuli), in addition, five genotypes were selected based on their phenotypic similarity, then mixed to form six mixture entries (Table 3.1) totalling 36 entries in the experiment. The genotypes were sourced from Pulse Breeding Australia (PBA) in Tamworth except for the ICCV lines which were sourced from ICRISAT India. Additionally, Sal, Sim, Lyle, Lyons, Austin and Doolin were sourced from the University of Sydney germplasm store. The PBA lines were selected because they are grown widely and also some of them have drought tolerance to some extent. The ICCV lines have been tested in ICRISAT India and there was a need to further test them for water use efficiency. The preceding crop in the experimental area was wheat in both seasons planted in rotation, such that chickpea is not planted in the same field where the previous crop was chickpea.

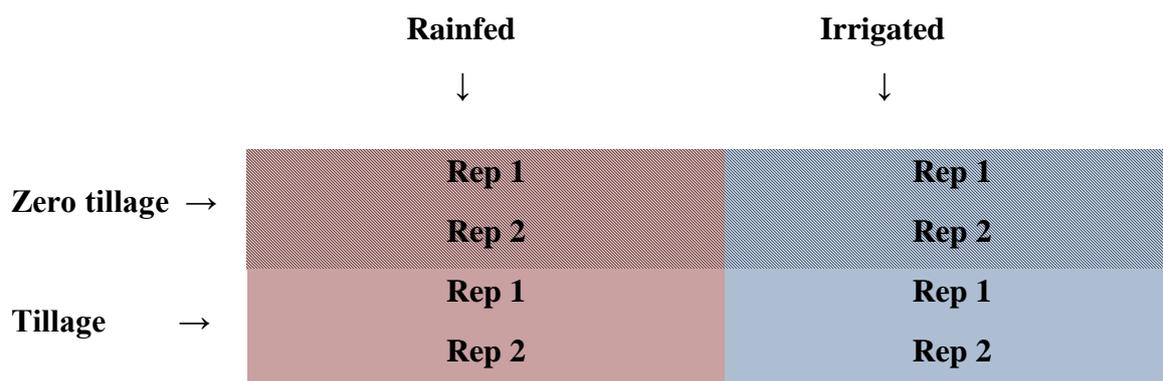


Figure 3.1: Narrabri experimental field layout in 2014 and 2015 for chickpea water use efficiency experiments

Table 3.1: List of chickpea genotypes for water use efficiency experiments at Narrabri

No.	Name	Type	No.	Name	Type
1	AMETHYST	Desi	19	JIMBOUR	Desi
2	FLIPPER	Desi	20	JIMBOUR#1	Desi
3	GENESIS KALKEE	Kabuli	21	FLIP 079C	Kabuli
4	HOWZAT	Desi	22	ICCV 05308	Kabuli
5	KYABRA	Desi	23	AUSTIN	Desi
6	PBA HATTRICK	Desi	24	DOOLIN	Desi
7	PBA SLASHER	Desi	25	HOWARD	Desi
8	PBA STRIKER	Desi	26	LYLE	Desi
9	SONALI	Desi	27	LYONS	Desi
10	TYSON	Desi	28	SAL	Desi
11	YORKER	Desi	29	SIM	Desi
12	GENESIS 079	Kabuli	30	THOMAS	Desi
13	GENESIS 090	Kabuli	31	Mix 1 (Yorker/Jimbour)	Desi
14	ICCV 96853	Desi	32	Mix 2 (Howzat/Flipper)	Desi
15	ICCV 98801	Desi	33	Mix 3 (Flipper/Jimbour)	Desi
16	ICCV 98813	Desi	34	Mix 4 (Yorker/Howzat)	Desi
17	ICCV 98816	Desi	35	Mix 5 (Howzat/Jimbour)	Desi
18	ICCV 98818	Desi	36	Mix 6 (Howzat/ 98813)	Desi

3.4 Field experiment sowing

Sowing was carried out using a six-row planter with 30 cm inter-row spacing in 2014 and a four-row planter with 50 cm inter-row spacing in 2015 resulting into 4 m by 2 m plots in both years. Plant population was maintained at 25 plants m⁻² for both years. The date of sowing was 28 May, 2014 and 11 June, 2015. The four-row planter was used in 2015 because the stubble in the no till area was high and it was difficult for the six-row planter to cut through it. Seeds

were dressed using P-Pickle[®] T (360 g/L thiram and 200 g/L thiabendazole) at 2 mL in 8 L of water with 1 kg of solution used per kg of seed, and later with Apron[®] XL 350 ES (350 g/L metalaxyl M) at 0.75 mL in 9.25 L of water with 10 mL of solution used per kg of seed, in both years. These fungicides were used to give protection against fungal diseases during the early stages (normally up to six weeks) of crop development. The seeds were inoculated with chickpea group N rhizobia (Nodulaid[®]) using the slurry method in 2014 and as a solution (water + inoculum) injected into the soil using a tank mounted on the planter in 2015 at the recommended label rates.

3.5 Field agronomic practices

Pre-emergence spray Terbyne[®] 750WG (750 g/kg terbuthylazine) was applied at 1 kg ha⁻¹ and Balance[®] 750WG (750 g kg⁻¹ isoxaflutole) at 100 g ha⁻¹ for weed control in the field. During the cropping season, any weeds present were pulled out manually in the experimental area. Prophylactic sprays using Ridomil Gold[®] at 2.5 kg ha⁻¹ were applied at flowering and mid-podding to protect the crop against phytophthora root rot (*Phytophthora medicaginis*) in both years. Unite[®] 720 (720 g/L chlorothalonil) was applied at the rate of 500 mL ha⁻¹ for the control of Ascochyta blight (*A. rabiei*) at early flowering in 2014 and at early flowering and early podding in 2015. Insect pests, mainly caterpillars (*Helicoverpa armigera*) and aphids, were controlled using Karate Zeon[®] (250 g/L lambda-cyhalothrin) at the rate of 36 mL/ha in 2015.

3.6 Data parameters

Several parameters were measured during the growing season and some post-harvest traits were also measured (Table 3.2). The main foci were agronomic, morphological, phenology and physiological data.

3.7 Field irrigation

Two irrigations were applied in both seasons using a lateral moving sprinkler irrigation system. In 2014, 35 mm was applied at flowering and early podding, whereas in 2015, 36 mm was applied at flowering and 26 mm at late podding/early maturity stage (represented as inverted arrows in Figure 3.3c and 3.3d).

3.8 Weather data

Weather data was collected from the nearest weather station at Narrabri Airport in 2014 and from the Managed Environment Facility weather station in a nearby field in 2015. Data for rainfall, temperature (maximum and minimum), radiation and evaporation were recorded from time of sowing to harvesting. During the growing season, total rainfall was considered as the

rainfall received during the active plant growing period, thus from sowing time to when the plants in the experiment reached 75% maturity.

3.9 Data analysis

Data were analysed using Genstat® edition 18 following the methods described in the individual chapters.

CHAPTER 4: WATER USE, WATER USE EFFICIENCY AND YIELD VARIATION IN CHICKPEA GENOTYPES

4.1 Introduction

Chickpea is mainly grown on stored soil water in areas where it is cultivated (Kashiwagi et al., 2005). As such, the crop has to strike a balance in water use to ensure that there is enough soil moisture towards the end of the growing season and at the same time to have extracted enough water to sustain yield. Legumes mainly have either a conservative water use strategy, where water is used sparingly, or a profligate water use strategy where the water use is more liberal (Bacelar et al., 2012). These water use strategies determine the survival of the crop, especially under water limiting conditions since their survival is dependent on moisture availability at the reproductive stage (Kato et al., 2008). This was emphasised by Zaman-Allah et al. (2011) who posited that chickpea genotypes that are drought susceptible used more water at the vegetative stage whereas the drought tolerant genotypes used less water at the vegetative stage and more water at the reproductive stage. Deep and profuse rooting systems are very important in accessing soil water from deep down the soil horizon (Kashiwagi et al., 2006b) and can give chickpea plants a reprieve under water limited conditions. Supplementary irrigation during the flowering and pod filling stages has been shown to increase seed yield as well (Silim and Saxena, 1993). Water use efficiency is an important trait in crops grown under stored soil water as well as under irrigation (Blum, 2005). Water use efficiency has various definitions depending on the level and measurement scale, but for the purpose of this chapter it will be defined as the ratio of grain yield to water used (Condon et al., 2004). There have been reports that there is genetic variation for WUE in various crops (Farquhar and Richards, 1984). This may give plant breeders an opportunity to exploit this trait in improving crop yields under water limiting conditions, especially under stored soil water. Improvement of WUE requires a multifaceted strategy (Wang et al., 2002) which includes breeding and management (Condon et al., 2004). Some of the management practices that increase WUE include crop sequencing since it ensures maximum use of available soil water (Merrill et al., 2007). Tillage and no till systems also affect water use efficiency in different ways and it is imperative to understand their effect in order to incorporate them in the management options. Early flowering in chickpea is used as a drought escape mechanism and helps the crop avoid seed yield losses as a result of terminal drought. This ensures that the plant will produce some grain even though there will be a yield penalty due to the low moisture conditions at the end of the growing season.

This in effect increases agronomic water use efficiency where seed yield is considered per unit amount of water used. Indeterminate flowering may cause the crop to delay in flowering and end up losing yield at the end of the growing season if moisture is inadequate.

Little attention has been paid to the pattern of water use in legumes and the relationship between water used and seed yield (Zhang et al., 2000b). Despite evaluation of WUE in chickpea in various studies, little has been achieved since these studies were focused on single factors affecting WUE. This causes variability of data from different studies due to failure of integration of various factors (Gan et al., 2010). Studies conducted by Angadi et al. (2008) showed WUE of $6.8 \text{ kg ha}^{-1} \text{ mm}^{-1}$ for chickpea grown on the Canadian Prairies whereas McKenzie et al. (2006) reported $15.8 \text{ kg ha}^{-1} \text{ mm}^{-1}$ for the same location. It is therefore important to incorporate more factors to get more reproducible data. Soil factors (tillage and fertility) also play a key role in minimising variation in the data. However, there have been limited studies on the effects of tillage systems on chickpea production. A few preliminary studies showed the benefits of no-till management were primarily due to soil moisture conservation and availability in the growing season (Rathore et al., 1998). There is also very little knowledge about how soil moisture status and WUE for chickpea is affected by cropping systems (Gan et al., 2010).

The hypotheses to be tested in this chapter include:

- whether there is genetic variation for WUE in chickpea and
- whether no till systems conserve more soil water and increase WUE in chickpea, relative to conventional cultivation.

This chapter aims to: i) discover whether there are differences in water use and WUE of chickpea genotypes, ii) evaluate the effect of tillage and irrigation management options on WUE, iii) establish the relationships among water use, WUE and yield and iv) establish heritability estimates for WUE under different management options.

4.2 Materials and methods

Thirty-six entries were grown for two years (2014 and 2015) at the IA Watson Plant Breeding Institute in Narrabri, under no till and till conditions with irrigation (well-watered/non-stress) and without irrigation (water stressed) as described under general Materials and Methods in Chapter 3. Soil moisture in the control plots was monitored on a fortnightly basis using a neutron probe moisture meter, CPN® 503DR Hydroprobe (Figure 4.1) from sowing on a

fortnightly basis until harvesting. A total of 16 (in 2014) and 32 (in 2015) aluminium neutron probe access tubes (Figure 4.2) were inserted immediately after sowing up to a depth of 150 cm spread across the whole experiment in all the control plots. The control plots in 2014 included PBA Hattrick and Tyson whereas in 2015 they included PBA Hattrick, Tyson, Amethyst and Sonali genotypes. Measurements were taken at 10, 20, 30, 40, 60, 80, 100, 120 and 134 cm in every tube.



Figure 4.1: Neutron probe moisture meter



Figure 4.2: Neutron probe access tube

The neutron probe moisture meter was set to take counts for 16 seconds and then data recording started. The data were converted to volumetric water content (θ) in millimetres using the equation (4.1) below from a soil calibration exercise in the Managed Environment Facility in Narrabri.

$$\theta = (C - 7863)/182.9 \quad (4.1)$$

Where, θ is the volumetric water content in millimetres and C is the neutron counts.

The soil water balance method (Equation 4.2) was used to estimate water use which was estimated to be equivalent to evapotranspiration from planting to physiological maturity as documented by Anwar et al. (1999).

$$WU = Et = (P + I) - \Delta SWC - Ro - D \quad (4.2)$$

Where WU is water use, Et is evapotranspiration, P is precipitation, I is irrigation, ΔSWC is change in soil water content from time of measurement 1 to 2 at a depth of 0-134 cm, Ro is run-off and D is drainage. Run-off was assumed to be zero since there was no major rain event to necessitate a run-off and the fields were effectively level. Drainage was set at zero because soil drained upper limit was not reached during the cropping season. Total water use was

considered as the initial water at the beginning of the season less the remaining water at the end of the season and also taking into consideration irrigation and precipitation.

The total seed yield was obtained by harvesting and threshing all the plants in the plot, weighing them and then converted to yield in kilograms per hectare.

Water use efficiency for grain production was calculated as the total grain produced divided by the total water used and expressed as $\text{kg ha}^{-1} \text{mm}^{-1}$. This was done for the control genotypes which had neutron probe access tubes fitted. For the rest of the genotypes, WUE was calculated by taking the average water use from the control genotypes in each environment type and divided by the total seed yield for each genotype in that environment type. Each year was considered separately.

Broad sense heritability was calculated as the ratio of genotypic to phenotypic variance (Equation 4.3) (Knapp and Bridges, 1987)

$$H^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_{ge}/e + \sigma^2_e/re) \quad (4.3)$$

Where σ^2_g is the genotypic variance, σ^2_{ge} is the genotype by year variance component and σ^2_e is the error term variance. “e” and “r” represents the year and replication, respectively.

The genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV) and environment coefficient of variation (ECV) were calculated as the ratio of the standard deviation of each variation to the trait mean as shown in Equations 4.4 to 4.6.

$$GCV = (\sqrt{\sigma^2_g}) / \bar{X}, \quad (4.4)$$

$$PCV = (\sqrt{\sigma^2_p}) / \bar{X}, \quad (4.5)$$

$$ECV = (\sqrt{\sigma^2_e}) / \bar{X} \quad (4.6)$$

Where, σ^2_g , σ^2_p , σ^2_e and \bar{X} are the genotypic variance, phenotypic variance, error variance and the trait mean, respectively.

Genetic advance (GA) as a percentage of the mean was calculated using Equation 4.7.

$$GA = ((K * \sqrt{\sigma^2_p} * H^2) / \bar{X}) * 100 \quad (4.7)$$

Where $\sqrt{\sigma^2_p}$ is the phenotypic standard deviation, H^2 is the heritability and K is the selection differential at 5% selection intensity (2.06)

Data were analysed using Genstat[®] edition 18 for all the measured traits using linear mixed models in Restricted Maximum Likelihoods (REML) (Patterson and Thompson, 1971) to estimate variance components. Tillage, moisture, year and genotypes were fitted in the fixed model whereas the range and rows were in the random model (Fixed model: Tillage X Moisture X Year X Genotype; Random model: Range.Row). To get least significant differences, the model was changed to tillage, moisture and genotypes in the fixed model and range and row were nested within the years in the random model (Fixed model: Tillage X Moisture X Genotype; Random model: year/(Range.Row)). Data on water use was analysed by considering Tillage X Moisture X Genotype in the fixed model. Tillage, moisture and year had two factor levels whereas genotypes had 36 factor levels. Data means, standard error of the means, coefficient of variation and least significant difference were tabulated.

4.3 Results

4.3.1 Precipitation and temperature

The total rainfall received in 2014 was 132.5 mm and 156.5 mm in 2015, respectively (Figure 4.3c and 4.3d). However, rainfall distribution during the flowering phase was better in 2014 than 2015. In general temperatures were higher in 2014 than in 2015 especially during the flowering and podding phase (Figure 4.3a and 4.3b).

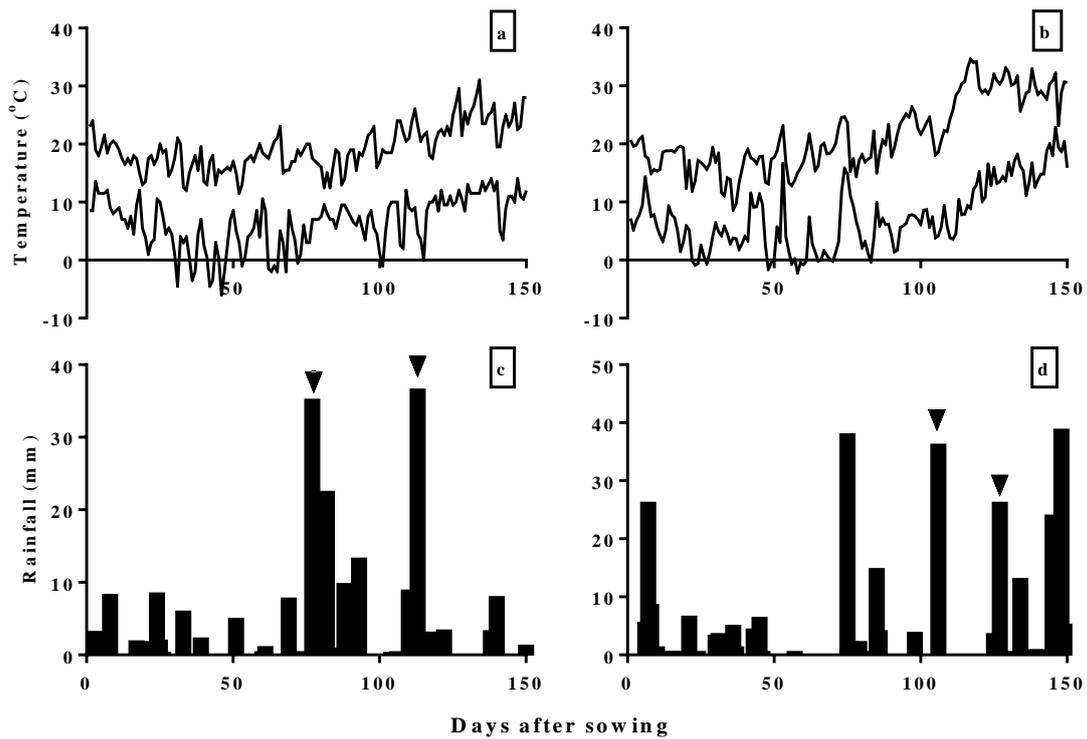


Figure 4.3: Daily maximum and minimum temperatures for 2014 (a) and 2015 (b) and rainfall for 2014 (c) and 2015 (d) at the water use efficiency experimental field site: Narrabri. Inverted arrows on the rainfall graphs show the amount and timing of irrigation water applied.

4.3.2 Seed yield

The combined two year seed yield average was 1722 kg ha^{-1} under irrigation and 1478 kg ha^{-1} under rainfed conditions (Figure 4.4a) with a range of 1223 to 2074 kg ha^{-1} under irrigation, and 1172 to 1849 kg ha^{-1} under rainfed conditions. Supplementary irrigation increased seed yield by 16.5% (Figure 4.4a). The average yield under no-till conditions was 1658 kg ha^{-1} which was 7.4% higher than the average yield under traditional tillage (Figure 4.4b). There was high seasonal variation with average yields in 2014 (1894 kg ha^{-1}) being significantly higher than in 2015 (1307 kg ha^{-1}) (Figure 4.4c).

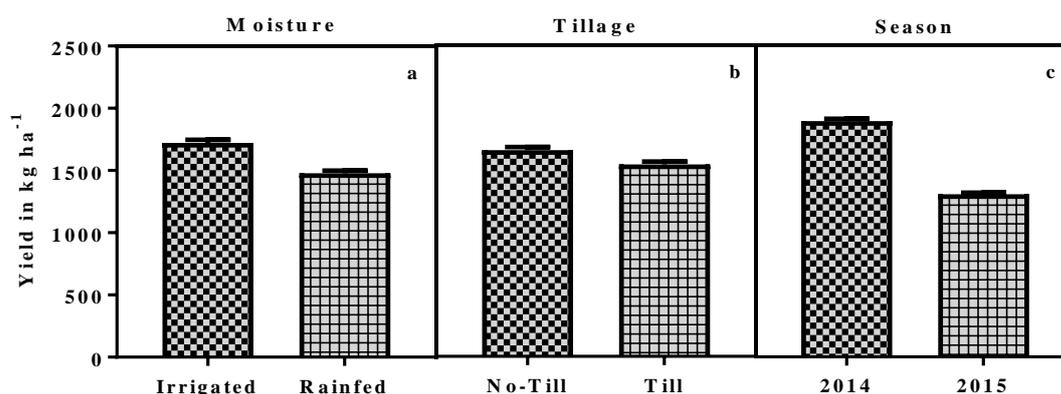


Figure 4.4: Mean chickpea grain yields under irrigation and rainfed conditions (a), no till and till systems (b), and different seasons (c). Error bars in the graph represent standard errors of the mean.

The highest yielding environment was the no-till, irrigated plot in 2014 with an average yield of 2148 kg ha⁻¹, whereas the lowest yield was from the standard till, rainfed plot in 2015 (Table 4.1). Sonali was the highest yielding genotype in both irrigated and rainfed no-till systems in 2014 with a yield of 2680 and 2210 kg ha⁻¹, respectively. The lowest yielding genotype in both environments was ICCV 05308 with a yield of 1446 and 1107 kg ha⁻¹ in irrigated and rainfed no-till systems, respectively. PBA Slasher had the highest yield in 2015 under no-till plus irrigation, whereas ICCV 96853 yielded the highest under no-till rainfed conditions. Genesis 079 had the highest yield under till plus irrigation in 2014, whereas Sonali had the highest yield under similar conditions in 2015. Sonali had the highest yield in 2014 under till and rainfed conditions, whereas PBA Slasher had the highest yield under the same conditions in 2015. However, the performance of these genotypes was not stable due to strong interactions among season, moisture regime and genotype.

Table 4.1: Mean chickpea seed yield (kg ha⁻¹) under different management and experimental conditions.

Genotype	No-Till		No-Till		Till		Till	
	Irrigated		Rainfed		Irrigated		Rainfed	
	2014	2015	2014	2015	2014	2015	2014	2015
AMETHYST	2336	1317	1360	1438	2227	1401	1725	972
AUSTIN	2019	1556	1409	1427	1785	1287	1673	1324
DOOLIN	2228	1570	1657	1439	1888	1306	1517	1150
FLIP 079C	2227	1044	1724	962	2100	1195	2092	1177

FLIPPER	1966	1344	1604	1053	1850	1485	1570	1063
GENESIS 079	2287	952	1756	900	2474	1301	1571	1183
GENESIS 090	1884	1476	1841	1330	2057	1335	1464	854
GENESIS KALKEE	1813	1012	1574	876	1623	863	1445	793
HOWARD	2013	1454	1705	1273	1848	1346	1629	1050
HOWZAT	2193	1370	1968	1471	2144	1262	1753	1256
ICCV 05308	1446	1293	1107	1338	1210	943	1650	1137
ICCV 96853	2557	1616	1990	1695	2340	1567	1890	1284
ICCV 98801	2266	1458	1668	1563	1968	1264	1887	1270
ICCV 98813	1544	1380	1290	1257	1654	1294	1291	1037
ICCV 98816	1986	1378	1428	1268	1615	1192	1702	1137
ICCV 98818	1769	1436	1637	1340	1693	1137	1535	1033
JIMBOUR	2428	1658	1796	1551	2075	1335	1854	1370
JIMBOUR#1	2049	1704	1703	1312	1916	1489	1775	1226
KYABRA	2171	1328	1904	1208	2076	1197	1933	1002
LYLE	2182	1506	1716	1244	1951	1270	1576	1212
LYONS	2128	1431	1616	1499	2047	1392	1579	1205
Mix 1 (Yorker/Jimbour)	2185	1493	1874	1284	1964	1292	1722	895
Mix 2 (Howzat/Flipper)	2170	1468	1592	1398	1987	1454	1668	1153
Mix 3 (Flipper/Jimbour)	2317	1455	1907	1388	1998	1308	1750	1120
Mix 4 (Yorker/Howzat)	2252	1360	1623	1468	2216	1363	1629	1037
Mix 5 (Howzat/Jimbour)	2368	1489	1983	1358	2207	1337	1823	1254
Mix 6 (Howzat/ 98813)	2295	1407	1769	1685	1932	1568	1792	1289
PBA HATTRICK	2340	1503	2000	1468	2154	1422	1778	1283
PBA SLASHER	2419	1859	1941	1326	2381	1635	1968	1388
PBA STRIKER	2257	1171	2063	1388	2232	1251	1716	1194
SAL	1850	1505	1608	1264	1806	1352	1513	1006
SIM	2050	1428	1648	1336	2065	1356	1737	1090
SONALI	2680	1492	2210	1666	2318	1675	2197	1324
THOMAS	2136	1627	1575	1251	1926	1164	1682	1242
TYSON	2460	1353	1965	1258	2285	1134	1839	1177
YORKER	2057	1434	1543	1296	1952	1220	1707	1024
Mean yield (kg ha ⁻¹)	2148	1426	1715	1341	1999	1316	1712	1145

Pooled SE	175	175	175	175	175	175	175	175
Pooled LSD @ 5%	348	348	348	348	348	348	348	348

4.3.3 Seed yield variation and interaction under different tillage and moisture regimes

There was a significant difference ($P < 0.001$) between the no-till and till systems with the no-till plots having higher yields than the till plots (Table 4.2). Irrigated plots had higher yields than the rainfed treatments. There was a significant difference ($P < 0.001$) in the yield of genotypes as well as their performance across the two seasons (2014 and 2015). There was a significant two-way interaction between year and tillage, year and moisture, and year and genotype, as well as a significant ($P < 0.001$) three-way interaction between tillage, moisture and year (Table 4.2), indicating that seed yield largely depends on seasonal weather conditions. The year effect was a key driver of the interaction and also explained a lot of the variation in the data.

Table 4.2: Wald statistic for main effects (tillage, moisture, genotype, season) and their interaction on chickpea seed yield

Fixed term	Wald statistic	
Tillage	60.15	***
Moisture	273.12	***
Genotype	401.57	***
Year	1641.74	***
Tillage.Moisture	0.85	
Tillage.Genotype	35.16	
Moisture.Genotype	42.51	
Tillage.Year	6.94	*
Moisture.Year	64.69	***
Genotype.Year	156.19	***
Tillage.Moisture.Genotype	41.12	
Tillage.Moisture.Year	15.67	***
Tillage.Genotype.Year	23.91	
Moisture.Genotype.Year	37.9	
Tillage.Moisture.Genotype.Year	30.46	

*= $P < 0.05$, ** = $P < 0.01$ and ***= $P < 0.001$

4.3.4 Water use

Soil water measurements at the start of the experiment showed that soil volumetric water content ranged from 354 – 453 mm in 2014, and 351 – 492 mm in 2015. There was higher average water use by plants under no till than till experimental plots in both years (Figure 4.5a). Water use under no till was 355 mm in 2014 and 301 mm in 2015. Plants under tillage used 332 mm water in 2014 and 296 mm in 2015 (Figures 4.5a and 4.5c, respectively). In general, more water was used in 2014 than 2015. Crops under irrigation used 359 mm in 2014 and 316 mm in 2015. Under rainfed conditions, crops used 328 mm in 2014 and 280 mm in 2015 (Figures 4.5b and 4.5d, respectively). Total water use in the 2014 growing season was 319 mm under the no-till rainfed regime, 278 mm in the till rainfed plots, 364 mm in no-till irrigated and 355 mm in the till irrigated plots. The total water use for 2015 was lower than in 2014 with no-till rainfed using 283 mm, till rainfed using 309 mm, no till irrigated using 364 mm and till irrigated using 355 mm of water.

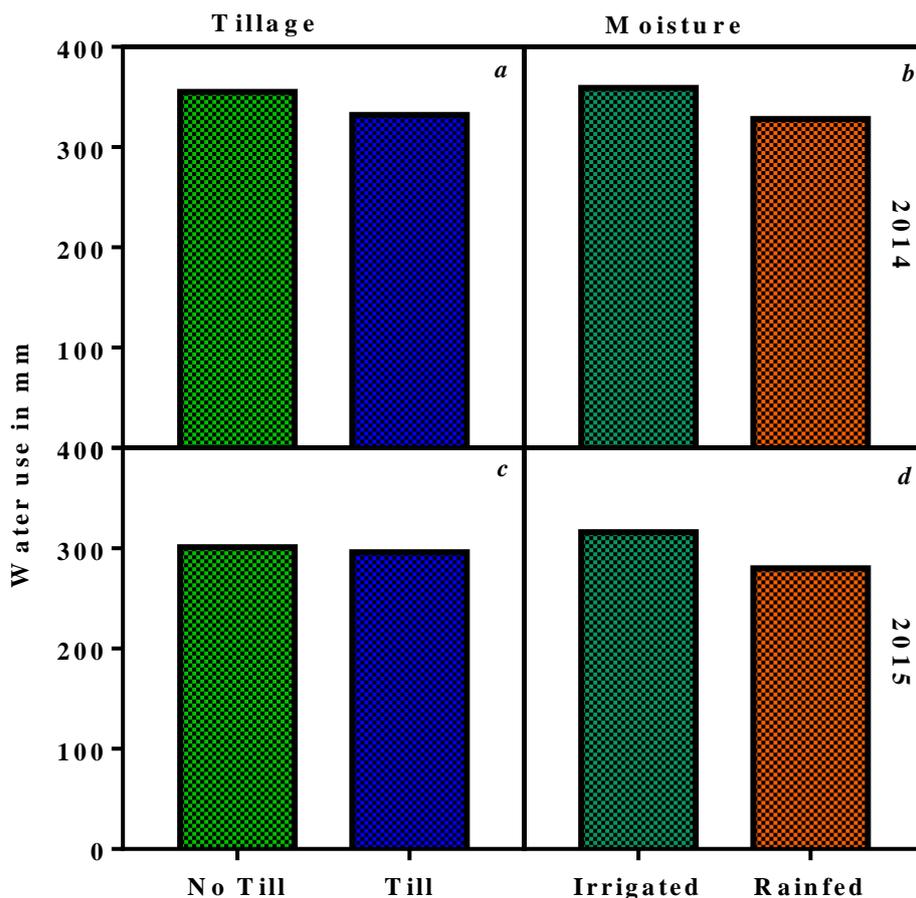


Figure 4.5: Mean chickpea water use under no till and till systems in 2014 (a) and 2015 (c), and under irrigation and rainfed conditions in 2014 (b) and 2015 seasons (d)

Plants accessed moisture in the top soil layer (up to 30 cm) in the early growing days and reached a peak extraction around the flowering period. In 2014, plants had deeper roots which extracted soil moisture from as far as 100 cm below the soil surface (Figure 4.6a), compared with a depth of 60 cm from flowering onwards in 2015 (Figure 4.6b). There was a sharp decline in soil water from flowering onwards in both 2014 and 2015 (Figures 4.6a and 4.6b). Soil moisture levels at 120 cm and 134 cm did not change over time meaning plants roots did not reach that far and deep water drainage was not occurring.

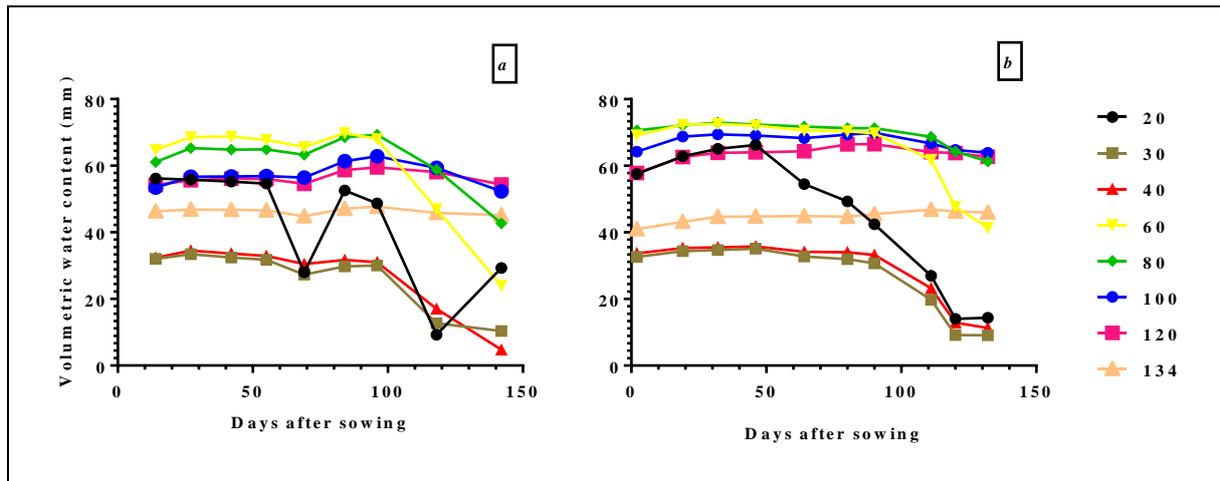


Figure 4.6: Mean volumetric water content (denoting root water access) at various soil depths during the growing season in 2014 (a) and 2015 (b). The legend on the right hand side shows soil depth in centimetres from the ground surface up to 134 cm deep in the soil profile.

4.4.5 Water use efficiency under different tillage and moisture regimes (individual analysis)

Water use efficiency under no-till irrigated conditions in 2014 ranged from 4.0 to 7.4 kg ha⁻¹ mm⁻¹ with a mean of 5.9 kg ha⁻¹ mm⁻¹. In total, 21 genotypes performed above the trial mean (Table 4.3). Under the same tillage and moisture conditions in 2015, WUE ranged from 3.0 to 5.8 kg ha⁻¹ mm⁻¹ with a mean of 4.5 kg ha⁻¹ mm⁻¹ with 22 genotypes above the trial mean. Under no-till and rainfed conditions, WUE ranged from 3.2 to 6.4 kg ha⁻¹ mm⁻¹ and 3.1 to 6.3 kg ha⁻¹ mm⁻¹ with means of 5.0 kg ha⁻¹ mm⁻¹ and 4.7 kg ha⁻¹ mm⁻¹ in 2014 and 2015, respectively (Table 4.3). The mean performance for WUE under till and irrigated conditions was 5.6 and 4.2 kg ha⁻¹ mm⁻¹ in 2014 and 2015, respectively (Table 4.3). The range in these conditions were 3.4 to 7.0 kg ha⁻¹ mm⁻¹ in 2014, and 2.7 to 5.2 kg ha⁻¹ mm⁻¹ in 2015, with 17 genotypes having better WUE than the trial mean in each year (Table 4.3). The range of WUE under till and rainfed conditions was 4.2 to 7.1 kg ha⁻¹ mm⁻¹ in 2014, and 2.8 to 5.2 kg ha⁻¹ mm⁻¹, with a mean of 5.5

kg ha⁻¹ m⁻¹ and 4.1 kg ha⁻¹ mm⁻¹ in 2014 and 2015, respectively. The number of genotypes that outperformed the trial mean in the same environments was 18 in 2014, and 19 in 2015 (Table 4.3). Of the eight environments tested, Sonali had the highest water use efficiency in five environments (no-till irrigated 2014, no-till rainfed 2014 and 2015, till rainfed 2014 and 2015), PBA Slasher in two (no-till irrigated 2015 and till irrigated 2015) and Genesis 079 in one environment (till irrigated 2014). The lowest WUEs were recorded in three environments for ICCV 05308 (no-till irrigated 2014, no-till rainfed 2014 and till-irrigated 2014), three for Genesis Kalkee (no-till rainfed 2015, till-irrigated 2015 and till rainfed 2015), with Genesis 079 and ICCV 98813 in one environment each (no-till irrigated 2015 and till rainfed 2014, respectively).

Table 4.3: Mean chickpea WUE among genotypes under different tillage, irrigation and seasonal conditions

Genotype	No-Till		No-Till		Till		Till	
	Irrigated		Rainfed		Irrigated		Rainfed	
	2014	2015	2014	2015	2014	2015	2014	2015
AMETHYST	6.4	4.2	3.9	5.0	6.3	4.3	5.6	3.3
AUSTIN	5.5	4.9	4.1	5.0	5.0	4.1	5.4	4.8
DOOLIN	6.1	4.9	4.8	5.1	5.3	4.2	4.9	4.1
FLIP 079C	6.1	3.3	5.0	3.4	5.9	3.8	6.7	4.2
FLIPPER	5.4	4.2	4.6	3.7	5.2	4.7	5.1	3.8
GENESIS 079	6.3	3.0	5.1	3.2	7.0	4.2	5.1	4.2
GENESIS 090	5.2	4.6	5.3	4.7	5.8	4.3	4.7	3.1
GENESIS KALKEE	5.0	3.2	4.6	3.1	4.6	2.7	4.7	2.8
HOWARD	5.5	4.6	4.9	4.5	5.2	4.3	5.3	3.8
HOWZAT	6.0	4.3	5.7	5.2	6.0	4.0	5.7	4.5
ICCV 05308	4.0	4.0	3.2	4.7	3.4	3.0	5.3	4.1
ICCV 96853	7.0	5.1	5.8	6.0	6.6	5.0	6.1	4.6
ICCV 98801	6.2	4.6	4.8	5.5	5.6	4.0	6.1	4.6
ICCV 98813	4.2	4.3	3.7	4.4	4.7	4.1	4.2	3.7
ICCV 98816	5.5	4.3	4.1	4.5	4.6	3.8	5.5	4.1
ICCV 98818	4.9	4.5	4.7	4.7	4.8	3.6	5.0	3.7
JIMBOUR	6.7	5.2	5.2	5.5	5.9	4.3	6.0	4.9
JIMBOUR#1	5.6	5.4	4.9	4.6	5.4	4.7	5.7	4.4

KYABRA	6.0	4.2	5.5	4.3	5.9	3.8	6.2	3.6
LYLE	6.0	4.7	5.0	4.4	5.5	4.1	5.1	4.4
LYONS	5.8	4.5	4.7	5.3	5.8	4.4	5.1	4.3
Mix 1 (Yorker/Jimbour)	6.0	4.7	5.4	4.5	5.5	4.1	5.6	3.2
Mix 2 (Howzat/Flipper)	6.0	4.6	4.6	5.0	5.6	4.6	5.4	4.1
Mix 3 (Flipper/Jimbour)	6.4	4.6	5.5	4.9	5.6	4.2	5.6	4.0
Mix 4 (Yorker/Howzat)	6.2	4.3	4.7	5.2	6.3	4.3	5.3	3.7
Mix 5 (Howzat/Jimbour)	6.5	4.7	5.7	4.8	6.2	4.3	5.9	4.5
Mix 6 (Howzat/ 98813)	6.3	4.4	5.1	5.9	5.4	5.0	5.8	4.6
PBA HATTRICK	6.5	4.5	5.8	5.0	6.4	4.9	5.7	4.7
PBA SLASHER	6.6	5.8	5.6	4.7	6.7	5.2	6.3	5.0
PBA STRIKER	6.2	3.7	6.0	4.9	6.3	4.0	5.5	4.3
SAL	5.1	4.7	4.6	4.5	5.1	4.3	4.9	3.6
SIM	5.6	4.5	4.8	4.7	5.8	4.3	5.6	3.9
SONALI	7.4	4.8	6.4	6.3	6.5	4.9	7.1	5.2
THOMAS	5.9	5.1	4.5	4.4	5.4	3.7	5.4	4.5
TYSON	6.7	4.2	5.6	4.5	6.1	3.8	6.0	4.0
YORKER	5.6	4.5	4.5	4.6	5.5	3.9	5.5	3.7
Mean	5.9	4.5	5.0	4.7	5.6	4.2	5.5	4.1
Pooled SE	0.66	0.58	0.66	0.58	0.66	0.58	0.66	0.58
Pooled LSD @ 5%	1.06	1.16	1.06	1.16	1.06	1.16	1.06	1.16

Where SE is the pooled standard error and LSD is the pooled least significant difference at 95% confidence interval.

4.3.6 Water use efficiency under different tillage and moisture regimes (combined analysis)

Combined analysis for WUE in the two years (2014 and 2015) was done for the four environments (no-till irrigated, no-till rainfed, till irrigated and till rainfed) and the range for no-till irrigated was 4.0 to 6.2 kg ha⁻¹ mm⁻¹ with a mean of 5.19 kg ha⁻¹ mm⁻¹ (Table 4.4). PBA Slasher had the highest WUE and ICCV 05308 had the lowest. Under the no-till rainfed system, the range for WUE was 3.8 to 6.4 kg ha⁻¹ mm⁻¹ with a mean of 5.85 kg ha⁻¹ mm⁻¹. Sonali had the highest WUE efficiency in this environment and Genesis Kalkee had the lowest. WUE ranged from 3.2 to 6.0 kg ha⁻¹ mm⁻¹ in the till and irrigated environment with a mean of 4.92

kg ha⁻¹ mm⁻¹ with PBA Slasher and ICCV 05308 having the highest and lowest WUE respectively. Under the no-till rainfed conditions, Sonali had the highest WUE and Genesis Kalkee the lowest with the range of 3.7 to 6.1 kg ha⁻¹ mm⁻¹ and a mean of 4.82 kg ha⁻¹ mm⁻¹ (Table 4.4).

Table 4.4: Mean chickpea WUE for combined analysis in 2014 and 2015*.

Genotype	No-Till	No-Till	Till	Till
	Irrigated	Rainfed	Irrigated	Rainfed
AMETHYST	5.3	4.5	5.3	4.4
AUSTIN	5.2	4.6	4.6	5.1
DOOLIN	5.5	4.9	4.7	4.5
FLIP 079C	4.7	4.2	4.9	5.5
FLIPPER	4.8	4.2	5.0	4.4
GENESIS 079	4.6	4.1	5.6	4.7
GENESIS 090	4.9	5.0	5.0	3.9
GENESIS KALKEE	4.1	3.8	3.7	3.7
HOWARD	5.0	4.7	4.8	4.5
HOWZAT	5.2	5.4	5.0	5.1
ICCV 05308	4.0	4.0	3.2	4.7
ICCV 96853	6.0	5.9	5.8	5.3
ICCV 98801	5.4	5.2	4.8	5.3
ICCV 98813	4.3	4.1	4.4	3.9
ICCV 98816	4.9	4.3	4.2	4.8
ICCV 98818	4.7	4.7	4.2	4.3
JIMBOUR	5.9	5.3	5.1	5.4
JIMBOUR#1	5.5	4.8	5.1	5.1
KYABRA	5.1	4.9	4.8	4.9
LYLE	5.4	4.7	4.8	4.7
LYONS	5.2	5.0	5.1	4.7
Mix 1 (Yorker/Jimbour)	5.3	5.0	4.8	4.4
Mix 2 (Howzat/Flipper)	5.3	4.8	5.1	4.8
Mix 3 (Flipper/Jimbour)	5.5	5.2	4.9	4.8
Mix 4 (Yorker/Howzat)	5.2	4.9	5.3	4.5
Mix 5 (Howzat/Jimbour)	5.6	5.3	5.2	5.2

Mix 6 (Howzat/ 98813)	5.4	5.5	5.2	5.2
PBA HATTRICK	5.5	5.4	5.7	5.2
PBA SLASHER	6.2	5.2	6.0	5.7
PBA STRIKER	4.9	5.4	5.1	4.9
SAL	4.9	4.6	4.7	4.3
SIM	5.1	4.7	5.1	4.8
SONALI	6.1	6.4	5.7	6.1
THOMAS	5.5	4.5	4.6	4.9
TYSON	5.4	5.1	5.0	5.0
YORKER	5.1	4.5	4.7	4.6
Mean	5.19	4.85	4.92	4.82
Pooled SE	0.56	0.56	0.56	0.56
Pooled LSD @ 5%	0.94	0.94	0.94	0.94

* LSD for the combined analysis (2014 and 2015) derived by including year in the random model

On average, no-till plants had a higher WUE ($5.02 \text{ kg ha}^{-1} \text{ mm}^{-1}$) than plants grown in the till plots ($4.87 \text{ kg ha}^{-1} \text{ mm}^{-1}$) and the irrigated plants ($5.05 \text{ kg ha}^{-1} \text{ mm}^{-1}$) had higher WUE than the rainfed ($4.84 \text{ kg ha}^{-1} \text{ mm}^{-1}$) (Figure 4.7-1 and 4.7-2, respectively). The highest environment mean for WUE was recorded in no-till irrigated (IRN) plots ($5.19 \text{ kg ha}^{-1} \text{ mm}^{-1}$) followed by till irrigated (IRC) ($4.92 \text{ kg ha}^{-1} \text{ mm}^{-1}$) (Figure 4.6-4). This was followed by no-till rainfed (RFN) ($4.85 \text{ kg ha}^{-1} \text{ mm}^{-1}$) and then till rainfed (RFC) ($4.82 \text{ kg ha}^{-1} \text{ mm}^{-1}$) which had the lowest WUE among the environments (Figure 4.7-4). Water use efficiency was higher in 2014 with a mean of $5.51 \text{ kg ha}^{-1} \text{ mm}^{-1}$ compared with 2015 with a mean of $4.38 \text{ kg ha}^{-1} \text{ mm}^{-1}$ (Figure 4.7-3).

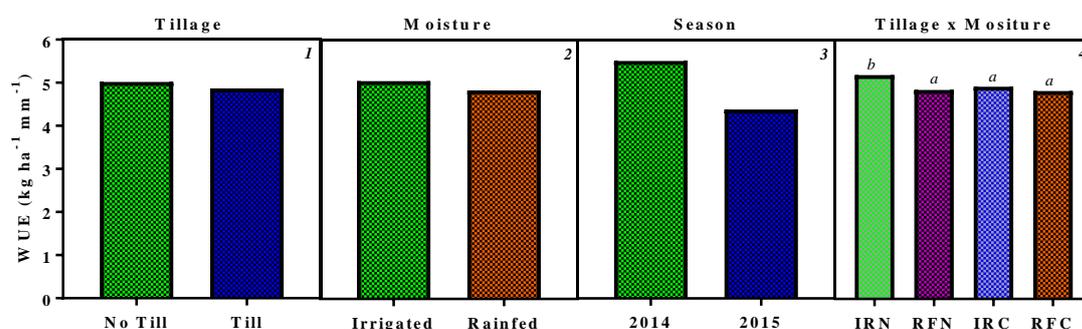


Figure 4.7: Chickpea WUE under different tillage (1), moisture (2), season (3) and tillage by

moisture interaction (4). IRN, irrigated no till; RFN, rainfed no till; IRC, irrigated till; and RFC, rainfed till. Different letters in the right panel (no.4) indicate significant difference at $P < 0.05$.

4.3.7 Genetic variation for water use and WUE under different tillage and moisture regimes

Water use was similar ($P > 0.05$) among the genotypes evaluated in both years (Table 4.5). However, there was a significant difference ($P < 0.01$ in 2014 and $P < 0.001$ in 2015, respectively) in water use between water regimes with more water being used under irrigation compared with rainfed conditions. There was a significant tillage effect ($P < 0.01$) on water use in 2014 but not in 2015. There was no significant interaction ($P > 0.05$) for water use among all the treatments.

Table 4.5: Variation for chickpea water use among genotypes under different tillage and moisture regimes

Source of variation	Mean sum of squares		
	2014	2015	Combined
Tillage	2096.3**	166.1	1365.9
Moisture	3971.5**	10000.0***	13932.1***
Genotype	815.7	105.2	2128.2
Tillage.Moisture	696.4	0.7	211.4
Tillage.Genotype	113.9	956.6	1275.1
Moisture.Genotype	549.3	895.2	876.4
Tillage.Moisture.Genotype	312.6	588.7	253.8
Residual	171.8	514.6	895.8

*= $P < 0.05$, ** = $P < 0.01$ and ***= $P < 0.001$

There were highly significant differences ($P < 0.001$) for the genotype, moisture, genotype and year main effects in both years (2014 and 2015) for all the environments except moisture main effect in 2015 (Table 4.6). Analysis for each individual year showed two way interactions between tillage and moisture for both years. Much of the variation in both years was accounted for by genotypic differences. Combined analysis for 2014 and 2015 showed that all the main effects were highly significant ($P < 0.001$) except for tillage which was significant at $P < 0.01$. In the combined analysis, significant two way interactions were observed in tillage by moisture, tillage by year, moisture by year, and genotype by year, whereas three way interactions were

observed for tillage by moisture by year. Much of the variation under the combined analysis was accounted for by variation in the year followed by genotypic differences.

Table 4.6: Components of variation in chickpea WUE in 2014 and 2015

Source of variation	Wald statistic		
	2014	2015	Combined
Tillage	6.15*	44.25***	10.28**
Moisture	69.07***	1.88	20.83***
Genotype	345.46***	173.41***	374.41***
Year			605.14***
Tillage.Moisture	40.18***	6.60*	5.71*
Tillage.Genotype	18.64	38.54	34.78
Moisture.Genotype	37.64	36.77	41.20
Tillage.Year			44.02***
Moisture.Year			46.98***
Year.Genotype			130.82***
Tillage.Moisture.Genotype	40.18	28.12	39.90
Tillage.Moisture.Year			40.28***
Tillage.Year.Genotype			24.68
Moisture.Year.Genotype			33.82
Tillage.Moisture.Year.Genotype			26.21

*=P<0.05, ** = P<0.01 and ***=P<0.001

4.3.8 Water use, water use efficiency and yield relationships under rainfed and irrigated conditions

There was a moderate positive correlation between water use and yield under rainfed conditions at $r^2 = 0.46$ (Figure 4.8a) and a high positive correlation between water use and yield under irrigated conditions $r^2 = 0.75$ (Figure 4.8c). The more the genotypes used water under irrigated conditions, the higher the yield. This was not the case always under rainfed conditions, where some genotypes would use a lot of water but the yield would still remain low. Water use efficiency was highly and positively associated with yield. However, the association was stronger with $r^2 = 0.96$ under irrigated conditions (Figure 4.8d) compared with rainfed conditions with $r^2 = 0.78$ (Figure 4.8b). Genotypes with high water use efficiency had the highest yield while those with low water use efficiency had the lowest yields.

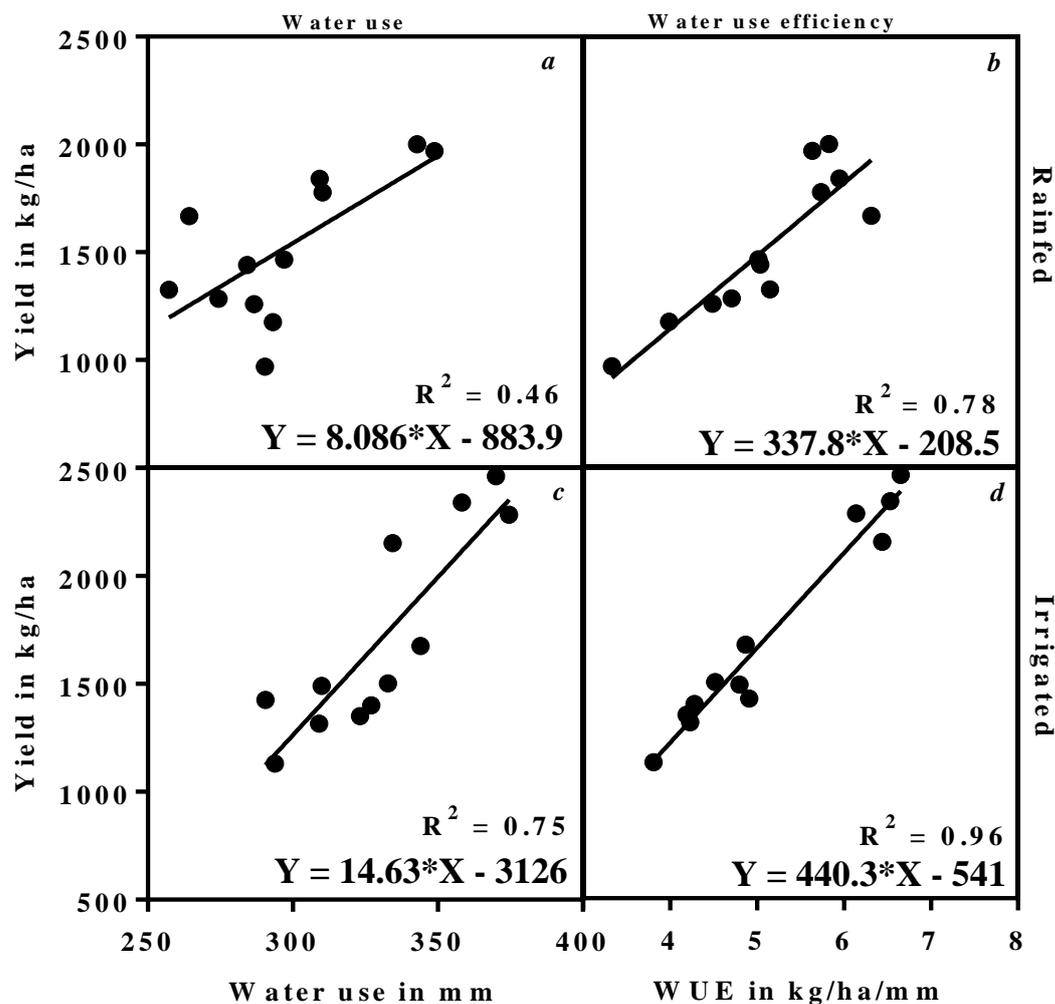


Figure 4.8: Relationships between water use, water use efficiency and yield. a) Water use vs yield under rainfed conditions, b) water use efficiency vs yield under rainfed conditions, c) water use vs yield under irrigated conditions d) water use efficiency vs yield under irrigated conditions

4.3.9 Heritability and genetic advance of WUE

Heritability was low under no-till systems with no-till irrigated, and no-till rainfed plants having heritability estimates of 36.4% and 43.3%, respectively (Table 4.7). High heritability was found under till systems where till rainfed had the highest heritability of 73% and till irrigated 71.3%. Genetic advance was higher under the till system compared with no-till which had moderate genetic advance.

Table 4.7: Heritability estimates and genetic advance for chickpea genotypes under different tillage and moisture regimes

Parameter	Heritability (%)	Genetic advance (GAM)
Till Irrigated	71.3	20.4
No-Till Irrigated	36.4	10.4
Till Rainfed	73.0	21.4
No-Till Rainfed	43.3	15.4

4.3.10 Genotypic, phenotypic and environment coefficient of variation for WUE under different tillage and moisture regimes

The genotypic coefficient of variation for WUE was low in all the four environments (Table 4.8). Phenotypic coefficient of variation was moderate in all the environments whereas environmental coefficient of variation was low under irrigated conditions and moderate under rainfed conditions irrespective of the tillage regime (Table 4.8).

Table 4.8: Coefficient of variation for WUE in different tillage and moisture regimes

Parameter	No-Till	No-Till	Till	Till
	Irrigated	Rainfed	Irrigated	Rainfed
Genotypic coefficient of variation	5.8	7.4	9.4	8.8
Phenotypic coefficient of variation	13.9	17.2	13.9	14.2
Environmental coefficient of variation	9.0	14.1	8.3	11.6

4.4 Discussion

The chickpea seed yields in the present study are similar to reports by Dalal et al. (1997) in their long-term experiment and Anwar et al. (2003) in their December sowing with full irrigation from flowering to podding. Supplementary irrigation applied twice at flowering and podding in this experiment increased seed yield with similar data reported by Silim and Saxena (1993) and Brown et al. (1989).

Chickpea water use was higher in the no-till than the tillage system. This may be due to higher moisture availability under the no-till system since water use in chickpea depends on the levels of soil water available as observed by Singh and Bhushan (1980) in an experiment conducted

in Dehra Dun in northern India. The higher soil water levels under a no till system may be a result of increased soil moisture conservation and storage (Verhulst et al., 2010, Marley and Littler, 1989, Felton et al., 1995), reduced soil temperatures and evapotranspiration due to the presence of crop residues which lower wind speeds at the soil surface (Hatfield et al., 2001, Jones et al., 1994). It may also be due to increased infiltration levels due to the presence of macropores formed by roots of the previous crop and earthworms in the soil profile. Water use in this experiment ranged between 296 mm to 355 mm on average, which was within the reported range by Anwar et al. (1999). However, Singh and Bhushan (1980) reported a range of 109 mm to 208 mm for rainfed experiments which was lower than in the present study. This may be due to different soil types, climate and soil moisture availability levels. There was no difference in the water use of the genotypes tested. Similar data have been reported by Brown et al. (1989). The plants used water from the top 30 cm during the vegetative phase and later accessed soil moisture deeper in the horizon. This was also reported by Brown et al. (1983).

Chickpea WUE was higher under no-till conditions than in the till system with similar findings reported by Herridge et al. (1995). WUE was higher under irrigated conditions than rainfed conditions. This was contrary to reports by Gan et al. (2010) who found that WUE was higher in rainfed conditions compared to irrigated conditions, whereas Anwar et al. (2003) did not find any significant differences between similar conditions. WUE was higher in 2014 than in 2015 which may have resulted from the weather conditions, especially rainfall distribution with higher rainfall in 2014 than 2015. More even rainfall distribution leads to better utilisation of soil moisture and consequently, higher grain yield. The diurnal range was lower in 2014 than in 2015 and plants also had deeper roots in 2014 than 2015 enabling them access to stored soil moisture from deep down the horizon. Such seasonal variation in WUE was also reported by Brown et al. (1989).

Water use efficiency among individual genotypes ranged from 3.2 to 6.4 kg ha⁻¹ mm⁻¹ under different tillage and moisture treatments based on a two year average. These values were in the range of findings by Gan et al. (2010) who reported WUEs between 5.3 to 6.7 kg ha⁻¹ mm⁻¹ in Saskatchewan. Dalal et al. (1997) reported a mean WUE value of 5.9 kg ha⁻¹ mm⁻¹ at Warra in Queensland, while Herridge et al. (1995) reported a mean of 5.8 kg ha⁻¹ mm⁻¹ in Glenhoma, New South Wales, whereas Beech and Leach (1988) reported 4.9 kg ha⁻¹ mm⁻¹ in Dalby, south eastern Queensland. The minor differences between the values in the present study and the ones reported by the other authors may be partly attributed to how water use was measured. One of the challenges in the present study was that the neutron probe access tubes were not

inserted in all the plots but only in the control plots. Water use for the other genotypes apart from the control genotypes was calculated using the average water use of the control genotypes in each environment type. This may have underestimated or overestimated water use efficiency of the other tested genotypes.

Genotypic variation in the tested genotypes was low; hence the need to diversify the genetic base of the materials in the present study through the introduction of new germplasm or hybridisation. Selection for genotypes with high WUE can be achieved under till systems in both rainfed and irrigated environments. This is because the tested genotypes showed high heritability and genetic advance scores under both tilled rainfed and irrigated systems. The high heritability recorded for plants grown under the till irrigated system may be associated with the breeding environment where these genotypes have been developed (Trethowan et al., 2012).

4.5 Conclusions

Chickpea genotypes in the present study did not show variation for water use but they varied significantly in their WUE. This variation can be exploited by choosing suitable parents contrasting for WUE to start a hybridisation program. Water use efficiency can be improved by adapting the no till system with supplementary irrigation if water is not limiting. However, if supplementary irrigation is not feasible, there are still yield benefits of planting chickpea under a no till system. More research is needed to identify more sources of genetic variation in chickpea which will enable breeding programs to develop new varieties with high water use efficiency.

CHAPTER 5: THE BASIS OF CHICKPEA YIELD FORMATION UNDER WATER LIMITED FIELD CONDITIONS.

5.1 Introduction

According to the Food and Agriculture Organization (FAO, 1983), drought is defined as ‘the percentage of years when crops fail from lack of moisture’. Agricultural drought is considered as a period where there is a decline in soil moisture which will eventually lead to crop failure (Mishra and Singh, 2010). The balance between plant water demand and supply is critical and water stress occurs if the demand outstrips the supply, especially in the top soil layer where there is a higher concentration of nutrients, soil microorganisms and root activity (Kulik, 1962). Water stress causes water limitation in the soil, hence limiting the amount of water available for crop growth and development.

Water stress can occur at any point in the growing season with varied effects on the crop. Intermittent drought occurs at any time during the growing season due to rainfall breaks, whereas terminal drought occurs towards the end of the growing season due to a steady decline in soil moisture (Canci and Toker, 2009). Chickpea is mainly grown on residual soil moisture in Australia and, as such, suffers from terminal drought (Sedgley et al., 1990, Turner, 2003, Leport et al., 1998, Krishnamurthy et al., 2010) with up to 50% yield losses (Varshney et al., 2013b). However, these yield losses can range from 30% to 100% depending on the environment, type of drought and genotype (Leport et al., 1999).

Drought tolerance research is imperative in identifying genotypes which can perform well in water limited environments. Sojka et al. (1981) defined drought tolerance as the ability of a plant to minimise yield losses under water limited conditions. Screening genotypes for yield potential and assessing their performance under differing moisture regimes is a key starting point in drought tolerance research (Ahmad et al., 2003). Various screening methodologies have been proposed which include selection of genotypes under water stressed conditions (Ceccarelli and Grando, 1991), selection under well-watered conditions (Betran et al., 2003, Richards, 1996) and selection under both well-watered and water stressed conditions (Fischer and Maurer, 1978, Clarke et al., 1992).

Plant breeders are mainly guided by yield while selecting for drought tolerance, hence proper screening and selection is necessary (Ganjeali et al., 2011). Different selection indices, which compare yield loss in stress conditions to normal conditions, have been established to aid in

the selection for drought tolerance (Mitra, 2001, Farshadfar et al., 2013). These indices have been used to identify drought tolerant genotypes in chickpea (Ganjeali et al., 2011), wheat (Talebi et al., 2009, El-Rawy and Hassan, 2014), barley (Nazari and Pakniyat, 2010), sunflower (Gholinezhad et al., 2014, Darvishzadeh et al., 2011), and oats (Akcura and Ceri, 2011). The indices provided a weighted method of identifying drought tolerant genotypes without entirely relying on yield which can give erroneous result.

Selecting genotypes that have high yield under water stressed conditions may also translate to high yield potential in well-watered conditions (Blum, 1988). However, Rosielle and Hamblin (1981) posited that selection of these genotypes under stress environments may not necessarily lead to high yields under well-watered conditions. A better approach would be to understand the physiological basis of yield formation under water limited environments and use these traits to select for drought tolerance. Selection of physiological traits, which are drought adaptive, coupled with high yield, potentially results in a plant with high yield and physiological shock absorbers against drought (Blum, 1983). The identification of traits of interest that can be used as an indirect selection criterion in a breeding or introgression program is referred to as physiological breeding (Jackson et al., 1996). Traits can be identified by using either the black box approach or the ideotype approach. In the black box approach, genotypes are evaluated under stress conditions and trait association with economic performance is measured, whereas under the ideotype approach, the desired traits in an ideal genotype in a given target environment are predicted (Fischer, 1981). In both methods, the target environment should be as close as possible to the treatments being administered in all the plots to minimise the occurrence of confounding factors that can affect trait expression (Reynolds et al., 2001).

By using physiological breeding strategies (Reynolds et al., 2012), coupled with selecting for drought tolerance using drought indices, one can identify drought tolerant genotypes that can perform well in water stressed and well-watered conditions. The research question is whether certain traits can be selected to confer drought tolerance in chickpea, and whether drought tolerance indices can be used to identify these marker traits in the field?

The aims of this chapter are to: i) identify drought tolerant and drought susceptible genotypes that can either be grown directly by farmers or used as parents in a breeding program, ii) identify the phenological, morphological and physiological basis of drought tolerance, iii) identify the most suitable selection indices for drought tolerance in chickpea, and iv) identify

phenological, morphological and physiological marker traits to aid selection of drought tolerant genotypes during the active growing season.

5.2 Materials and methods

A total of 36 entries were grown over two years (2014 and 2015) at the IA Watson Plant Breeding Institute in Narrabri, as described in the general Materials and Methods in Chapter 3. For the purposes of this chapter, only the well-watered and water stressed treatments are considered because yield differences between no-till and till were minimal, and there was no tillage by genotype interaction effect.

Data on phenology, physiological and morphological traits were recorded from the vegetative stage through to maturity during the growing season. Grain was harvested from a 4 m by 2 m plot for each entry and data recorded. Data recorded included percent early ground cover. This was done by taking pictures using a Nikon™ camera of the plot to cover four rows and then it was analysed using the CSIRO Canopy Cover Software to give percent ground cover. Days to first flower was recorded as the day the first open flower was sighted in a plot. Days to 50% flowering was recorded as day when 50% of the plants in a plot have at least one open flower. Days to last flower was recorded as the day when the last open flower was sighted in the plot. Flower duration was calculated as days to last flower minus the days to first flower. Normalised Difference Vegetation Index (NDVI) measurements were done using a Greenseeker™ machine at early podding and late podding. Plant height was measured using a ruler from the base of the stem at ground level to the tallest growing tip at late flowering and late podding. Chlorophyll content was measured using a SPAD meter at mid and late podding stages. Number of leaflets per leaf was counted by getting an average of 10 fully grown leaves per plot sampled at the fifth leaf from the top at flowering. Single leaf area was obtained by measuring with a ruler average leaf area from 5 leaves sampled from 5 plants, 1 leaf per plant at flowering. Single leaflet size and length were measured using a ruler as an average of 10 fully grown leaves per plot sampled at the fifth leaf from the top at flowering. Number of pods per plant was obtained by counting and obtaining the mean of 5 representative plants per plot at maturity. Pod biomass was obtained by taking a sample of 5 plants in a plot, drying them and weighing their mass and then getting the average mass of the 5 plants. Pod harvest index was calculated as seed yield from pod biomass samples divided by pod biomass whereas shoot harvest index was calculated by grain yield divided by biological yield. One thousand weight was obtained by sampling 100 seeds at 10% moisture content and weighing them and multiplying by 10.

Various drought susceptibility indices (Table 5.1) were calculated from the yield data collected. They included mean relative performance (Rosielle and Hamblin, 1981, Reddy et al., 2009) where a higher value denotes tolerance, and relative efficiency index (Singh et al., 2011) which selects genotypes with high yield potential and are drought tolerant with high values being desirable. High values according to the stress tolerance index (Fernandez, 1992), drought resistance index (Lan, 1998), yield index (Gavuzzi et al., 1997) and yield stability index (Bousslama and Schapaugh, 1984) are correlated with drought tolerance.

Linear regression was run for the drought indices and yield using the formula

$$Y_i = \alpha + \beta X_i + \varepsilon_i$$

Where Y_i is the score for the dependent variable for the i^{th} term, $a + b X_i$ are a linear function relating X (of the i^{th} term) to Y , and e_i is the error term.

Heritability estimates were estimated using the formula in equation 5.1 (Knapp and Bridges, 1987).

$$H = (\sigma^2_g) / (\sigma^2_g + (\sigma^2_{ge}/e) + (\sigma^2_e/re)) \quad (5.1)$$

Where H is the broadsense heritability, σ^2_g is the genotypic variance, σ^2_{ge} is the genotype by environment interaction variance, σ^2_e is the error variance, e is the number of environments (years) and r is the number of replications.

Genetic advance (GA) was calculated as shown in the equation 5.2 (Singh and Chaudhary, 1979) below and then converted to a percentage of the mean.

$$GA = ((K * \sqrt{\sigma^2_p} * H^2) / \bar{X}) * 100 \quad (5.2)$$

Where $\sqrt{\sigma^2_p}$ is the phenotypic standard deviation, H^2 is the heritability and K is the selection differential at 5% selection intensity (2.06).

Yield data was analysed using Genstat® edition 18 by subjecting it to generalised linear mixed models (GLM). Tillage regime, water regime and genotypes were fitted in the fixed model whereas the range and row nested into years were fitted in the random model. Mean yield for well-watered and water stressed conditions were tabulated and used to calculate the drought indices. Physiological and morphological traits explaining most of the variation under water limited conditions were identified by regressing the traits against grain yield in multiple linear regressions. All traits that did not significantly explain variation in yield in each run were

eliminated until all the traits that remained were significant at the 95% confidence interval. Selection of drought indices was done using principal component analysis and plotting a principal component scatter plot to observe their relationships with each other and the genotypes.

Table 5.1: Drought tolerance indices for evaluating chickpea yield under water-limiting conditions

Index	Abbreviation	Equation	Equation no.
Mean Relative Performance	MRP	$(Y_{si}/Y_s) + (Y_{pi}/Y_p)$	(5.3)
Relative Efficiency Index	REI	$(Y_{si}/Y_s) * (Y_{pi}/Y_p)$	(5.4)
Stress Tolerance Index	STI	$(Y_{si} * Y_{pi}) / (Y_p)^2$	(5.5)
Drought Resistance Index	DRI	$(Y_{si} *(Y_{si}/Y_{pi})) / (Y_s)$	(5.6)
Yield Index	YI	Y_{si} / Y_s	(5.7)
Yield Stability Index	YSI	Y_s / Y_p	(5.8)

Where Y_{si} is the yield under stress for the i^{th} genotype, Y_{pi} is the yield under well-watered conditions for the i^{th} genotype, Y_s is the mean grain yield under stress conditions and Y_p is the mean grain yield under well-watered conditions.

5.3 Results

5.3.1 Phenological, morphological and physiological traits for yield formation under water stressed conditions

Twenty-one traits accounted for 91% of the total variation in yield from the multiple linear regression (Table 5.2). The traits included phenological, morphological, physiological and yield components with confidence levels ranging from $p < 0.05$ to $p < 0.001$. Important phenological traits include days to first flower, days to 50% flowering and days to last flower. Flowering is important, especially in areas where there is water limitation towards the end of the growing season. Early flowering ensures there is adequate soil moisture at the reproductive phase in contrast to late flowering where there is high risk of soil water deficit and a loss in yield potential. Important morphological traits included leaf characteristics and plant height. Leaf area plays a key role in water loss through the transpiration stream – large leaf surface areas lose more water compared with small surface areas. Important physiological traits include NDVI, chlorophyll content and early ground cover. A high NDVI during the reproductive phase was associated with high yield, however a high NDVI towards the end of the growing season was associated with low yield. Similar to NDVI, a high chlorophyll content at mid podding was associated with high yield and low yield towards the end of the growing season.

Early season ground cover resulted in high yields at the end of the season. Yield component traits that explained much of the variation in grain yield included the number of pods per plant, pod and shoot biomass, pod and shoot harvest index and 1000 seed weight. Moderate biomass for pod and shoot, as well as moderate seed weight, resulted in high yields at the end of the growing season. A high harvest index is desirable since it resulted in high yields as well.

All the traits measured had high heritability (greater than 60%) apart from NDVI at early podding which had a low heritability of 43% (Table 5.2). Thousand seed weight had the highest heritability of 99% closely followed by morphological traits (leaf characteristics) and phenological traits (days to first flower, days to 50% flowering and flower duration, except days to last flower which was lower than the rest). Physiological traits and yield component traits had notably lower heritability estimates compared with phenological and morphological traits. Early ground cover, flowering duration, NDVI at late podding, leaf area and leaflet length, number of pods per plant, pod biomass, shoot biomass, shoot harvest index and one thousand seed weight had high heritability estimates and genetic advance. The lowest genetic advance was recorded for the pod harvest index and NDVI at early podding stage.

Table 5.2: Traits explaining variation in chickpea yield under water stressed conditions, correlations with grain yield, heritability and genetic advance

Trait	Wald			
	statistic	Correlation	Heritability	GA (%)
Early ground cover (%)	14.2**	0.10	79.6	50.5
Days to first flower	31.66***	-0.18	97.0	14.2
Days to 50% flowering	18.63***	-0.23	95.3	12.4
Days to last flower	24.69***	-0.36*	78.0	2.6
Flowering duration (days)	24.62***	0.12	95.2	29.7
NDVI at early podding	58.92***	0.55*	43.0	4.7
NDVI at late podding	8.32*	-0.52*	83.7	31.0
Plant height at late flowering	20.72***	0.10	88.9	14.5
Plant height at late podding	29.84***	0.04	92.5	14.9
Chlorophyll content at mid podding (SU)	5.38*	0.02	71.7	7.5
Chlorophyll content at late podding (SU)	9.61**	-0.35*	73.3	16.6
Number of leaflets per leaf	13.42**	-0.10	96.3	11.7
Single leaf area (cm ²)	25.64***	-0.04	98.3	89.7

Single leaflet area (cm ²)	35.79***	-0.03	98.4	91.0
Leaflet length (cm ²)	28.16***	0.02	97.7	37.4
Number of pods per plant	11.43**	-0.18	74.7	50.4
Pod biomass per plant (g)	19.11***	-0.31	85.7	82.7
Pod harvest index	9.6**	0.10	56.2	3.5
Shoot biomass	25.85***	-0.41*	84.7	67.2
Shoot harvest index	47.88***	0.24	84.5	22.9
One thousand seed weight (g)	9.05**	-0.39*	99.1	53.1

Where SU is SPAD Units, * = P<0.05, ** = P<0.01 and *** = P<0.001

5.3.2 Grain yield and drought indices

Grain yield ranged from 1222 kg ha⁻¹ to 2074 kg ha⁻¹ under well-watered conditions and 1170 kg ha⁻¹ to 1850 kg ha⁻¹ under water stressed conditions (Table 5.3). On average, the well-watered moisture regime resulted in a higher yield (1722 kg ha⁻¹) than the water stressed moisture regime (1478 kg ha⁻¹) with drought causing a 14% reduction in grain yield. The highest yielding genotype under well-watered conditions was PBA Slasher followed by Sonali, whereas under water limited conditions, Sonali was the highest yielding genotype. By ranking the genotypes based on their performance in well-watered and water stressed conditions, Sonali, PBA Slasher, ICCV 96853 and Jimbour were classified as stable, whereas Amethyst dropped from a ranking of 7 to 30, and Genesis 079 dropped from a ranking of 14 to 31 under well-watered and water stressed conditions, respectively (Table 5.3). This demonstrates that Amethyst and Genesis 079 have high yield potential but are vulnerable to water stressed conditions, hence the high loss in grain yield. Based on the grain yield ranking and drought indices, PBA Slasher, Sonali, ICCV 96853 and Jimbour were identified as drought tolerant, whereas Amethyst and Genesis 079 were drought susceptible. All the indices ranked Sonali as the most tolerant genotype except for the yield stability index which ranked it seventh.

Table 5.3: Grain yield and drought tolerance indices for chickpea genotypes grown under well-watered and water stressed conditions

Genotype	Grain yield (kg ha^{-1}) (WW)	Grain yield (kg ha^{-1}) (WS)	Rank under WW	Rank under WS	MRP	REI	STI	DI	YI	YSI
PBA SLASHER	2074	1657	1	3	2.33	1.35	1.16	0.77	1.12	0.75
SONALI	2041	1850	2	1	2.44	1.48	1.27	0.97	1.25	0.88
ICCV 96853	2020	1714	3	2	2.33	1.36	1.17	0.84	1.16	0.82
JIMBOUR	1873	1643	4	4	2.20	1.21	1.04	0.84	1.11	0.91
PBA HATTRICK	1855	1630	5	6	2.18	1.19	1.02	0.83	1.10	0.80
Mix 5 (Howzat/Jimbour)	1850	1605	6	8	2.16	1.17	1.00	0.81	1.09	0.77
AMETHYST	1818	1372	7	30	1.98	0.98	0.84	0.60	0.93	0.81
TYSON	1806	1562	8	11	2.11	1.11	0.95	0.78	1.06	0.88
Mix 6 (Howzat/ 98813)	1800	1632	9	5	2.15	1.15	0.99	0.86	1.10	0.85
Mix 4 (Yorker/Howzat)	1799	1441	10	22	2.02	1.02	0.87	0.67	0.97	0.93
JIMBOUR#1	1791	1503	11	14	2.06	1.06	0.91	0.73	1.02	1.07
Mix 2 (Howzat/Flipper)	1771	1455	12	18	2.01	1.01	0.87	0.69	0.98	0.85
Mix 3 (Flipper/Jimbour)	1771	1540	13	12	2.07	1.07	0.92	0.78	1.04	0.92
GENESIS 079	1756	1352	14	31	1.93	0.93	0.80	0.60	0.91	0.83
LYONS	1751	1473	15	16	2.01	1.01	0.87	0.72	1.00	0.90
DOOLIN	1749	1441	16	21	1.99	0.99	0.85	0.69	0.97	0.92
HOWZAT	1743	1614	17	7	2.10	1.10	0.95	0.87	1.09	0.88
ICCV 98801	1738	1598	18	9	2.09	1.09	0.94	0.85	1.08	0.84
Mix 1 (Yorker/Jimbour)	1735	1445	19	20	1.98	0.98	0.85	0.70	0.98	0.89
LYLE	1727	1440	20	23	1.98	0.98	0.84	0.70	0.97	0.83
PBA STRIKER	1727	1589	21	10	2.08	1.08	0.92	0.85	1.07	0.84
SIM	1723	1452	22	19	1.98	0.98	0.84	0.71	0.98	0.83
THOMAS	1713	1434	23	24	1.96	0.96	0.83	0.70	0.97	0.82
KYABRA	1695	1514	24	13	2.01	1.01	0.87	0.79	1.02	0.87
GENESIS 090	1688	1374	25	29	1.91	0.91	0.78	0.65	0.93	0.80
YORKER	1666	1392	26	26	1.91	0.91	0.78	0.68	0.94	0.87
HOWARD	1663	1415	27	25	1.92	0.92	0.79	0.70	0.96	0.91
AUSTIN	1661	1459	28	17	1.95	0.95	0.82	0.74	0.99	0.88
FLIPPER	1659	1322	29	33	1.86	0.86	0.74	0.61	0.89	0.80
FLIP 079C	1642	1489	30	15	1.96	0.96	0.82	0.78	1.01	0.92
SAL	1628	1348	31	32	1.86	0.86	0.74	0.65	0.91	0.83
ICCV 98816	1544	1385	32	28	1.83	0.84	0.72	0.72	0.94	0.84
ICCV 98818	1510	1387	33	27	1.82	0.82	0.71	0.74	0.94	0.91
ICCV 98813	1469	1216	34	35	1.68	0.70	0.60	0.58	0.82	0.84

GENESIS KALKEE	1328	1170	35	36	1.56	0.61	0.52	0.60	0.79	0.87
ICCV 05308	1222	1309	36	34	1.59	0.63	0.54	0.81	0.89	0.84

Where WW is well watered, WS is water stressed, MRP is mean relative performance, REI is relative efficiency index, STI is stress tolerance index, DI is drought resistance index and YI is yield index.

5.3.3 Grain yield relationships under well-watered and water stressed conditions

There was a moderately strong positive relationship between grain yield under well-watered and water stressed conditions (Figure 5.1). This shows that genotypes with the highest yield potential under well-watered conditions generally yielded well under water stressed conditions as well although there were some exceptions. This sort of plasticity is important in plant breeding programs.

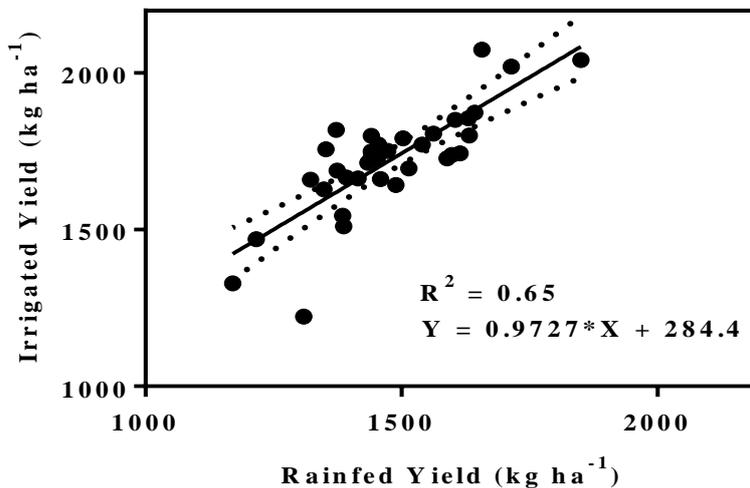


Figure 5.1: Relationship between irrigated (well-watered) and rainfed (water stress) yield for the different chickpea genotypes analysed for drought tolerance

5.3.4 Correlation analysis for grain yield and drought indices

All the slopes had a significant ($P < 0.05$) deviation from zero except for yield stability index which was non-significant ($P > 0.05$). The intercepts and slopes were also different. The mean relative performance index was highly and positively correlated with grain yield for both well-watered and water stressed conditions with a coefficient of determination (R^2) of 0.91 and 0.90, respectively (Figure 5.2a). This implies selecting for genotypes with a high relative performance index will lead to high yield potential. Both relative efficiency index and stress tolerance index have similar coefficient of determinations for well-watered and water stressed

conditions. Under well-watered conditions the R^2 was slightly lower at 0.89 than under water stressed conditions ($R^2 = 0.91$) (Figure 5.2b and 5.2c). The drought resistance index had a weak and positive relationship with grain yield under well-watered conditions, however it was not significant (Figure 5.2d). Still, this index had a high and positive relationship with grain yield under water stressed conditions suggesting its suitability for selection under drought stress conditions. The yield index had a moderate positive correlation with grain yield, and a strong positive correlation with grain yield under well-watered and water stressed conditions respectively (Figure 5.2e). However, the yield stability index was not associated with grain yield in either well-watered or water stressed conditions (Figure 5.2f).

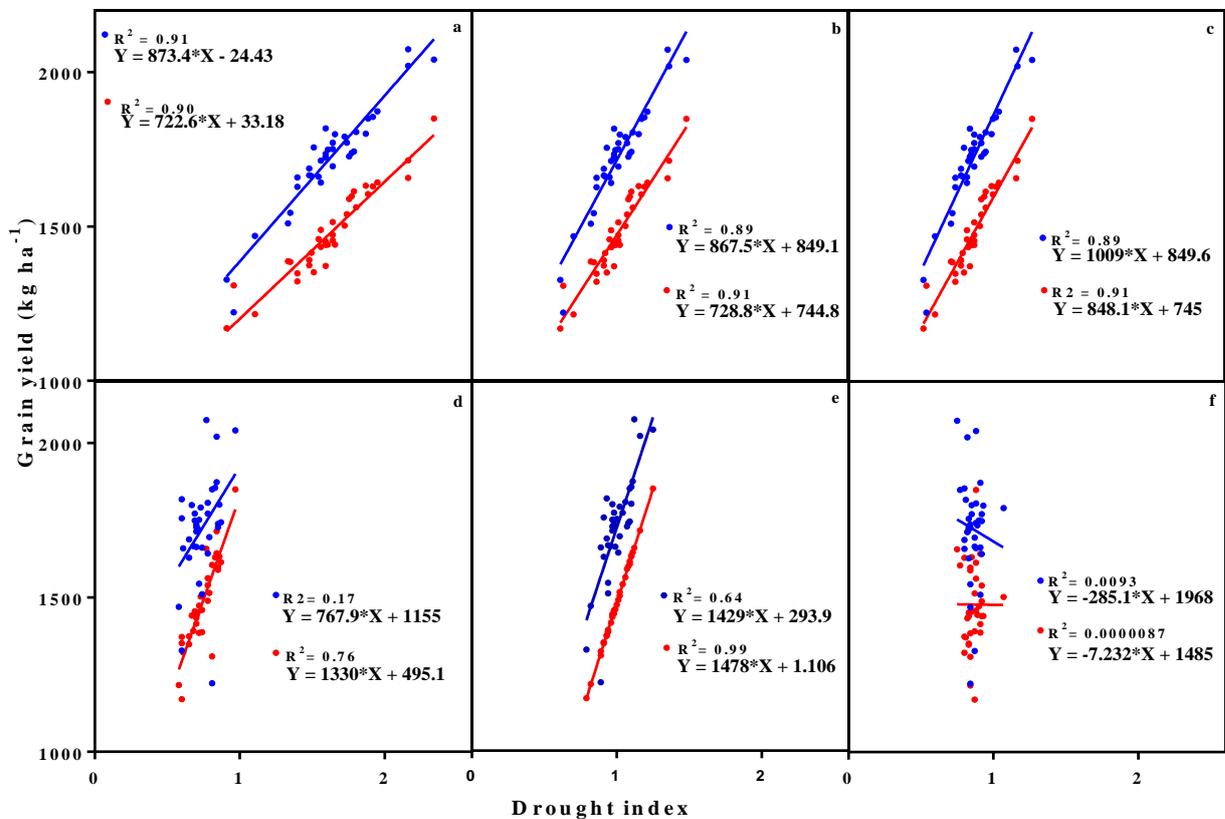


Figure 5.2: Linear regression of chickpea grain yield against six drought indices shown for well-watered (blue) and water-stressed (red) growing conditions. Blue data points represent well-watered conditions and red data points represent water stressed conditions. Each plot represents grain yield on the Y-axis and a specific drought index on X-axis where a) is mean relative performance, b) is relative efficiency index, c) stress tolerance index, d) is drought resistance index, e) is yield index and f) is yield stability index.

5.3.5 Selection of the best drought tolerance index for chickpea

The first principal component explained 92.72% of the total variation in drought tolerance, whereas the second principal component explained 4.47% of the total variation (Figure 5.3). Genotypes 7, 9 and 14 (PBA Slasher, Sonali and ICCV 96853, respectively) clustered near each other and are considered drought tolerant, whereas the drought susceptible entries 1 and 12 (Amethyst and Genesis 079, respectively) clustered together when analysed by the different drought indices (Figure 5.3). The drought response index, stress tolerance index, mean relative performance and relative efficiency index were the most discriminating for identifying drought tolerant genotypes, whereas the yield index and yield stability index were not able to efficiently identify drought tolerant genotypes. The stress tolerance index, mean relative performance and relative efficiency indices were positively correlated to each other. These indices were also positively correlated with the other indices except for the yield stability index.

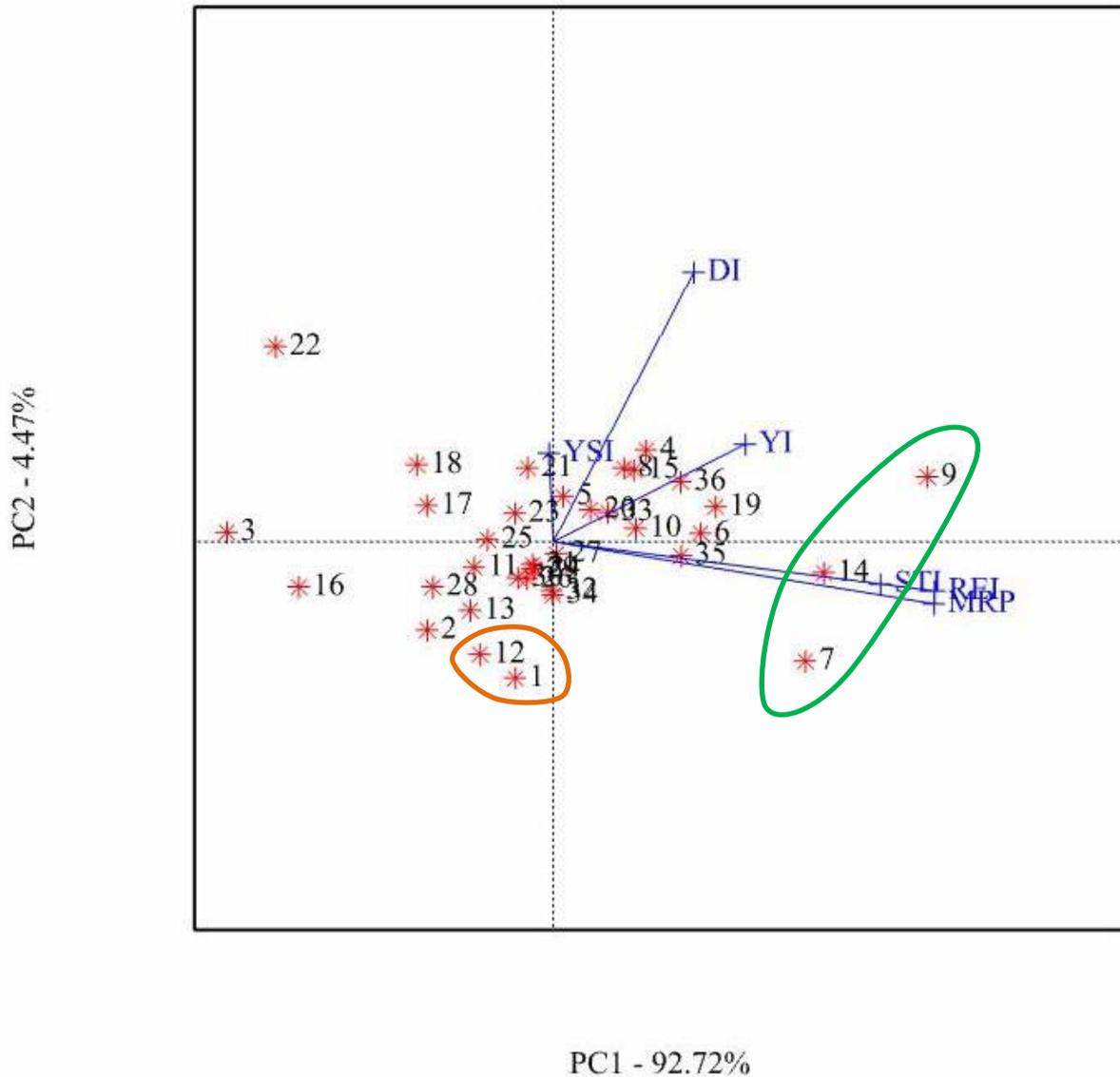


Figure 5.3: Principal component scatter plot for chickpea genotypes and drought indices. MRP, mean relative performance; REI, relative efficiency index; STI, stress tolerance index; DI, drought resistance index; YI, yield index. The green oval shape groups the drought tolerant genotypes and the orange oval shape groups drought susceptible genotypes.

5.3.6 Effect of water deficit on important traits associated with chickpea grain yield under water limited conditions

In general, water deficit caused the reduction of trait means except for a few instances where the means increased. Early ground cover had a mean of 20.4% which was reduced by 7% under water stressed conditions compared with well-watered conditions (Table 5.4). Most phenological traits had minimal change except in flowering duration which decreased by 13.2%, thus; genotypes under well-watered conditions flowered almost five days later

compared with water stressed conditions. There was a 1.9% reduction in NDVI during early podding compared with a 42.2% reduction in NDVI at late podding in water stressed compared with well-watered conditions. This is probably indicative of the difference in soil moisture from early podding to the late podding stages. Plant height was shorter under water stressed than well-watered conditions with a 5.7% and 9.1% reduction at the mid and late podding stages, respectively. On the contrary, chlorophyll content at the mid and late podding stages increased by 4.1% and 1.9%, respectively, under water stressed conditions. Number of leaflets per leaf also increased from an average of 13.7 under well-watered conditions, to 14 under water stressed conditions, denoting a 1.9% increase. Other leaf traits including single leaf area, single leaflet area and leaflet length decreased by 10.2%, 12.3% and 4.6%, respectively, under water stressed conditions. Yield components were more affected by water stress compared with the other traits analysed. The numbers of pods per plant were reduced from 38.9 to 31.3 when plants were exposed to water stressed conditions. Pod biomass and shoot biomass were reduced by 28.4% and 25.1%, respectively, under water deficit conditions. The pod harvest index was similar between the treatments (0.79 to 0.80) whereas and the shoot harvest index reduced by 2.2% by the water stress conditions. One thousand seed weight increased from 212 g to 217 g under water stressed conditions denoting a 2.2% increase (Table 5.4).

Table 5.4: Trait means and per cent change due to water deficit in chickpea genotypes

Trait	Trait mean (WW)	Trait mean (WS)	Change (%)
Early ground cover (%)	20.4	19.1	-7.0
Days to first flower	87.4	86.6	-1.0
Days to 50% flowering	98.2	97.2	-1.1
Days to last flower	127.6	122.0	-4.5
Flowering duration	40.2	35.5	-13.2
NDVI at early podding	0.7	0.7	-1.9
NDVI at late podding	0.5	0.3	-42.2
Plant height at late flowering	62.9	59.5	-5.7
Plant height at late podding	70.0	64.1	-9.1
Chlorophyll content at mid podding (SU)	67.7	70.6	4.1
Chlorophyll content at late podding (SU)	56.9	58.0	1.9
Number of leaflets per leaf	13.7	14.0	1.9

Single leaf area (cm ²)	7.7	7.0	-10.2
Single leaflet area (cm ²)	0.6	0.5	-12.3
Leaflet length	1.3	1.2	-4.6
No of pods per plant	38.9	31.3	-24.4
Pod biomass per plant (g)	13.9	10.9	-28.4
Pod harvest index	0.8	0.8	1.1
Shoot biomass (cm ²)	28.3	22.6	-25.1
Shoot harvest index	0.4	0.4	-2.2
One thousand seed weight	212.0	216.8	2.2

Where SU is SPAD Units and NDVI is normalised difference vegetation index.

5.3.7 Associations between trait relationships and chickpea drought indices

The phenological, morphological, physiological and yield component traits were associated with drought indices either positively or negatively but not all associations were significant (Table 5.5). Days to 50% flowering and days to last flower had a negative and significant correlation with drought resistance index but did not have any significant relationship with the other drought indices. The NDVI at early podding was significantly and positively associated with all the indices, except for drought resistance index, where the association was not significant, and yield stability index where the association was negative (Table 5.5). The NDVI at late podding had a negative and significant relationship with all the indices, except for yield stability index, where the association was not significant at the 95% confidence interval. The chlorophyll content at late podding was significantly and negatively correlated with all the indices except drought response index and yield stability index. However, chlorophyll content at mid podding was not significantly associated with any of the drought indices. Leaflet length had a positive and significant relationship with the drought response index only. Pod biomass per plant had a significant and negative correlation with mean relative performance, relative efficiency index, and stress tolerance index, and a non-significant relationship with yield index and yield stability index. Similar relationships were observed between these indices and shoot biomass also except the yield index was significantly and negatively related. Thousand seed mass was significantly and negatively correlated with all the drought indices except for drought resistance index and yield stability index. In general, mean relative performance, relative efficiency index and stress tolerance index were correlated with the indices in a similar fashion closely followed by the yield index. These indices were mainly correlated with physiological traits and yield components. The drought resistance index exhibited a different trend from the

other indices but was significantly correlated with phenology (days to 50% flowering and days to last flower), morphological traits (leaflet length), physiological traits (NDVI at late podding). The yield stability index was not significantly correlated with any trait.

Table 5.5: Correlation between drought indices and important traits in chickpea grown under water deficit conditions

Trait	MRP	REI	STI	YI	DI	YSI
Early ground cover	0.14	0.14	0.14	0.10	0.01	0.04
Days to first flower	-0.09	-0.11	-0.11	-0.18	-0.32	0.08
Days to 50% flowering	-0.14	-0.16	-0.16	-0.23	-0.35	0.06
Days to last flower	-0.27	-0.29	-0.29	-0.36	-0.44	0.14
Flower duration	0.03	0.05	0.05	0.12	0.26	-0.05
NDVI at early podding	0.62	0.61	0.61	0.55	0.31	-0.17
NDVI at late podding	-0.56	-0.56	-0.56	-0.52	-0.36	-0.08
Plant height at late flowering	0.15	0.12	0.12	0.10	-0.02	0.10
Plant height at late podding	0.06	0.04	0.04	0.04	-0.03	-0.02
Chlorophyll content at mid podding (SU)	-0.03	-0.03	-0.03	0.02	0.08	0.10
Chlorophyll content at late podding (SU)	-0.42	-0.40	-0.40	-0.35	-0.17	0.06
Number of leaflets per leaf	-0.11	-0.10	-0.10	-0.10	-0.07	-0.19
Single leaf area (cm ²)	-0.24	-0.20	-0.20	-0.04	0.31	-0.09
Single leaflet area (cm ²)	-0.23	-0.19	-0.19	-0.03	0.32	-0.07
Leaflet length	-0.17	-0.13	-0.13	0.02	0.34	-0.08
Number of pods per plant	-0.22	-0.22	-0.22	-0.18	-0.03	-0.01
Pod biomass per plant (g)	-0.48	-0.45	-0.45	-0.31	0.05	-0.07
Pod harvest index	0.29	0.26	0.26	0.10	-0.23	0.01
Shoot biomass (cm ²)	-0.56	-0.54	-0.54	-0.41	-0.05	-0.02
Shoot harvest index	0.19	0.21	0.21	0.24	0.30	-0.07
1000 seed mass	-0.55	-0.51	-0.51	-0.39	-0.06	-0.09

MRP, mean relative performance; REI, relative efficiency index; STI, stress tolerance index; DI, drought resistance index; YI, yield index; YSI, yield stability index; SU, SPAD units. Figures in bold indicate significance at a 95% confidence interval ($p < 0.05$).

5.4 Discussion

Plant breeders and growers require genotypes that are high yielding in non-stress conditions and have minimal yield losses under stress conditions (Ud-Din et al., 1992). It is therefore

imperative to consider rankings coupled with selective indices because a single drought tolerance selection criteria may be misleading (Khalili et al., 2012). There was a significant correlation ($R^2 = 0.65$) between non-stress yield and water-stress yield suggesting that some genotypes that yield highly under non-stress conditions also yield highly under stress conditions. This means that direct selection of chickpea genotypes under non-stress conditions may be a predictor of good performance under stress conditions.

The best drought tolerance indices should have a high correlation with both non-stress yield and stress yield (Mitra, 2001, Blum, 1988). This helps in selecting genotypes which show plasticity such that in years with adequate rainfall, these genotypes take advantage of adequate moisture and give higher yields, and in years with low rainfall, they still produce and do not experience total crop failure. The relative efficiency index, stress tolerance index, drought resistance index, yield index had stronger correlations with yield in stressed plants compared with non-stress yield. These findings concur with those reported by (Sahar et al., 2016). The relative efficiency index, stress tolerance index, drought resistance index and yield index had a significant and positive relationship with yield and this is in agreement with findings by Kumar et al. (2014), Sahar et al. (2016) and Singh et al. (2011) in studies conducted in rice, bread wheat and sorghum, respectively. Stress tolerance index had a positive and significant correlation with non-stress yield with a coefficient of determination of 0.91. Similar data were reported by Nazari and Pakniyat (2010) in barley genotypes whereas Talebi et al. (2009) reported an R^2 of 0.79 in durum wheat which was slightly lower. Stress tolerance index was a better predictor of drought tolerance than mean relative performance (Talebi et al., 2009, Nazari and Pakniyat, 2010) which is in agreement with data reported in the present study. This is because stress tolerance index was highly correlated with yield and it identified genotypes with high yield potential and high drought tolerance. Stress tolerance index and relative efficiency index were identical based on the biplot analysis indicating similar genotype rankings with respect to drought tolerance. Based on the biplot constructed from the principal component analysis (PC1 and PC2), Mean relative performance, relative efficiency index and stress tolerance index were closely related and were the best predictors to identify drought tolerant genotypes in chickpea with high yield potential.

Since grain yield is highly affected by the interaction between genotype and environment, it is more practical to identify traits that are associated with yield under water stressed environments and use them as selection criteria (Ludlow and Muchow, 1990). Twenty one phenological, morphological and physiological traits were identified as important in explaining yield

variation under water stressed conditions (Table 5.3). Ramamoorthy et al. (2016) identified days to 50% flowering, shoot biomass at maturity, harvest index and number of pods as important traits under water stressed conditions. These are among the 21 traits identified in the present study. Early ground cover was associated with high yielding genotypes at the end of the growing season. This may be attributed to the fact that there is high moisture loss from the ground as a result of evaporation, hence early ground cover reduces these losses (Siddique et al., 2001). Early flowering genotypes performed better than late maturing genotypes in the present study because genotypes that mature early are able to avoid terminal drought at the end of the growing season (Toker et al., 2007).

Genotypes with high NDVI values at the early podding stage and high chlorophyll content at the mid podding stage had high yields and were drought tolerant. These data are similar to other reports (Maalouf et al., 2011). However, genotypes that had high NDVI values and chlorophyll content values towards the end of the growing season were low yielding under water limited conditions. Genotypes with small leaves had higher yields under water stressed environments probably due to reduced evaporative surface area thereby conserving water in the soil. This may also be attributed to the fact that smaller leaves contribute to an increased rate of partitioning to grains (Ramamoorthy et al., 2016).

Low shoot biomass in the present study was associated with low yields under water stressed conditions. This was contrary to reports by Kashiwagi et al. (2015) who found higher shoot biomass led to high yields and better drought tolerance under water stressed conditions. This discrepancy may be due to the different genotypes used in the experiments and the differences in the environments.

The shoot harvest index indicates the ability of a plant to partition assimilates and the reallocation of stored assimilates into grain yield (Turner et al., 2001). Shoot harvest index, number of pods per plant and days to first flower are important traits to consider under water limited conditions with similar findings reported by (Toker and Canci, 2005). Mean shoot harvest index was 0.39, which is slightly lower than the 0.42 reported by Siddique et al. (2001) in an experiment conducted at Mullewa in Western Australia. Genotypes with high shoot harvest index are normally high yielding under water stressed conditions (Krishnamurthy et al., 2013, Beebe et al., 2008).

High heritability coupled with genetic advance is favourable because it implies additive gene action or cumulative contribution of alleles in the formation of a phenotype), whereby the effect

of environment on genotype is minimal. Selecting for such traits is attractive to the plant breeder because it means faster genetic gains can be made. Days to 50% flowering had high heritability which is similar to data reported by Ramamoorthy et al. (2016). The 1000 seed mass had the highest heritability in the present study which is similar to findings by Hamwieh and Imtiaz (2015) and Ramamoorthy et al. (2016) who reported heritability estimates of 84-97% and 96% under water stressed conditions, respectively. Hay (1995) reported a high heritability estimate for harvest index which is similar to data in the present study.

Water deficit reduced the expression of most traits except for chlorophyll content, number of leaflets per leaf, pod harvest index and 1000 seed mass. Days to first flower, days to 50% flowering and days to last flower were earlier than in the non-stress conditions with similar findings reported by (Ramamoorthy et al., 2016). There was a slight reduction in NDVI at the early podding stage, however, there was a 42% difference in NDVI at the late podding stage between water stressed and well-watered conditions. The lower NDVI at late podding may be attributed to leaf senescence due to water stressed conditions. Plants were shorter under water stressed conditions than in well-watered conditions most likely due to a reduction in cell expansion and enlargement due to low plant water status (Manivannan et al., 2007). There was a reduction in leaf area and number of pods per plant under water stressed conditions compared with the well-watered conditions and similar findings were reported by Randhawa et al. (2014). Water stressed conditions caused a 25% reduction in shoot biomass which may be attributed to reduced cell division as a result of impaired cyclin dependent kinase activity (Schuppler et al., 1998a).

Since drought tolerance indices are based on yield, one has to wait until harvesting is completed to compute them and select the genotypes which show tolerance (El-Hendawy et al., 2017). However, by use of traits that are associated with these indices in the field during the active crop growth period, plant breeders can engage in early selection of promising genotypes which will eventually be drought tolerant. NDVI was positively and significantly correlated with mean relative performance, relative efficiency index, stress tolerance index and yield index at the early and late podding stages. A similar finding was reported by El-Hendawy et al. (2017) in an experiment using spring wheat lines where NDVI was correlated with yield index and stress tolerance index. Other stress tolerance indicator traits based on mean relative performance, relative efficiency index, stress tolerance index and yield index include chlorophyll content at late podding which can be measured during the active crop growth period. Days to 50% flowering, days to last flower and leaflet length can be used as a proxy

for drought resistance index but may not provide adequate information since drought resistance index is not as accurate in identifying drought tolerant chickpea genotypes with high yield potential. Yield components (pod biomass, shoot biomass and 1000 seed mass) are analysed at the same time as grain and can be used to confirm the crop performance with respect to drought tolerance at the end of the season.

The identification of traits associated with drought tolerance in the field gives plant breeders an ability to engage in early selection of drought tolerant genotypes while still actively growing in the field. This also helps the breeder look at other market preferred traits as well as agronomic appearance of the genotype to help in decision making.

5.5 Conclusions

Grain yield under water stressed and well-watered conditions was positively correlated. Hence, selection for high yield potential under similar environments can lead to high yields under water stressed conditions. Sonali, PBA Slasher and ICCV 96853 were identified as drought tolerant genotypes with high yield potential. These genotypes can be used as parents in a chickpea breeding program to improve drought tolerance of existing commercial cultivars, or grown directly by farmers since they are released varieties. Growing these genotypes can give high yields under well-watered conditions and have low yield penalty under water stressed conditions, providing more profitability and risk mitigation for the grower. Use of yield ranking scores coupled with drought indices is recommended for the identification of high potential genotypes with drought tolerance. In the present study, mean relative performance, relative efficiency index and stress tolerance index were identified as the best indices for identifying drought tolerant chickpea genotypes. High heritability coupled with genetic advance can be used to identify traits that are controlled by additive gene action. Some of these traits include flowering duration, early ground cover, NDVI at late podding, number of pods per plant, leaf area and leaflet length, shoot biomass, pod biomass, 1000 seed mass and shoot harvest index. Water stress reduced the expression of several characters with NDVI at late podding, number of pods per plant, pod and shoot biomass being the traits most affected. Several traits were identified as markers for drought tolerance during the active chickpea growing season. By using NDVI at the early podding and late podding stages, as well as chlorophyll content at late podding, one can identify genotypes with potentially high yield and high drought tolerance.

CHAPTER 6: EFFECT OF GENOTYPE BY ENVIRONMENT BY MANAGEMENT INTERACTIONS ON CHICKPEA PHENOTYPIC STABILITY

6.1 Introduction

In Australia, the main chickpea growing regions are Northern New South Wales and Queensland which have a sub-tropical climate, and Western Australia which has a Mediterranean climate (Wells, 2013). It is also grown in smaller acreages in South Australia and Victoria. Narrabri, which is in northwest New South Wales, has a summer dominant rainfall with a median annual rainfall ranging from 600-800 mm (Dang et al., 2015). Chickpea in this area is grown during winter which is characterised by high temperatures towards the end of the growing season as well as low and variable in-season rainfall (Freebairn et al., 1991). This variance makes repeatability of yield results difficult and a challenge for plant breeders and growers alike who aim to sustain yields under various growing environments. In an effort to stabilise yield results, various management options are adopted including no-till practices and supplementary irrigation. No-till systems are beneficial because they improve soil structure (Page et al., 2013), increase soil aggregate stability (Chan and Mead, 1988, Li et al., 2007) and improve water storage (Radford et al., 1995, Felton et al., 1995) as a result of increased infiltration rates and reduced water evaporation. The increase in infiltration rate may be attributed to earthworm activity and plant roots from the previous crop which creates continuity of macropores.

While certain adaptable genotypes can perform well in a diverse range of environments, some only perform well in specific environments. The mean performance of a genotype denotes its average performance whereas the stability measure indicates its variability across a number of environments (Yan et al., 2001). The lack of stability in yield is influenced by the genotype by environment interaction (Fox and Geiger). This interaction complicates the selection of genotypes in a breeding program by offsetting expected responses (Pande et al., 2013, Gauch and Zobel, 1997). It is further complicated by the fact that not all stable genotypes are high yielding across a wide range of environments; thus, they may be highly stable but have low yield potential implying stability alone is not necessarily a good thing.

To dissect the Genotype x Environment Interaction (GxE), it is imperative to perform multi-environments trials (MET) which entail growing genotypes across a wide range of environments (Annicchiarico, 2002). Multi-environment trials data analysis allows one to

decipher the relationships between environments and explores the possibility of grouping these environments into mega-environments.

By subdividing the environment into smaller homogeneous environments (mega-environments), plant breeders can have more environment specific genotypes, thus presenting the opportunity of exploiting repeatable GxE across years (Gauch and Zobel, 1997, Yan et al., 2001). Alternatively, they can develop superior genotypes across a range of environments which show a high level of phenotypic stability and yield potential (Kanouni et al., 2015). For breeders to do this, they need to incorporate appropriate selection methods that integrate high yield potential and stability (Gauch et al., 1996). The genotype main effect and genotype by environment interaction (Staggenborg and Vanderlip, 2005) biplot allows for the selection of genotypes which are stable and have high yield potential, while addressing mega-environment differentiation at the same time, thus matching genotype performance with the mega-environment (Yan et al., 2001). The GGE biplot simultaneously provides a visualisation of stability, mean performance and delineates the mega-environments providing plant breeders with a powerful analysis tool (Yan and Kang, 2002). The ideal genotypes in a biplot should exhibit high principal component (PC) 1 scores which denote high yields and low PC2 scores which represent high stability (Hamayoon et al., 2011). The ideal environment discriminates genotypes based on genetic differences as well as the target environment for which they are selected for (Gauch and Zobel, 1997). The genotype (G) and the GxE are the main sources of variation in the biplot genotype evaluation whereas the environment (E) is not relevant in biplot analysis (Yan and Tinker, 2006, Gauch and Zobel, 1997). The GGE biplot thus takes G and GxE into account and excludes the environmental and residual effect.

Extensive research on genotype stability has been carried out using various stability measures (Lin et al., 1986). However, little attention has been paid to selecting chickpea genotypes that are both stable and have high yield potential. The hypothesis for this chapter was there was GxE in the evaluated chickpea genotypes and that the test environments were highly discriminating and representative.

The objectives of this chapter were to: i) measure the extent of genotype by environment interaction in chickpea grown under varying environmental conditions, ii) explore the possibility of delineating the target environments into mega-environments, iii) identify stable chickpea genotypes with high yield potential and iv) identify the best performing genotypes for specific mega-environments.

6.2 Materials and methods

A field experiment was conducted at the IA Watson research station at The University of Sydney in Narrabri, northwest New South Wales as described under the general Materials and Methods in Chapter 3. The total number of entries was 36 (as listed in Table 3.1 in Chapter 3) and they were planted in an alpha lattice design replicated twice each year and grown for two years. The entries were planted in a combination of no till and till, with and without irrigation. Every combination in each year was considered as a separate environment to give a total of eight environments (Table 6.1).

Yield data were analysed using Genstat® edition 18 to determine the effect of season on yield variation. This was done by using REML analysis and fitting tillage, moisture regimes, genotypes and year in the fixed model, and range and row in the random model. Further analysis was performed to determine if there was GxE in the tested materials by using each tillage by moisture by year combination as a single environment. Genotype by environment was assigned to the treatment structure whereas the replicate was assigned to the blocking structure. GGE biplots were constructed using the GGE function in Genstat®. Weather data (temperature, rainfall and rainfall distribution) for each genotype at the vegetative, flowering and podding phenophases were computed and analysed to determine the means for each phenophase.

Table 6.1: Field environments with different tillage and moisture regimes for analysis of chickpea phenotypic stability

Environment	Code	Management regime
1	IRC14	Irrigation, under tillage, 2014 season
2	IRC15	Irrigation, under tillage, 2015 season
3	IRN14	Irrigation, under no till, 2014 season
4	IRN15	Irrigation, under no till, 2015 season
5	RFC14	Rainfed, under tillage, 2014 season
6	RFC15	Rainfed, under tillage, 2015 season
7	RFN14	Rainfed, under no till, 2014 season
8	RFN15	Rainfed, under no till, 2015 season

6.3 Results

6.3.1 Weather data

There were significant differences ($P < 0.05$) in all the weather parameters measured in 2014 and 2015, except for minimum temperature at the flowering phase (Table 6.2). Mean minimum temperature was lower in 2014 compared with 2015 with a similar trend observed in mean maximum temperature in 2014 compared to 2015. Rainfall was lower in 2014 with 74.7 mm recorded during the vegetative phase compared with 2015 which received almost double the amount (140.9 mm). Rainfall events were more common in 2015 with 28 rainy days recorded compared with 22 in 2014. Mean minimum temperature at flowering was similar in both years at 7.5°C, whereas the mean maximum temperature at the same phenophase was almost 5°C lower in 2014 (20.7°C) compared with 2015 (25.3°C). Rainfall was more than double, and rain events close to sixfold, in 2014 at the flowering phase compared with 2015 at a similar phenophase. The mean minimum temperature at the podding phase was more than 3°C lower in 2014 (11.3°C) than 2015 (14.6°C), with the same trend observed in the mean maximum temperatures of 25.3°C and 30.2°C in 2014 and 2015, respectively. Rainfall distribution was slightly better in 2015 than in 2014. In general, the 2015 season was hotter than the 2014 season and also had higher rainfall although it was poorly distributed.

Table 6.2: Average weather conditions for each environment experienced by chickpea genotypes analysed for phenotypic stability

Phenophase	Weather code	IRN	RFN	IRC	RFC	IRN	RFN	IRC	RFC	2014	2015
		14	14	14	14	15	15	15	15	means	means
Vegetative	MnT	4.7	4.7	4.7	4.6	5.5	5.2	5.5	5.2	4.7 ^a	5.3 ^b
	MxT	17.2	17.2	17.2	17.2	19.7	19.3	19.7	19.2	17.2 ^a	19.4 ^b
	RF	79.1	73.7	75.4	70.6	141.8	140.2	141.4	140.2	74.7 ^a	140.9 ^b
	RD	23.4	22.3	22.5	21.6	28.5	28.0	28.4	28.0	22.4 ^a	28.2 ^b
Flowering	MnT	7.7	7.4	7.7	7.3	8.1	7.2	7.8	7.0	7.5 ^a	7.5 ^a
	MxT	21.0	20.5	20.9	20.3	25.9	25.0	25.5	24.6	20.7 ^a	25.3 ^b
	RF	78.6	50.0	81.9	53.1	43.0	7.6	46.7	10.5	65.9 ^a	27.0 ^b
	RD	12.5	13.2	13.5	13.9	2.9	1.5	3.2	2.0	13.2 ^a	2.4 ^b
Podding	MnT	11.5	11.0	11.5	11.1	15.0	14.3	14.8	14.2	11.3 ^a	14.6 ^b
	MxT	25.9	24.8	25.7	25.0	30.1	30.3	30.2	30.4	25.3 ^a	30.2 ^b
	RF	47.3	11.0	47.1	9.9	46.6	17.1	43.2	16.1	28.8 ^a	30.7 ^b

RD	4.5	2.1	4.3	2.0	5.9	4.0	5.4	3.4	3.2 ^a	4.7 ^b
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MnT, mean minimum temperature; MxT, mean maximum temperature; RF, rainfall; RD, rainfall distribution. Environment codes are listed in Table 6.1. Means followed by a different letter in each row denotes that they are significantly different at $P < 0.05$.

6.3.2 Grain yield under different environments

Chickpea mean grain yield was higher in 2014 than in 2015 with different environments producing different yields. In general, no till environments had higher yields than till, and irrigated environments yielded more than rainfed. The highest yielding environment was IRN14 with a mean of 2148 kg ha⁻¹ followed by IRC14 at 1999 kg ha⁻¹ (Figure 6.1). RFC14 and RFN14 environments had very similar grain yields of 1712 kg ha⁻¹ and 1714 kg ha⁻¹, respectively. The environment with the lowest yield was RFC15 with a mean of 1145 kg ha⁻¹. The environment yield ranking was; IRN14 > IRC14 > RFN14 > RFC14 > IRN15 > RFN15 > IRC15 > RFC15. There was more grain yield variability in 2014 than in 2015 with IRC15 and IRN15 environments resulting in very similar grain yield.

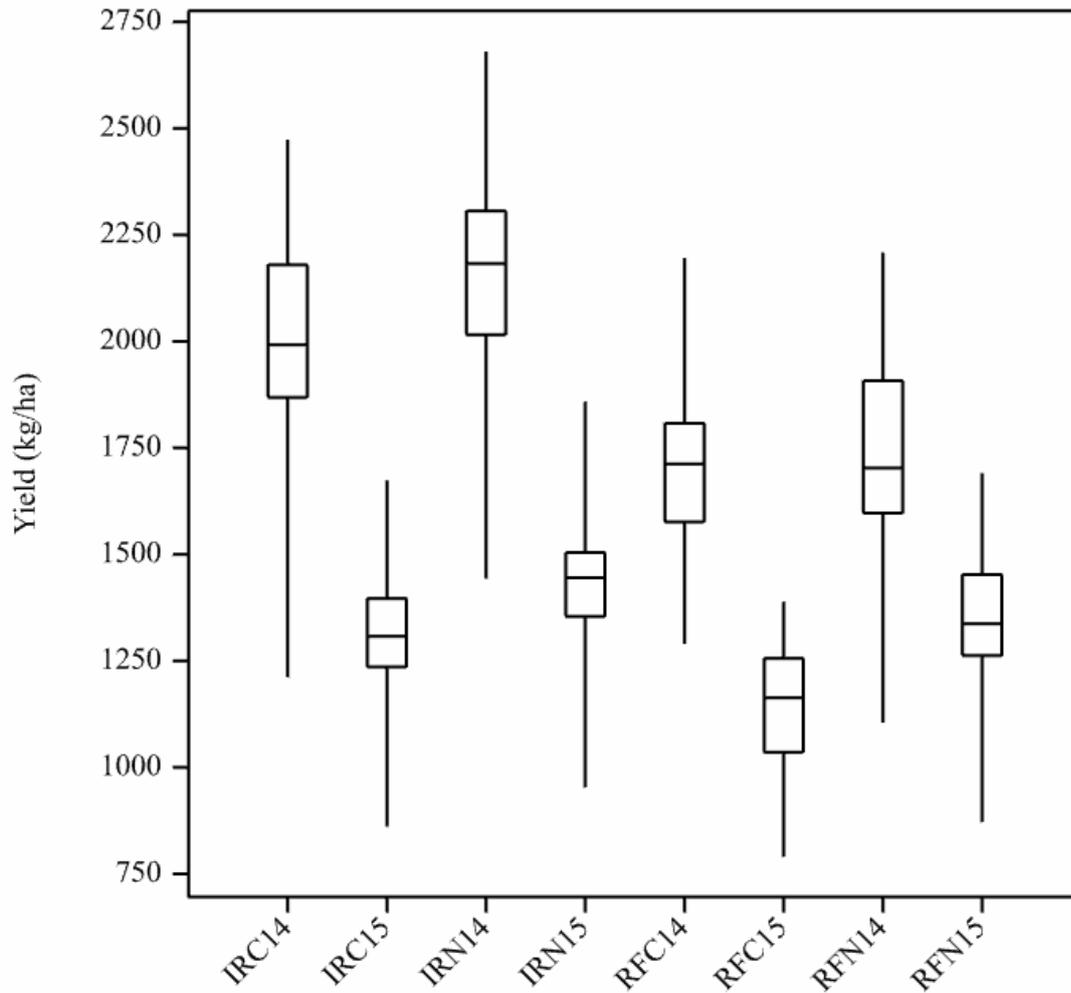


Figure 6.1: Chickpea grain yields for different tillage and moisture regime environments over two years (2014 and 2015). IRC14 and IRC 15 means irrigation + tillage in 2014 and 2015 season, respectively. IRN14 and IRN15 means irrigation + no till in 2014 and 2015 season, respectively. RFC14 and RFC15 stands for rainfed + tillage in 2014 and 2015 season, respectively. RFN14 and RFN15 stands for rainfed + no tillage in 2014 and 2015 season, respectively.

6.3.3 Factors accounting for grain yield variation

Tillage (no till and till), moisture (irrigated and rainfed), genotype and year (2014 and 2015) main effects were significant at 95% confidence interval and explained a large proportion of the variation in the grain yields observed (Table 6.3). The genotype main effect explained 14.2% of the variation in grain yield and moisture levels explained 9.6%. Tillage had the lowest main effect factor explaining only 2.1% of the total variation in grain yield. The largest variation in grain yield was explained by the year (part of environment) main effect which accounted for 58% of the total variability. There was a significant genotype by year interaction

($P < 0.05$) which accounted for 5.5% of the total variation in grain yield. Moisture regime and year had a significant interaction and accounted for 2.3% variation, and the tillage by year effect was also significant and accounted for 0.2% variation in grain yield. There was a significant three-way interaction between tillage, moisture regime and year and it accounted for 0.6% of the total variation in yield. The remaining interactions were not significant and accounted for the remainder of the variation in yield.

Table 6.3: The main factors accounting for grain yield variation in chickpea grown across different environments.

Parameter	TSS	Percent of TSS
Tillage	60.2	2.12***
Moisture	273.1	9.64***
Genotype	401.6	14.18***
Year	1641.7	57.97***
Tillage.Moisture	0.9	0.03
Tillage.Genotype	35.2	1.24
Moisture.Genotype	42.5	1.50
Tillage.Year	6.9	0.25***
Moisture.Year	64.7	2.28***
Genotype.Year	156.2	5.52***
Tillage.Moisture.Genotype	41.1	1.45
Tillage.Moisture.Year	15.7	0.55***
Tillage.Genotype.Year	23.9	0.84
Moisture.Genotype.Year	37.9	1.34
Tillage.Moisture.Genotype.Year	30.5	1.08

Values followed by an asterisk(s) indicate significant difference at * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

6.3.4 Genotype, environment and genotype by environment interaction

There was a significant genotypic difference ($P < 0.001$) among the genotypes tested which accounted for 12.6% of the total variation observed (Table 6.4). The test environments were significantly different and accounted for 66% of the total variation in grain yield. The interaction between genotype and environment was significant, indicating the genotypes had different yield rankings in the different environments. The genotype, and genotype by environment interaction accounted for cumulative variance of 24.6% of the total variation observed in grain yield.

Table 6.4: Combined analysis of variance (ANOVA) for genotype and environment effects on mean chickpea grain yields

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.	% TSS
Rep stratum	1	16641	16641	0.54		
Genotype	35	11992315	342638	11.11	<0.001	12.6
Environment	7	62672976	8953282	290.37	<0.001	66.0
Genotype.Environment	245	11412558	46582	1.51	<0.001	12.0
Residual	286	8818513	30834			9.3
Total	574	94909369				

Where d.f is degrees of freedom, s.s is sums of squares, m.s is mean sums of squares, v.r is variance ratio, Fpr is the Fischer test probability and TSS is total sums of squares.

6.3.5 Test environment evaluation

The first PC accounted for 59% of the total variation in yield, PC2 accounted for 17% of the total variation and together, PC1 and PC2 accounted for 76% of the total variation in yield (Figure 6.2). The 2014 environments were positively correlated with each other with IRC14 and RFN14 showing higher similarity compared with RFC14 and IRN14. The highest dissimilarity between the 2014 environments was between IRC14 and RFC14 which is signified by the wider angle between their environmental vectors formed from the origin in Figure 6.2. The similarity in the 2015 environments was based on tillage practices rather than moisture regimes. IRN15 and RFN15 had a narrow angle between the two environmental vectors with a similar trend observable between IRC15 and RFC15 (Figure 6.2). The highest level of similarity in test environments in 2015 was between IRC15 and RFC15. There was a negative correlation between IRN15 and IRC14 because the angle between their environmental vectors was greater than 90° indicating a moderately large GEI. RFN15 and IRC14 had no relationship as evidenced by the 90° angle between their environmental vectors.

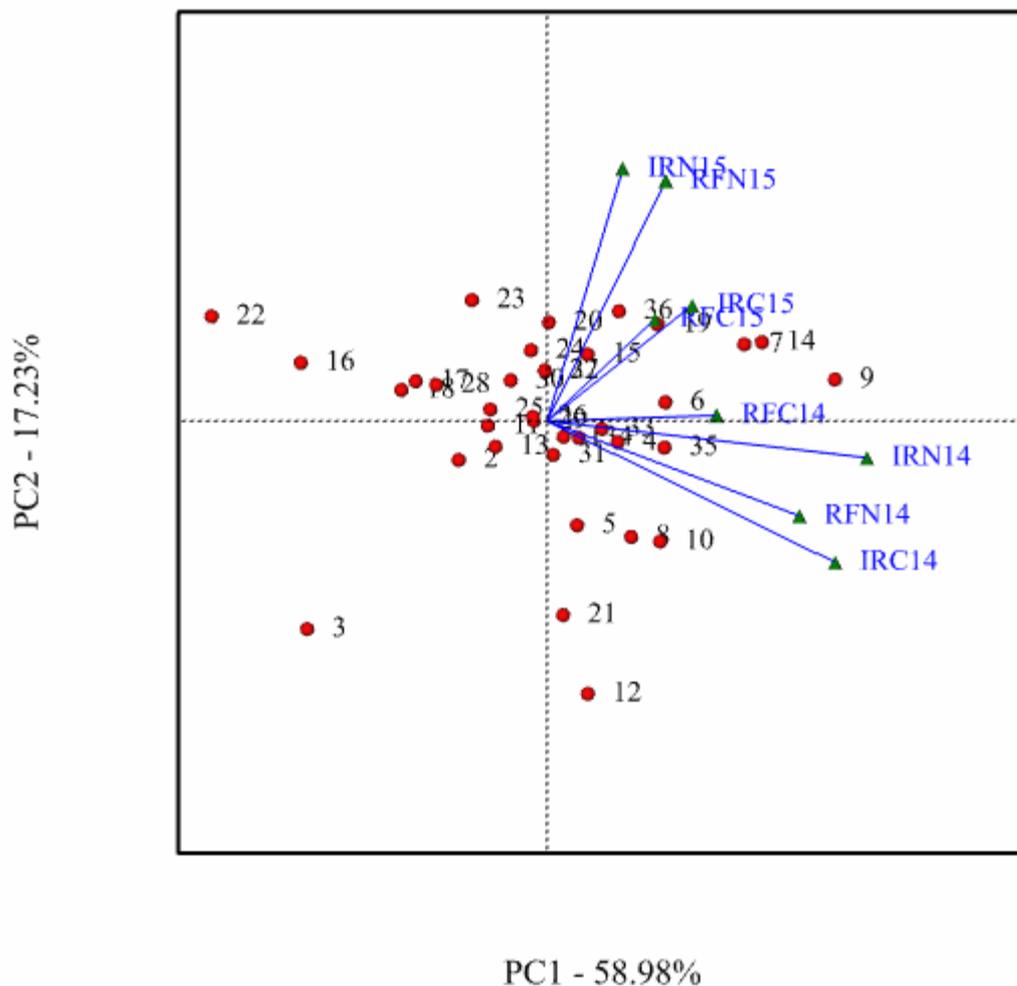


Figure 6.2: Environment scatter plot for evaluation of the test environment and chickpea genotypes. Red spheres indicate genotypes (see Table 6.1 for genotype codes) and green/blue arrows indicate environments. The larger the angle between two blue lines, the larger the difference between the test environments.

6.3.6 The ideal test environment

The length of the environmental vector in the principal component is relative to the standard deviation of the particular environment and indicates the discriminating ability of that environment. The most discriminating environments for grain yield were IRC14 and IRN14 whereas the least discriminating were RFC14, RFC15 and IRC15 (Figure 6.3). Representative environments have small angles between them and the average environmental axis. The most representative environments were RFC15, IRC15 and RFC14 followed by IRN14 and RFN14. The least representative environments were IRN15 and RFN15 even though they were discriminating. An ideal environment should be both discriminating and representative. IRN14 was the ideal environment because it was both discriminating and representative and located

near the centre of the concentric circles in Figure 6.3. This environment was characterised by slightly higher and better rainfall distribution patterns at the vegetative phase compared to other environments in the 2014 season. However, a lower rainfall was recorded when compared to the 2015 season. IRN14 had a relatively high rainfall with good distribution at flowering and it was cooler than the 2015 environments. The other environments close to the ideal were RFN14 and RFC14 indicating that 2014 was generally a better growing season than 2015. IRN15 and RFN15 were discriminating but not representative so they may be useful for selecting specifically adapted genotypes.

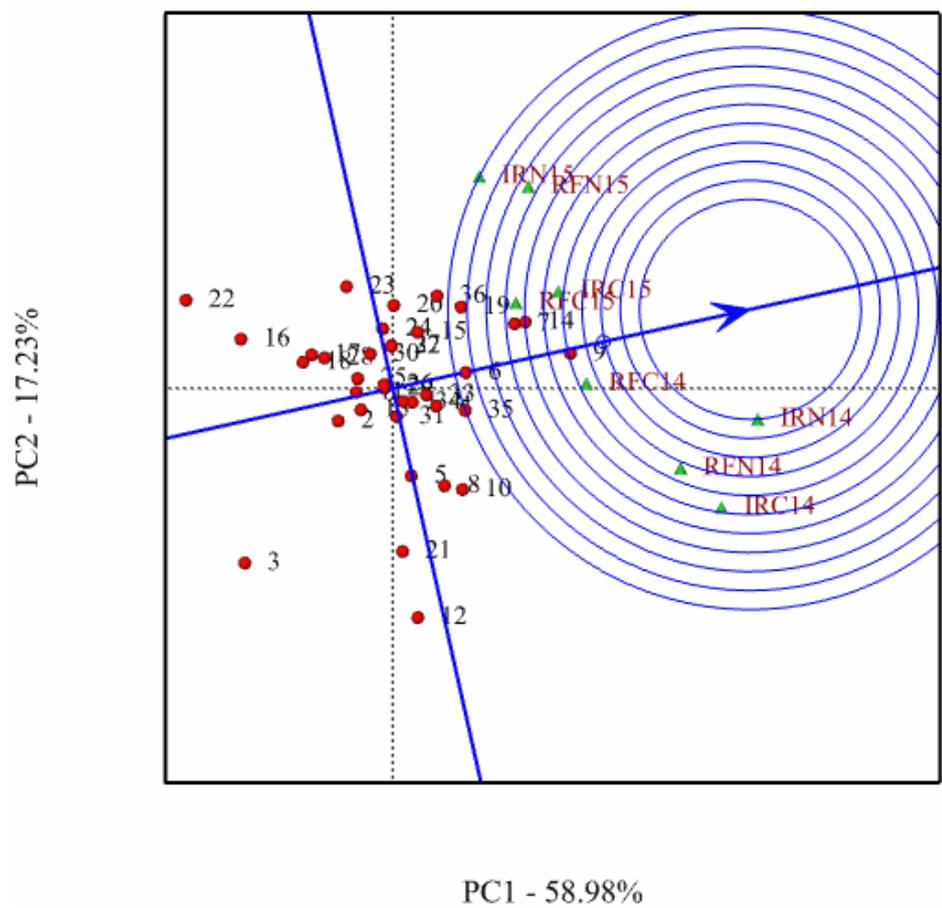


Figure 6.3: Test environment comparison scatter plot for evaluating genotype and environment interactions in chickpea yield. Red spheres indicate genotypes (see Table 6.1 for genotype codes) whereas green triangles indicate environments. The arrow in the middle of the concentric rings denotes the ideal environment and the further away a particular genotype is from the centre, the less ideal it is. The concentric rings help one visualise how far a genotype is from the ideal environment.

6.3.7 Mean grain yield performance and stability test

Genotypic stability is measured by the length of the perpendicular line to the average environment axis on either side and the proximity of the genotype to the average environment coordinate in a PC analysis biplot (Figure 6.4). The most stable genotypes were PBA Hattrick (6), Jimbour (19) and ICCV 98801 (15) however they were not the highest yielding. Sonali (9) was less stable compared with PBA Hattrick but had high yield potential, hence making it a good target for plant breeders (Figure 6.5). ICCV 96853 (14) and PBA Slasher (6) were less stable than PBA Hattrick but both out-yielded this genotype. Sonali exhibited higher GEI than both PBA Slasher and ICCV 96853 based on the length of the perpendicular line to the average environment axis. The most unstable genotype and low yielding genotype was ICCV 05308 (22) followed by ICCV 98813 (16). Genesis 079 (12) was unstable but had close to average yield across all the test environments. Amethyst (1), Lyle (26) and Sim (29) had very little contribution to both genotype and GxE since they clustered near the biplot origin. Both ICCV 05308 (22) and Genesis 079 (12) expressed high GxE and had low and average yield potential, respectively.

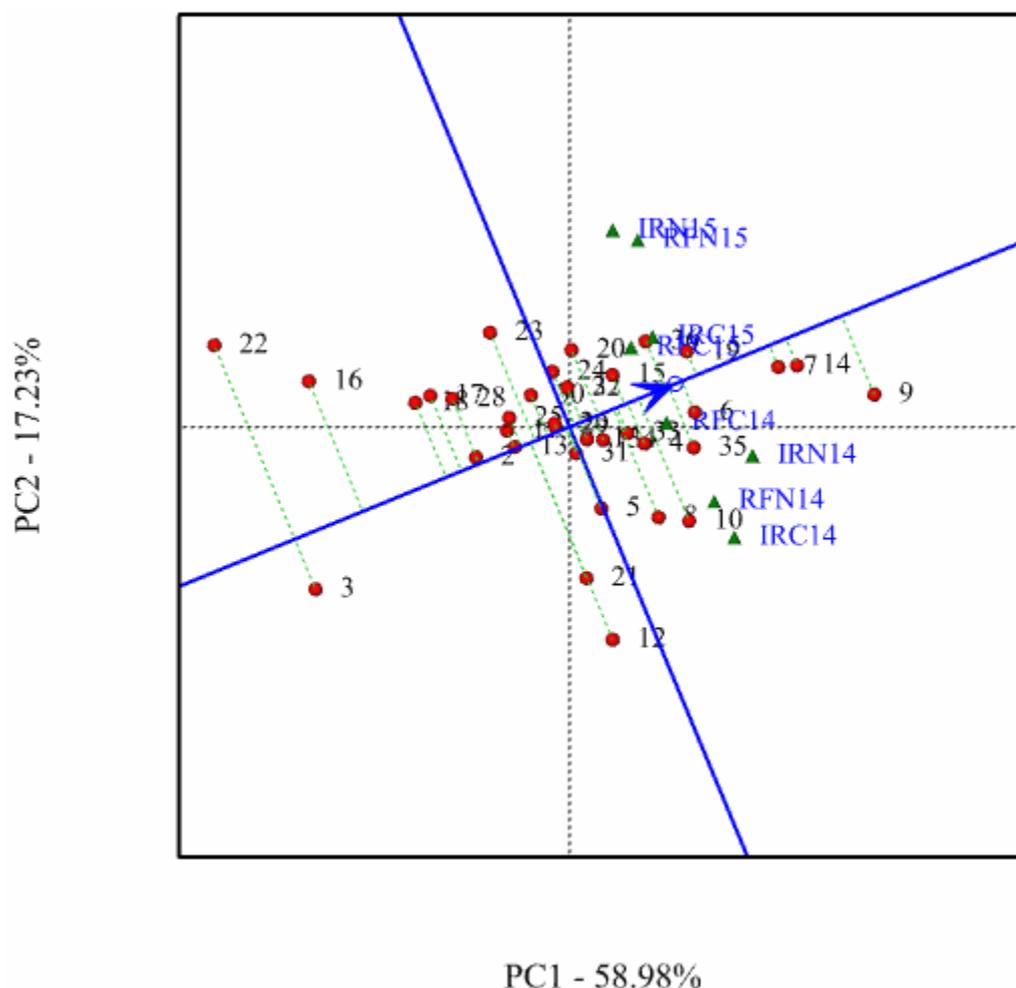


Figure 6.4: Principal component analysis scatter plot for evaluating grain yield performance and stability in chickpea genotypes. Red spheres indicate genotypes (see Table 3.1 for genotype codes) and green triangles indicate environments.

6.3.8 Selecting the ideal genotype

The ideal genotype is that which is located in the middle of the concentric circles (Figure 6.5) and other genotypes near the centre of the concentric circles are considered equally as good. The best genotype, which had high yield potential and stability, was Sonali (9) (Figure 6.5). It was closely followed by PBA Slasher (7) and ICCV 96853 (14) with PBA Hattrick (6) slightly behind them. Genotypes ICCV 05308 (22), ICCV 98813 (16), Genesis Kalkee (3) and Genesis 079 (12) were distant from the ideal genotype making them less preferable for growing. Sonali had high yields in 2014 and the environments for this genotype could be ranked on yield as follows; IRN14 > IRC14 > RFN14 > RFC14.

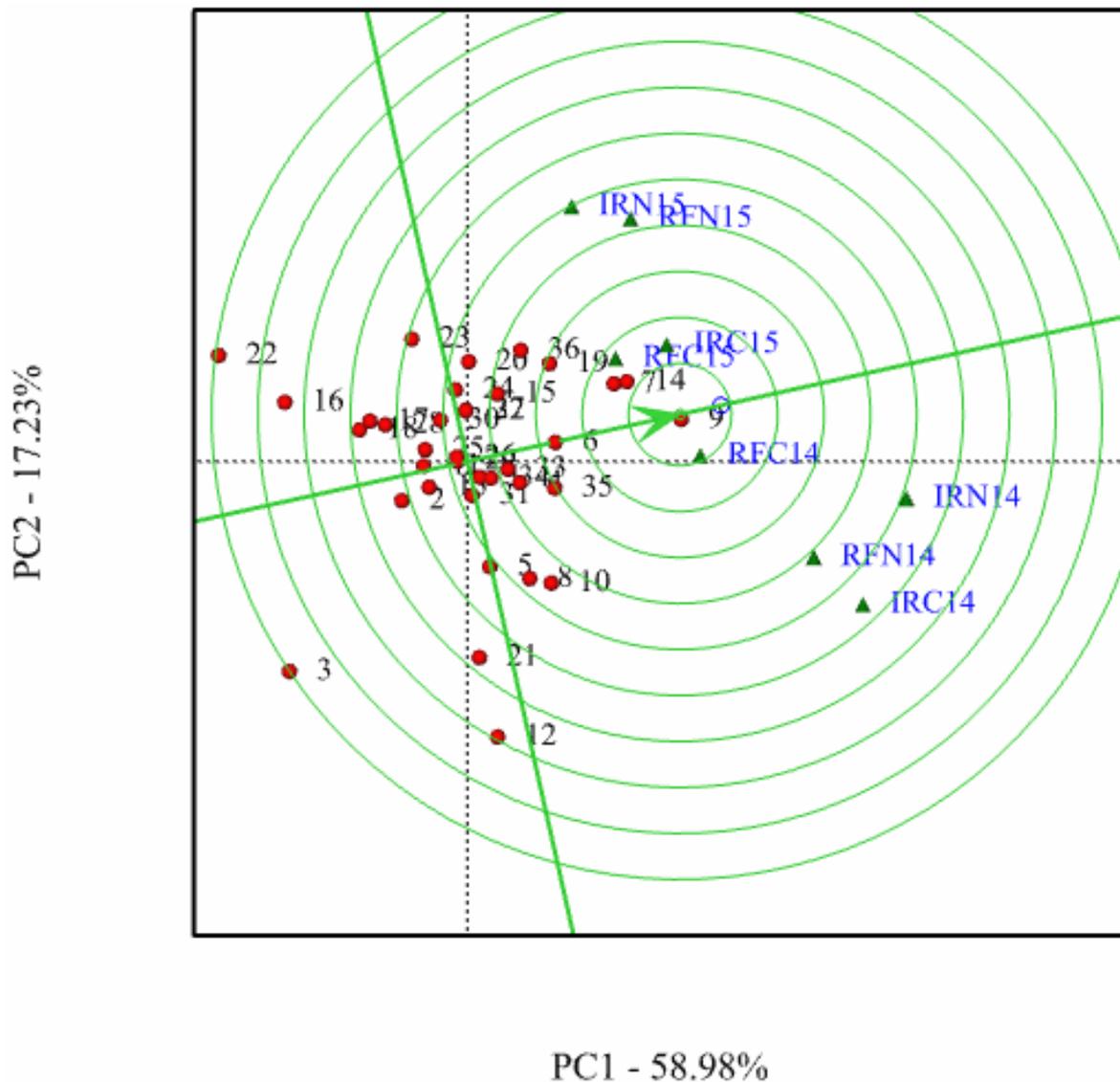


Figure 6.5: Scatter plot for evaluating the ideal chickpea genotype. Red spheres indicate genotypes (see Table 6.1 for genotype codes) and green triangles indicate environments.

6.3.9 Mega-environment analysis

The genotypes in the mega-environment (MGE) plot fell into seven sections delineated by the perpendicular lines from the origin and the environments fell into two sections (Figure 6.6). The eight environments were grouped into two MGE with IRC15, RFC15, RFC14, RFN14, IRN14 and IRC14 clustering into one mega-environment (MGE1) and IRN15 and RFN15 in the other mega-environment (MGE2). The till regimes (RFC14, RFC15, IRC14, IRC15) clustered in the same mega-environment in both test years indicating repeatability of results under tillage. The vertex genotypes which were located the furthest in each sector were joined using equality lines to form a polygon such that all the other genotypes were inside the polygon (Yan and Tinker, 2006). These vertex genotypes were the most responsive in each section of

the plot. Sonali was the vertex genotype in the MGE1 cluster, therefore the best performer, closely followed by PBA Slasher and ICCV 96853 which were above average performers. The equality line in MGE1 connects Sonali (9), ICCV 96853 (14), PBA Slasher (7) and Jimbour (19) so the performance ranking for MGE1 is as follows; Sonali > ICCV 96853 > PBA Slasher > Jimbour. There were no specific high yielding genotypes in MGE2 since it lacked a vertex genotype. Genesis Kalkee (3), ICCV 05308 (22) and ICCV 98813 (16) were below average performers in all the test environments.

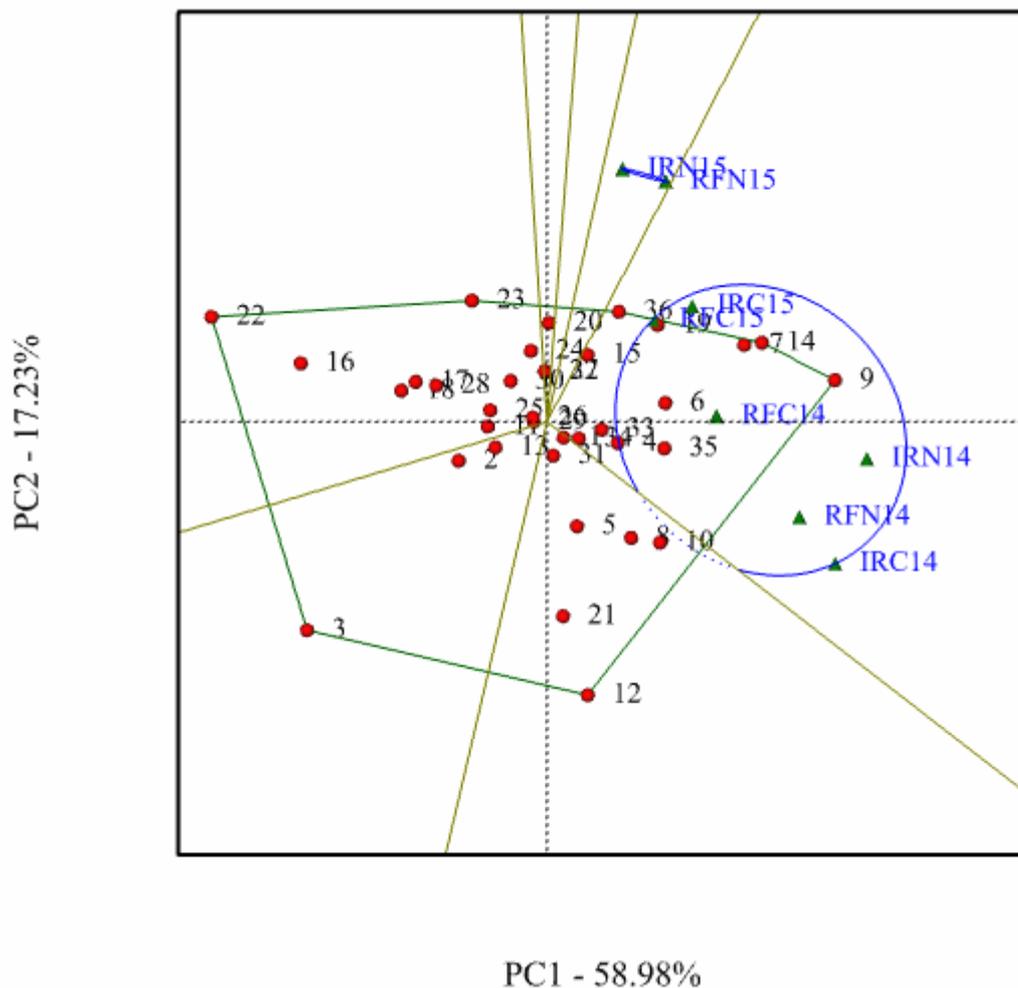


Figure 6.6: Mega environment scatter plot for evaluating chickpea yield across environments. Red spheres indicate genotypes (see Table 3.1 for genotype codes) and green triangles indicate environments. The green line represents the equality line for joining vertex genotypes.

6.4 Discussion

Rainfall is the most important factor affecting crop production in rainfed agriculture (Godwin, 1990). Rain distribution plays a key role as well in explaining variation in yield. Gangopadhyaya and Sarker (1965) reported about 75% of the total variation in maize yield was

accounted for by rainfall distribution. In the present study, rainfall and rainfall distribution between 2014 and 2015 caused significant differences at various chickpea phenophases. There was less rainfall during the vegetative phase in 2014 than in 2015, however the yields were higher in 2014 indicating that this may not be a critical stage for yield requiring high moisture levels. There was a large difference in rainfall and its distribution during the flowering phase in 2014 compared to 2015 with 2014 receiving more and better distributed rainfall. This may have contributed substantially to the high yields that were observed in 2014 compared with 2015 as the reproductive phase is the most sensitive to water stress (Nayyar et al., 2006, Mafakheri et al., 2010). The year effect was the largest contributor to the variation in yield observed between the two years with similar findings reported for chickpea in northern New South Wales in Australia (Haigh et al., 2005). The difference observed in rainfall and its distribution at the podding stage in 2014 and 2015 was not as large as that observed during the flowering stage. Temperature plays a key role in determining chickpea yield with temperatures less than 10°C (Chaturvedi et al. (2009) and more than 30°C (Summerfield et al. (1984) causing a reduction in grain yield. Minimum mean temperature differences were not large during the vegetative and flowering phases in 2014 and 2015. Notably, 2015 was warmer than 2014 by 5°C in terms of mean maximum temperature at both flowering and podding stages with the podding stage exposed to temperatures greater than 30°C in 2015. This may have contributed to the lower yields recorded in 2015.

The ideal test environment in terms of discriminating ability and representativeness was IRN14 followed by RFN14. Both were no till environments suggesting that no till may be beneficial in farming systems through improved soil aggregate stability (Chan and Mead, 1988), improved soil structure (Page et al., 2013) and increased water storage (Radford et al., 1995). No till environments (IRN14, RFN14, IRN15 and RFN15) were the most discriminating compared with till environments (RFC14, RFC15 and IRC15) except for IRC14 which was as discriminating as the no till environments.

Genotype stability is only effective if it is accompanied by high yields. The most desirable genotypes are those which show high stability and have high yield potential. In the GGE biplot, genotypes with a high PC1 score are high yielding and a low PC2 score are stable (Maqbool et al., 2015). In the present study, PBA Slasher and ICCV 96853 had both high stability and high yield potential. Sonali was less stable than PBA Slasher and ICCV 96853 but out-yielded both those genotypes. Genotypes that have low stability but high yield potential may be selected for

a specific environment, whereas genotypes that have low yield and high stability are the most undesirable in a breeding program (Yan and Wu, 2008)

Extensive breeding programs strive to save costs by reducing the number of testing sites. It is therefore important to identify testing sites which are highly discriminating and at the same time representative. This allows the plant breeder to effectively reduce the number of test sites and costs while at the same time managing the selection process effectively such that no desirable genotypes are discarded (Imtiaz et al., 2013). In the present study, two mega-environments were identified; MGE1 comprising of IRC15, RFC15, RFC14, RFN14, IRN14 and IRC14, and MGE2 comprising of IRN15 and RFN15. The two MGE accounted for 76% of the total GEI which was explained by the genotype-mega environment variance component. IRN14 and RFN14 represent the rest of MGE1 as good test environments and either IRN15 or RFN15 would suffice for MGE2. This can reduce the test sites from eight to three, which is a cost effective strategy. By identifying the MGE, selection based on individual MGE can be done so that the best adapted genotypes are cultivated (Yan et al., 2001). In the present study, the best adapted genotypes for MGE1 are Sonali, PBA Slasher and ICCV 96853. There is no specifically adapted genotype for MGE2.

6.5 Conclusions

The analysis presented in this chapter revealed that there was significant GxE in chickpea grown under varying environmental conditions. The year effect was the largest contributor to the observed variation in yield and this was driven by the weather conditions in each season. Rainfall and rain distribution played a key role in yield formation in the test environments with seasons that had high rainfall which was well distributed yielding better than others.

The GGE biplot is an effective tool in selecting good test environments, ideal genotypes and assessing the possibility of grouping the environment into mega-environments. In the present study, GGE successfully grouped the environment into two MGE and ideal genotypes relative to the performance of the other genotypes in similar environmental conditions were identified. Sonali, PBA Slasher and ICCV 96853 were identified as suitable genotypes for cultivation under rainfed or irrigated regimes with no till or tillage, hence showing a wider adaptation.

CHAPTER 7: DEVELOPMENT OF A DROUGHT TOLERANT CHICKPEA IDEOTYPE FOR THE AUSTRALIAN GRAIN BELT

7.1 Introduction

Plant breeders have selected for yield empirically over the years (Donald, 1968) based on genetic variation. This variation is caused by mutation, recombination of genes during reproduction and lateral gene transfer. Plant breeders use this variation and knowledge of gene, environment and management interactions to develop high yielding crop cultivars. Further yield increases are achieved through conservation of soil moisture, control of pests and diseases and the use of fertilisers (Johnson, 1984). Breeding programs traditionally select the highest yielding genotypes in any given environment and cross these to generate high yielding progenies for advancement. The challenge with this approach is that very little is known about the physiological, morphological and biochemical drivers of yield in different genotypes in different environments. Furthermore, the heritability of yield is generally low (Ludlow and Muchow, 1990) because the expression of this polygenic trait is significantly influenced by the environment, including drought, thus reducing the repeatability of results (Johnson and Geadelmann, 1989).

Under drought, secondary traits linked to yield which exhibit higher heritability than yield could be selected (Ludlow and Muchow, 1990, Blum, 1988). This ideotype approach is an alternative strategy to empirical breeding (Peng et al., 1994) and allows the breeder to predict the ideal genotype in the target environment. An ideotype is a biological plant model which behaves in a known manner when exposed to a distinct environment (Donald, 1968). Donald's concept was to consolidate several important traits that may manifest in different genotypes into one ideal genotype that would perform better than the individual parents. Definition of the plant type (Rasmusson, 1987) provides plant breeders with clear cut objectives based on defined traits (Rasmusson, 1991) that provide a blueprint for pyramiding traits (Mock and Pearce, 1975). Thus ideotype breeding is more analytical than traditional empirical selection and breeding.

One of the most important steps in ideotype breeding is the identification of the target environments (Mock and Pearce, 1975, Trethowan, 2014) and the target ideotype should perform optimally in these environments. Some of the key factors to consider in the target environment include temperature, soil moisture and soil fertility (Mock and Pearce, 1975).

Each ideotype is normally designed for a certain target environment and could possibly be grown in areas which lie in the same environmental type or mega-environment. The next step is identification of the physiological and morphological traits that contribute to yield either directly or indirectly. These traits should show genetic diversity to be incorporated into an ideotype breeding program (Rasmusson, 1987). Ideally the target traits should be easy to measure and highly heritable, however this should not preclude traits that are laborious to measure if they are important and correlated with yield (Rasmusson, 1987). Trait relationships must also be carefully considered because pleiotropy, trait compensation and inferior donor germplasm may influence the target ideotype thus reducing breeding progress (Rasmusson, 1991). The identified traits can then be pyramided in one genotype (Mock and Pearce, 1975).

Crop modelling has recently become an important enabling tool in plant breeding (Tardieu, 2003, Hammer et al., 2006). From a modelling perspective, an ideotype is a set of defined crop parameters that drive growth and development in defined environmental conditions (Rotter et al., 2015). High quality long-term data is an imperative for model calibration and the generation of accurate simulation results (Rotter et al., 2015). These ideotype models can also be refined to capture variability in the climate (Rotter et al., 2015).

Models have been a powerful tool in ideotype design and testing *in silico* (Semenov and Stratonovitch, 2013). Data on multiple sites over many years can be produced without running actual field trials, which reduces the cost of plant breeding. Chapman et al. (2002) emphasised that models provide an understanding of the temporal and spatial environmental effects on crops, especially when experimentation is not possible. Crop modelling can also be used to assess crop responses to environmental factors (White et al., 2002).

Several crop ideotypes have been developed including rice (Khush, 1995) and wheat (Semenov and Stratonovitch, 2013). The software tool APSIM simulates cropping systems using climate, soil, management and crop genetic coefficients to predict the economic yield (Keating et al., 2003). The APSIM model uses the supply and demand concept of important plant growth resources (light, water, nitrogen and carbon) to create a plant phenotype (Hammer et al., 2001).

There has been no attempt to develop and model the performance of a drought tolerant chickpea ideotype from a defined chickpea germplasm gene pool and compare the ideotype performance with drought tolerant and drought susceptible chickpea genotypes under different management practices (no tillage and full tillage systems) in the Australian grain belt.

This chapter aims to; i) develop a chickpea ideotype, ii) characterise the chickpea growing environments based on soil moisture deficits at various growth stages across the Australian grain belt, iii) identify the critical stages where drought occurs to better match phenology to environment, and iv) assess the performance of selected chickpea cultivars and a target ideotype across the Australian grain belt.

7.2 Materials and methods

7.2.1 Field experiments

Data from an experiment conducted at The University of Sydney's IA Watson Grains Research Centre at Narrabri (latitude 30.275616° S and longitude 149.803547° E) in 2014 and 2015 as described under Materials and Methods in Chapter 3 were used to develop the chickpea ideotype, and parameterise and validate the APSIM-Chickpea model (Version 7.8). The larger experiment comprised 30 entries (25 desi and 5 kabuli types – refer to Table 3.1) and for the purpose of the ideotyping presented in this chapter, five desi genotypes were chosen; Amethyst, Kyabra, PBA Hattrick, Tyson and Sonali. These genotypes were selected because of their differential response to drought based on yield rankings in well-watered and water stress conditions, as well as stress tolerance index. For example, Sonali has a high yield and is drought tolerant with a field stress tolerance index of 1.27 calculated according to (Fernandez, 1992). Tyson is reported to be drought tolerant (Sarma et al., 2011) but showed moderate tolerance in these field experiments with a stress tolerance index of 0.95. Tyson has also been used as a parent in breeding programs to develop new varieties (Lake et al., 2016). Amethyst had a stress tolerance index of 0.84 and was classified as drought susceptible based on the field evaluation at Narrabri. PBA Hattrick, widely cultivated by farmers in northern NSW had a stress tolerance index of 1.02 whereas Kyabra had a stress tolerance index of 0.87. Hence, PBA Hattrick had moderate drought tolerance and Kyabra was drought susceptible.

7.2.2 Chickpea ideotype development

The chickpea ideotype was designed following the recommendations of Rasmusson (1987), Martre et al. (2015) and Rotter et al. (2015). Field data obtained from the two seasons (2014 and 2015) in Narrabri was used to construct the chickpea ideotype. The data were subjected to analysis using Genstat® edition 18 to generate means, test genetic variation of traits at 95% confidence levels, and generate least significant differences (LSD) at $P < 0.05$ using the linear mixed models in the REML function (Patterson and Thompson, 1971). Multiple linear regression analysis was subsequently used to identify traits that significantly explained yield

variation. The measured traits were also subjected to correlation analysis following the method described by Snedecor and Cochran (1987). Trait relationships with yield and individual inter-relationships were considered and traits optimised to a maximum (Marinho et al., 2014) or minimum depending on their correlation with yield (Figure 7.1). The maximum and minimum values were chosen as relevant and the LSD used to establish a range for the trait (Figure 7.1). The use of trait ranges was intended to give breeders some flexibility while targeting traits. The optimised values were generated and assigned to the ideotype and then subjected to analysis (Laurila et al., 2012) using Genstat® edition 18.

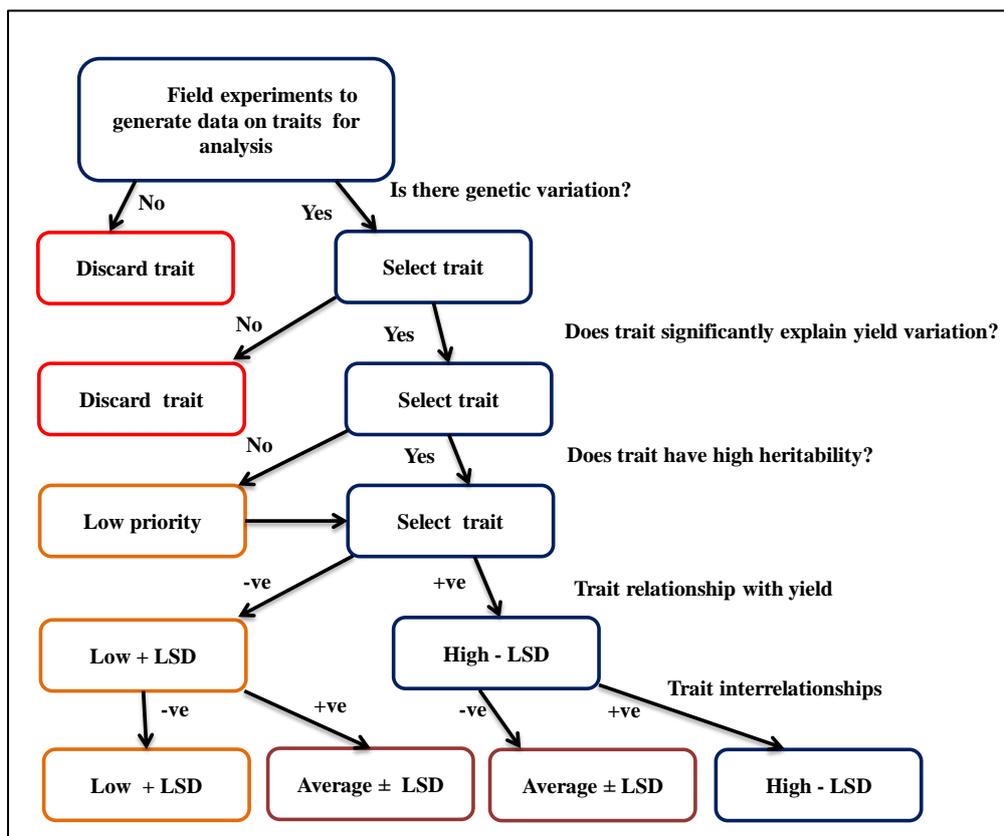


Figure 7.1: Flow diagram for chickpea ideotype construction. LSD, least significant difference at $P < 0.05$; +ve, positive correlation; -ve, negative correlation.

7.2.3 Environmental characterisation: the soil water deficit approach

Soil water deficit at important phenophases (e.g. flowering, grain filling) of chickpea were estimated using the APSIM-Chickpea model. Fifty locations within the Australian grain belt based on the chickpea National Variety Trials (NVT) sites (<http://www.nvtonline.com.au/>) were selected. The critical chickpea planting window for each location was obtained from the chickpea sowing guides provided by each state. For each location, the SoilMapp iPad® application developed by Commonwealth Scientific and Industrial Research Organisation

(CSIRO) was used to search the Australian Soil Resource Information System (ASRIS) map discovery database to obtain the relevant soils. Once the soil type was identified for each location, it was selected from the APSIM soils repository and used for analysis. The SILO climate database for the period from 1905 to 2004 was used. Sowing was conducted when the cumulative rainfall in three consecutive days was greater than 15 mm within the sowing window. The sowing rule for each genotype was set to begin when there was at least 200 mm of allowable available soil water. The planting density for each genotype was set at 25 plants per m² with a 30 mm depth and an inter-row spacing of 300 mm. The initial surface residue in the no-till management system was set at 1000 kg ha⁻¹ with a 0.6 fraction of standing residue remaining. No fertilisers were applied to either no-till and till systems. In the historical analysis, 100 year weather, soil type and sowing rules for each location were considered. Simulations (60 000) were performed denoting combinations of six genotypes (including the ideotype), two management systems (till and no-till), 100 years and 50 locations. The crop growing season was divided into five stages; juvenile, floral initiation, flowering, start of grain filling, end of grain filling and maturity. The soil water deficit was derived from the water supply/water demand ratio (Lake et al., 2016, Kholová et al., 2013) and used to analyse soil moisture stress levels at each growth stage. The soil water deficit values were then subjected to average link cluster analysis using Euclidean distances in Genstat® edition 18. The output was used to identify various stress environments in the Australian grain belt. An index of 1 indicated no moisture stress (no drought) and 0 very low moisture (severe drought) as described by Kholová et al. (2013), with an index less than 0.7 considered a drought event (Lake et al., 2016).

7.3 Results

7.3.1 Chickpea ideotype

A total of 21 parameters were identified through multiple linear regression on yield and they accounted for 91% of the total variation at $P < 0.001$ (Table 7.1). High yielding genotypes developed ground cover early in the season and also had high NDVI both at early and late podding stages. These genotypes also produced their first flower earlier in the season and finished flowering earlier. Genotypes that continued flowering and had a late date to last flower were associated with low NDVI at flowering and low shoot harvest index, hence rendering NDVI an undesirable trait. However, a longer flowering period was associated with longer leaves and higher yield. Plant height had no clear correlation with yield but shorter machine harvestable plants were preferred because they were associated with early flowering, longer flower duration and high NDVI scores which all contributed positively to yield. Genotypes

with high chlorophyll content at mid-podding and low chlorophyll content at late-podding produced higher yield. Leaf characteristics (number of leaflets per leaf, single leaflet area and single leaf area) were not significantly correlated with yield. Average-sized leaves should be selected as opposed to small leaves because larger leaf area was associated with early flowering, longer flowering duration and longer leaves, all of which are desirable for increasing yield. Average shoot harvest index was selected because plants with high shoot harvest index also had slower development of ground cover, lower chlorophyll content at mid podding and lower NDVI. On the other hand, they flowered earlier and were shorter. All these traits influence yield in opposite directions, hence the average was chosen. Similarly, plants with high pod harvest index also had high NDVI. However, they had short narrow leaves, were taller, flowered later and had lower seed mass.

Table 7.1: Wald statistic, correlations and decisions used to construct the chickpea ideotype

Parameter	Wald		
	statistic	Correlation	Decisions
Early ground cover (%)	14.2**	0.10	H - LSD
Days to first flower	31.66***	-0.18	L + LSD
Days to 50% flowering	18.63***	-0.23	L + LSD
Days to last flower	24.69***	-0.36*	L + LSD
Flower duration (days)	24.62***	0.12	H - LSD
NDVI at early podding	58.92***	0.55	H - LSD
NDVI at late podding	8.32*	-0.52*	L + LSD
Plant height at late flowering (Krupinsky et al.)	20.72***	0.10	L + LSD
Plant height at late podding (Krupinsky et al.)	29.84***	0.04	L + LSD
Chlorophyll content at mid podding (SU)	5.38*	0.02	H - LSD
Chlorophyll content at late podding (SU)	9.61**	-0.35*	L + LSD
Number of leaflets per leaf	13.42**	-0.10	AV ± LSD
Single leaf area (cm ²)	25.64***	-0.04	AV ± LSD
Single leaflet area (cm ²)	35.79***	-0.03	AV ± LSD
Leaflet length (cm ²)	28.16***	0.02	AV ± LSD
Number of pods per plant	11.43**	-0.18	AV ± LSD
Pod biomass per plant (g)	19.11***	-0.31	L + LSD
Pod harvest index	9.6**	0.10	AV ± LSD
Shoot biomass	25.85***	-0.41*	L + LSD

Shoot harvest index	47.88***	0.24	AV ± LSD
1000 seed weight (g)	9.05**	-0.39	L + LSD

Wald statistic is from the multiple linear regression Wald tests for dropping terms. Significant terms at various levels of confidence were picked; * = P<0.05, ** = P<0.01, *** = P<0.001. Correlations are between the considered traits and yield. Decision on ideotype optimisation based on trait ranges and relationship with yield and other traits. L, low; H, high; AV, average; LSD, least significant difference at 5%; SU, SPAD Units.

The early ground cover ranged from 13.2 – 25.9% with the selected ideotype at 23.2% (Table 7.2). Days to first flower, 50% flowering and days to last flower ranged from 68 – 93, 80 – 103 and 118 – 124, respectively, with the ideotype classified as 70, 82 and 119 days in the same trait order. Sonali was closest to the ideotype in days to flowering whereas the other genotypes flowered later. All genotypes stopped flowering around the same time regardless of when they started to flower. Flower duration ranged from 31 – 50 days with the ideotype classified at 48 days. NDVI at early podding ranged from 0.66 – 0.74 and 0.22 – 0.41 at late podding. Both NDVI and chlorophyll measures at the podding stages of the five selected genotypes were comparable to the ideotype. Variation in number of leaflets was low compared to leaf area. Number of pods per plant ranged from 21 – 54, and pod biomass ranged from 6.4 – 31.6 g. Shoot biomass varied greatly (13.6 – 52.6 g), however the range in shoot harvest index was relatively narrow (0.33 – 0.48). The ideotype values for shoot biomass and shoot harvest index were 17.7 g and 0.39, respectively. Seed weight also varied greatly with an observed range of 139 – 392 g and the ideotype was classified as 148 g.

Table 7.2: Trait range, genotype and ideotype values for evaluating chickpea drought tolerance through APSIM modelling

Parameter	Trait range	PBA					
		Amethyst	Kyabra	Hattrick	Sonali	Tyson	Ideotype
Early ground cover (%)	13.2-25.9	15.7	22.2	18.9	15.1	16.2	23.2
Days to first flower	68-93	88	88	87	77	86	70
Days to 50% flowering	80-103	99	99	98	88	97	82
Days to last flower	118-124	120	122	121	118	120	119
Flower duration (days)	31-50	32	34	34	41	34	48
NDVI at early podding	0.66-0.74	0.70	0.71	0.72	0.69	0.70	0.72
NDVI at late podding	0.22-0.41	0.28	0.28	0.29	0.22	0.25	0.25

Plant height at late flowering	49-64	58	64	64	56	54	51
Plant height at late podding	54-69	62	68	69	60	56	55
Chlorophyll at mid pod (SU)	65-74	69	74	71	65	66	72
Chlorophyll at late pod (SU)	49-68	52	54	56	49	52	51
Number of leaflets per leaf	12-15	14	14	12	14	14	14
Single leaf area (cm ²)	4-21	6	7	6	8	5	7
Single leaflet area (cm ²)	0.3-1.6	0.4	0.5	0.5	0.6	0.3	0.5
Leaflet length (cm ²)	1.0-2.2	1.2	1.2	1.2	1.3	1.0	1.2
Number of pods per plant	21-54	42	30	34	32	35	31
Pod biomass per plant (g)	6.4-31.6	12.4	10.5	10.0	10.5	8.5	8.8
Pod harvest index	0.75-0.82	0.81	0.81	0.80	0.79	0.81	0.80
Shoot biomass	13.6-52.6	25.0	24.8	21.6	18.1	16.2	17.7
Shoot harvest index	0.33-0.48	0.42	0.34	0.37	0.48	0.43	0.39
1000 seed weight (g)	139-392	151	224	206	192	139	148

SU, SPAD units

All five selected genotypes were compared to the ideotype based on their performance against the 21 parameters used for ideotype construction. Sonali was the closest to the ideotype with 76% resemblance (Figure 7.2). This resemblance was primarily based on phenology (days to first flower, days to 50% flowering, days to last flower and flower duration), leaf characteristics and number of pods per plant. The next closest resemblance to the ideotype was Tyson at 73.2% similarity. This resemblance was based on pod biomass, NDVI, plant height and chlorophyll content. Kyabra and PBA Hattrick were the most closely related pair of genotypes with 90.3% similarity, followed by Tyson and Amethyst with 83.7% similarity. Sonali and Tyson showed drought tolerance under field conditions (Narrabri) with stress tolerance indices of 1.27 and 0.95, respectively, compared to the drought susceptible cultivar Amethyst (0.84).

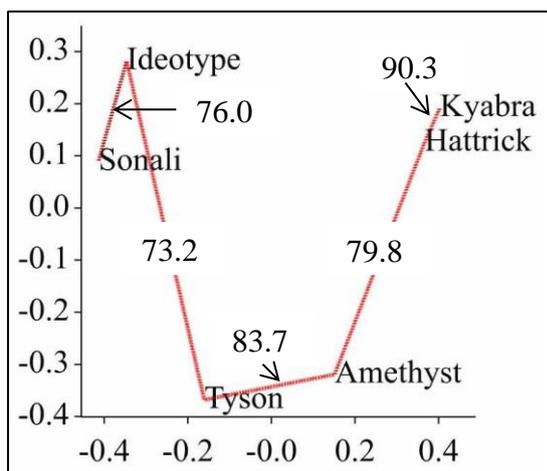


Figure 7.2: Evaluation of chickpea for drought tolerance using minimum spanning tree for genotype similarity. Genotypes close to each other along the line are more similar than those further away in the tree. The x-axis is dimension 1 and the y-axis is dimension 2 of the Genstat output.

7.2 Validation of the APSIM-Chickpea model

The simulated days to flowering compared to the observed days to flowering in the Narrabri field experiment returned a coefficient of determination of 0.6 and a root mean square error of 12 (Figure 7.3a). When the 1:1 line was fitted, it showed that the simulated values were slightly underestimated. The coefficient of determination for simulated and observed yield was 0.7 with a root mean square error value of 823 (Figure 7.3b), thus the simulated yield was slightly overestimated.

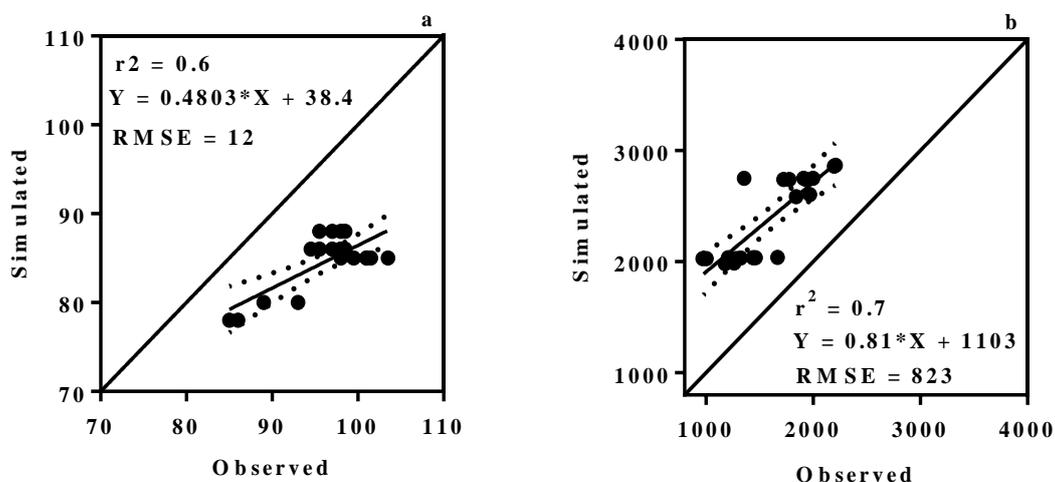


Figure 7.3: Evaluation of chickpea traits using APSIM modelling. (a) Days to 50% flowering

(days) and (b) grain yield (kg ha^{-1}) for observed and simulated data. R^2 is the coefficient of determination and RMSE is the root mean square error.

7.3 Simulated yield

The simulated yield from the 50 locations ranged from 760 to 3902 kg ha^{-1} showing the diversity of production environments investigated (Figure 7.4a). No till environments had a slightly higher average yield of 2559 kg ha^{-1} compared to 2492 kg ha^{-1} under till (Figure 7.4b). The chickpea ideotype had the highest average yield of 2678 kg ha^{-1} compared to Sonali, PBA Hattrick, Amethyst, Kyabra and Tyson which yielded 2553, 2513, 2487, 2487 and 2457 kg ha^{-1} , respectively (Figure 7.4b).

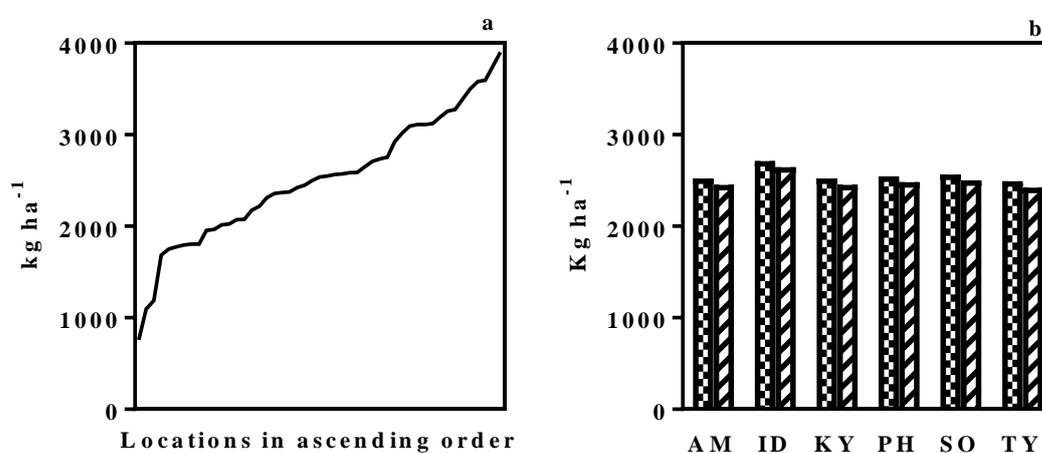


Figure 7.4: Evaluation of chickpea yields across different production environments (a) Simulated yield (kg ha^{-1}) range representing 50 locations from the lowest yielding location to the highest (b) Actual yield (kg ha^{-1}) of individual genotypes under no-till (checked) and till (diagonal lines) environments. AM, Amethyst; ID, Ideotype; KY, Kyabra; PH, PBA Hattrick; SO, Sonali; TY, Tyson.

7.4 Environmental characterisation and soil water deficit patterns

Cluster analysis performed on the soil water deficit output from APSIM grouped the environments into three major clusters and two ungrouped environments at 95% similarity value (Figure 7.5 and Table 7.3). The first cluster was comprised of four sites only; Albany, Hamilton, Minlaton, Riverton. The second cluster represented 33 locations making it the largest group, and the third cluster comprised 10 locations. The two ungrouped locations were Bourke and Rudall. The complete cluster groups and names are listed in Table 7.3.

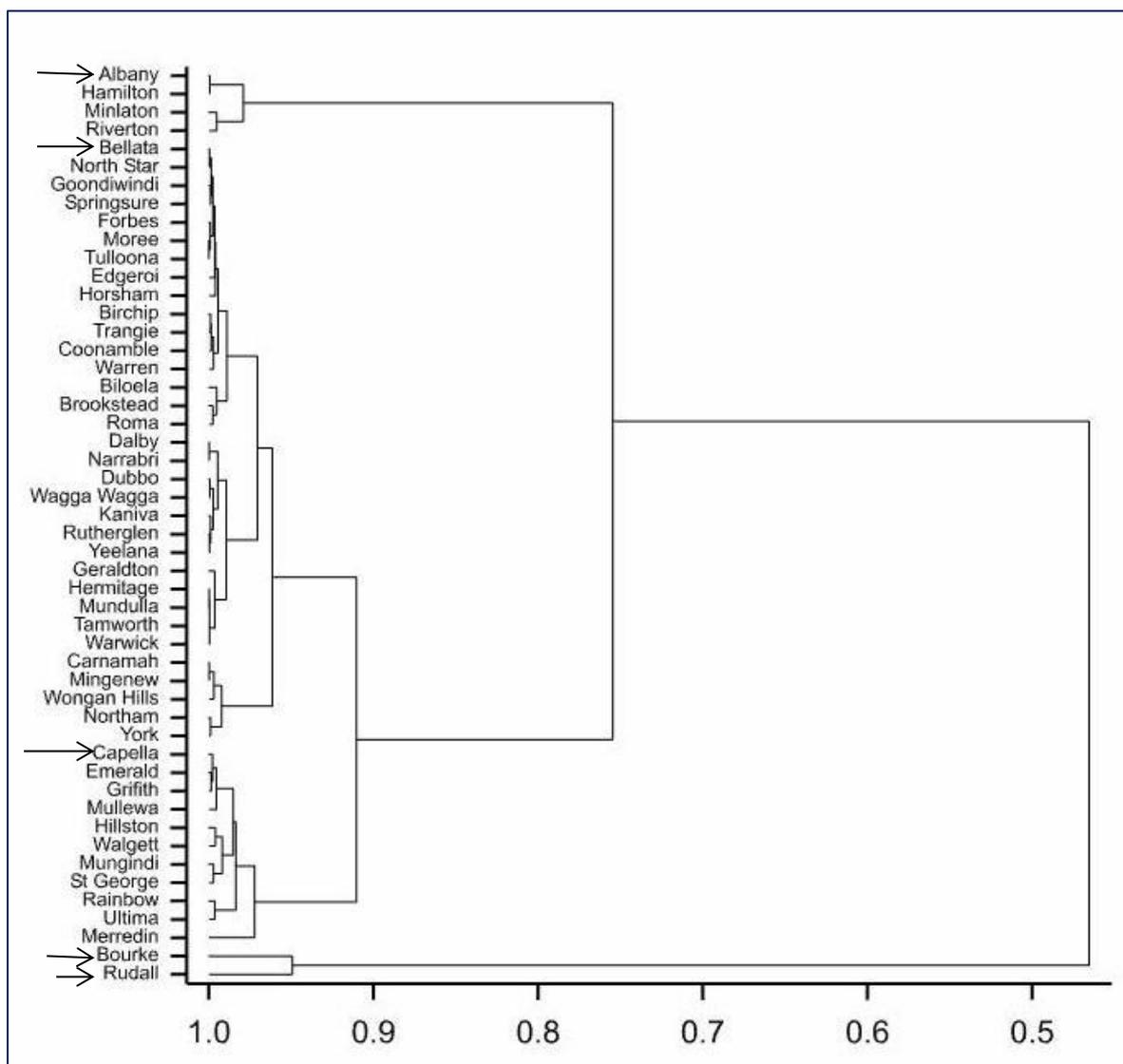


Figure 7.5: Dendrogram of Australian chickpea production environment characterisation based on soil moisture deficit. Arrows indicate the start of a new cluster or group.

Table 7.3: Australian chickpea production environmental clusters based on soil water deficit

Cluster 1		Cluster 3	
Number	Location	Number	Location
1	Albany	1	Capella
2	Hamilton	2	Emerald
3	Minlaton	3	Griffith
4	Riverton	4	Hillston
		5	Merredin
		6	Mullewa
Cluster 2		7	Mungindi
Number	Location	8	Rainbow
1	Bellata	9	St George
2	Biloela	10	Walgett
3	Birchip		

4	Brookstead		
5	Carnamah		
6	Coonamble		
7	Dalby		
8	Dubbo		
9	Edgeroi		
10	Forbes		
11	Geraldton		
12	Goondiwindi		
13	Hermitage		
14	Horsham		
15	Kaniva		
16	Mingenew		
17	Moree		
18	Mundulla		
19	Narrabri		
20	North Star		
21	Northam		
22	Roma		
23	Rutherglen		
24	Springsure		
25	Tamworth		
26	Trangie		
27	Tulloona		
28	Wagga Wagga		
29	Warren		
30	Warwick		
31	Wongan Hills		
32	Yeelana		
33	York		

Ungrouped	
1	Rudall
2	Bourke

In the first cluster, genotypes flowered and matured on average at 89 and 175 days, respectively (Figure 7.6a). The second cluster flowered slightly earlier at 86 days after sowing and matured earlier at 159 days. The third cluster was the earliest flowering and maturing of the three clusters at 79 and 147 days, respectively. The ungrouped locations flowered at 70 days and matured at 128 days on average. Cluster 1 was the highest yielding (3645 kg ha⁻¹) followed by clusters 2 (2700 kg ha⁻¹) and 3 (1801 kg ha⁻¹) (Figure 7.6b). The two ungrouped locations had a low mean yield of 928 kg ha⁻¹.

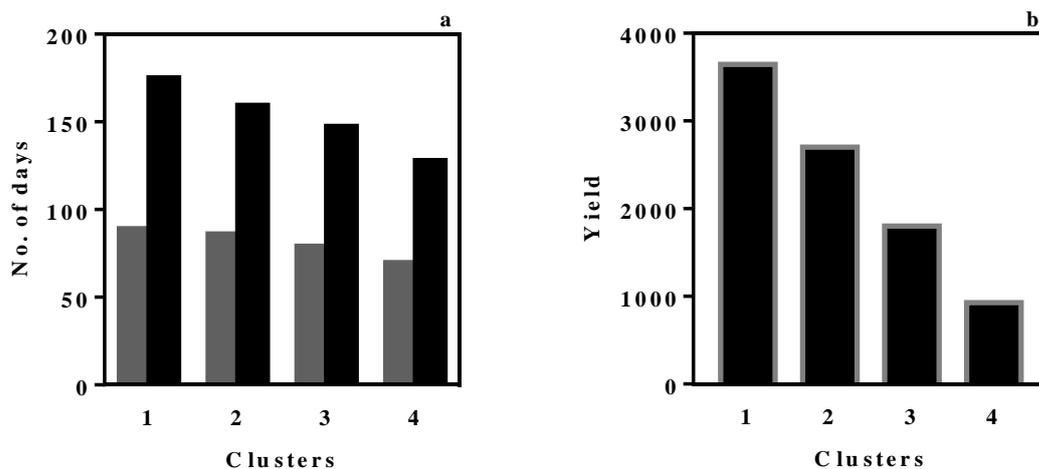


Figure 7.6: Evaluation of APSIM-predicted chickpea traits for drought tolerance based on soil water deficit clusters. (a) Mean days to 50% flowering (grey bars) and maturity (black bars) and (b) mean grain yield (kg ha⁻¹). Numbers on the x-axis represent the cluster numbers.

The first cluster had a 97% chance of yielding over 2500 kg ha⁻¹ in every season and less than a 0.3% chance of yielding less than 1000 kg ha⁻¹ (Figure 7.7). Cluster 2 had a 60% chance of exceeding 2500 kg ha⁻¹ per year and an approximately 30% chance of yielding between 1000-2500 kg ha⁻¹. The third cluster had a 30% chance of yielding 2500 kg ha⁻¹ or more with an equal chance of yielding 1000 kg ha⁻¹ or below. The two ungrouped locations had a mean yield of 928 kg ha⁻¹. All the simulated genotypes produced similar yield patterns with little variation in the frequencies in all the clusters with the ideotype performing better in all comparisons (Figure 7.7).

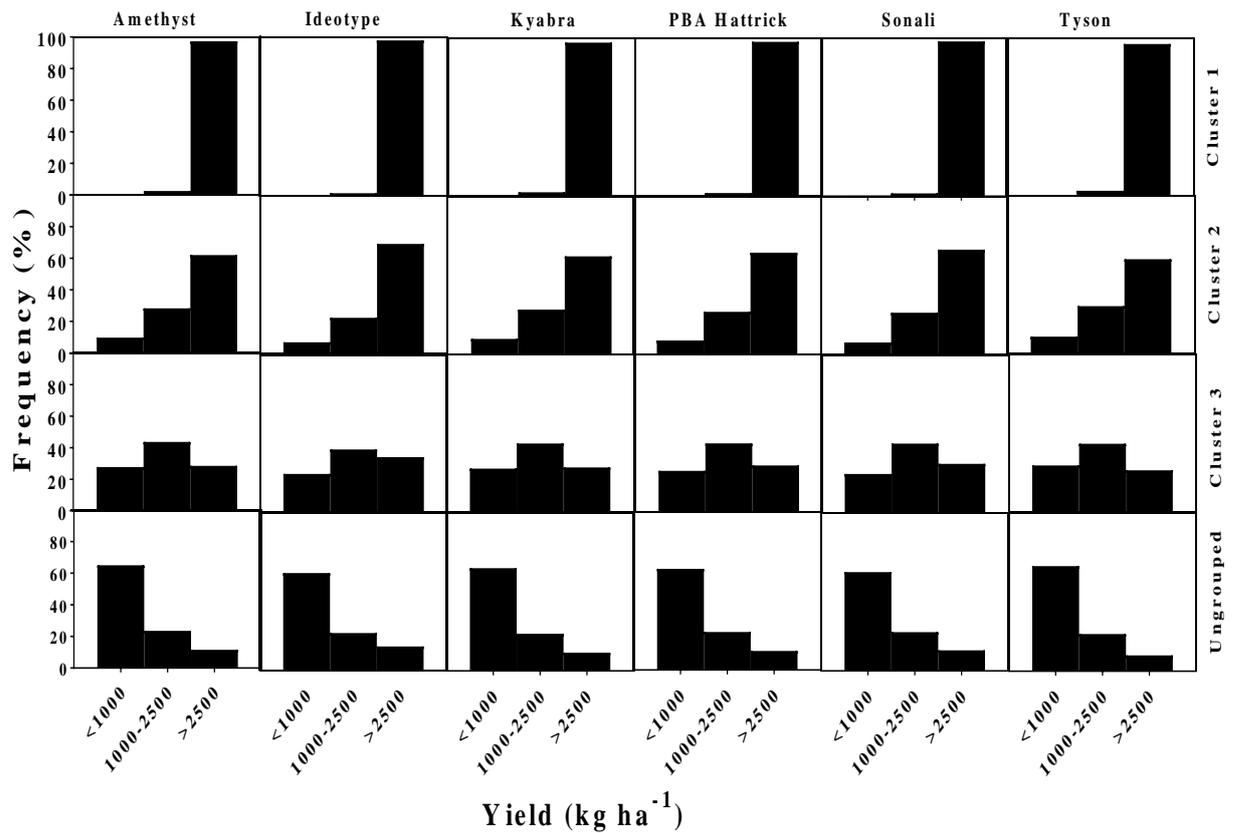


Figure 7.7: Frequency predictions (%) for chickpea yield based on cluster groupings (identified in Figure 7.5).

7.5 Stress timing and the critical period for yield penalty

There was adequate soil moisture on average at all locations during the juvenile development stages (Figure 7.8). However, a gradual decline in soil moisture occurred from the juvenile stage to flowering in all three clusters. The two ungrouped locations (Bourke and Rudall) experienced a sharp moisture decline immediately after the juvenile stage. Cluster 1 maintained soil moisture all the way to maturity with a gentle decline during the grain filling period, levelling off at maturity. Cluster 2 and 3 experienced a sharp moisture decline from flowering until the end of grain filling. While terminal drought was experienced in both clusters 2 and 3, the intensity of drought was greater in cluster 3. The two ungrouped locations experienced both intermittent and terminal drought.

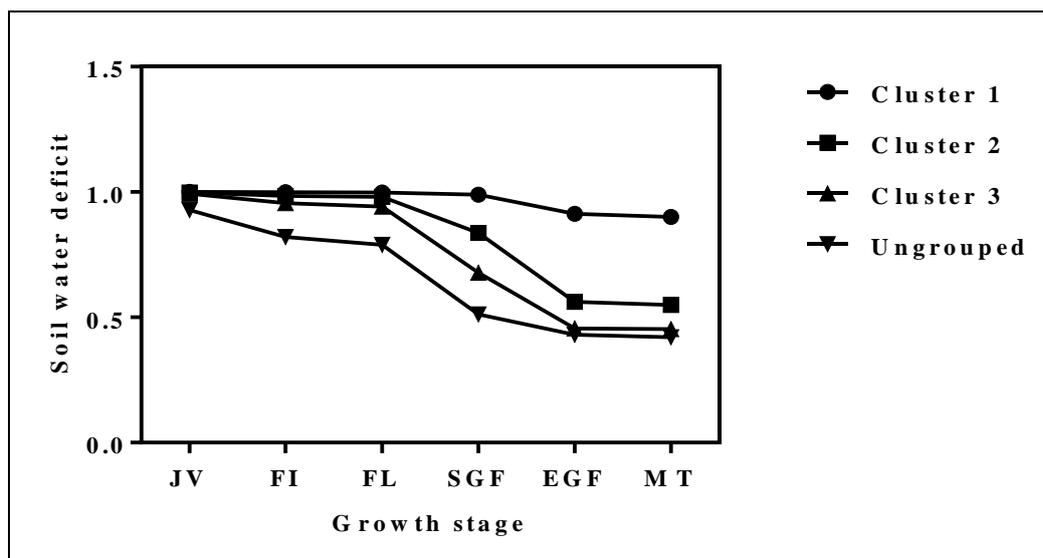


Figure 7.8: APSIM-predicted soil water deficits in different growth stages over a 100 year period x 50 locations x six varieties. JV, juvenile stage; FI, floral initiation; FL, flowering; SGF, start of grain filling; EGF, end of grain filling; MT, maturity stage.

Multiple linear regression of all growth stages was significant ($P < 0.001$) and accounted for 96.2% of the total variation in grain yield. The start of grain filling was the critical point where drought most severely affected yield (Table 7.4). However, stress later in grain-filling also limited yield but to a lesser extent. These results show that the whole grain filling period is very sensitive to any soil water deficit.

Table 7.4: Multiple linear regression of various growth stages in relation to chickpea yield

Summary of analysis					
<i>Source</i>	<i>d.f.</i>	<i>s.s.</i>	<i>m.s.</i>	<i>v.r.</i>	<i>F pr.</i>
Regression	2	22550219	11275109	619.05	<.001
Residual	47	856032	18213		
Total	49	23406251	477679		

Wald tests for dropping terms				
<i>Term</i>	<i>Wald statistic</i>	<i>d.f.</i>	<i>F statistic</i>	<i>F pr.</i>
swdSGF	493.6	1	493.64	<0.001
swdEGF	10.8	1	10.8	0.002

Where swdSGF is soil water deficit at the start of grain filling and swdEGF is soil water deficit at the end of grain filling, d.f is degrees of freedom, s.s is sums of squares, m.s is mean sums of squares, v.r is variance ratio, Fpr is the Fischer test probability

7.6 Discussion

A target crop ideotype, as defined by Donald (1968), is a developed biological model with predictable behaviour in a known environment. Defining the target environment constitutes an important step in ideotype breeding (Trethowan, 2014). The ideotype developed in the present study is a stress ideotype (Sedgley et al., 1990) suited for areas which experience terminal drought. One of the proposed traits for this ideotype is early ground cover (Singh et al. (1993); Toker et al. (2007)). This enables the plant to cover the bare ground quickly, thereby reducing water loss associated with evaporation from the soil (Sekhon et al., 2010). Early flowering is important especially in areas which experience terminal drought because the plant can complete pod setting before the onset of water stress (Jain, 1975; Singh et al., 1993; Toker et al., 2007). However, there is often a trade-off between early flowering and high yield potential which may limit yield in cooler, wetter years. Short machine harvestable plants are desirable in water limited environments partly because they will not waste resources in the stem and are less susceptible to lodging. Small leaflets which reduce water loss through evapotranspiration are desirable and adopted for the ideotype designed in the present study. Similar proposals were made by Toker et al. (2007), Saxena (2003) and Saxena and Johansen (1990). High chlorophyll content at mid podding was associated with higher yields under drought conditions whereas high chlorophyll later in the growing season resulted in lower yields (Jain, 1975; Nayyar et al., 2005). This is probably a function of slightly later development, thus exposing the plant to moisture stress during late pod filling. High harvest index is an important determinant of yield under moisture limited conditions (Siddique and Sedgley (1985) Jain (1975). Sonali and Tyson were closer to the ideotype than the widely grown cultivar PBA Hattrick in terms of harvest index.

APSIM is a dynamic crop simulation model that takes into account management options in farming systems to simulate both biological and physical processes (Keating et al., 2003). It has been effectively parameterised for various crops including mungbean, peanut and chickpea (Robertson et al., 2002), wheat and soybean (Mohanty et al., 2012), pearl millet (Akponikpè et al., 2010), sorghum (Whish et al., 2005) and maize (Archontoulis et al., 2014). In the present study, the comparison between simulated and observed field data returned a coefficient of determination for days to flowering of 0.6 and 0.7 for yield. These data are comparable to Carberry (1996) and Robertson et al. (2002) who each reported a coefficient of determination of 0.7 for days to flowering and yield in chickpea, respectively.

Grain yield ranged from 760 to 3902 kg ha⁻¹ in the Australian grain belt environments and similar diversity was reported by Chauhan et al. (2008). These authors reported six clusters of Australian environmentally-based locations compared to just three in India. This diversity reflects the importance of yield stability for both plant breeders and grain growers. However, this challenge can be tackled by exploiting genotype by environment by management interactions and matching crop phenology to the target environment. The majority of the locations had simulated yields greater than the break-even yield for chickpea of 1 t/ha reported by Whish et al. (2007) which makes chickpea a profitable venture for farmers. High yield in some locations, coupled with the benefits of soil amelioration that chickpea provides, should lead to wider adoption of chickpea in the Australian grain belt farming systems. The yield in the no-till production systems was consistently higher than the till system as observed by others (Dalal, 1989, Horn et al., 1996). This advantage is perhaps due to water conserved in the no-till system that becomes available later in the growing season (Rathore et al., 1998).

Kholová et al. (2013) used the soil moisture deficit approach to characterise sorghum growing environments. Lake et al. (2016) and Chenu et al. (2011) used the same approach to characterise chickpea and wheat growing environments, respectively. The present study grouped environments into three distinct clusters with two arid locations (Bourke, Rudall) remaining ungrouped. This classification differs slightly from Lake et al. (2016) who reported four clusters. Nevertheless, the stress patterns are similar to the Lake study with the majority of locations classified as limited by terminal drought. However, in the current study no environments recovered from terminal drought as reported by Lake et al. (2016). Stress generally started at the reproductive phase, with early podding/start of grain filling being the most sensitive to drought. A similar finding was reported by (Thudi et al., 2014).

7.7 Conclusions

Ideotype breeding can increase chickpea drought tolerance and hence sustain yields across the Australian grain belt and areas with similar climates. *In silico* testing is a more efficient way to evaluate chickpea genotype performance in a wide range of environments. The developed chickpea ideotype outperformed the other genotypes in a wide range of environments and was closely followed by Sonali which was identified as a drought tolerant genotype. Since Sonali had 76% similarity to the ideotype, it can be used as a target for incorporating the ideotype traits. Incorporating traits associated with drought tolerance into commercially grown genotypes can lead to faster adoption of drought tolerant genotypes and resilient chickpea production systems.

Based on the soil water deficit approach the Australian chickpea growing environment was characterised into three main clusters. The same approach can be used to characterise the growing environments for any crops grown in the Australian grain belt as well as other parts of the world where drought is a major problem. By characterising the growing environments, it is possible to match crop phenology with the environment and target specific drought environments. This could lead to minimal losses from terminal drought by ensuring the reproductive phase which is most sensitive to drought is reached in a period when soil moisture is not limiting. Short season crops can be grown in areas where drought starts early in the season, whereas longer maturing genotypes can be grown in areas where soil moisture is adequate. Similarly, the framework for developing chickpea ideotype can be used to develop ideotypes of other crops which are important strategies in adapting to adverse environments.

8.0: GENERAL DISCUSSION

8.1 Introduction

Chickpea is an important legume that provides dietary protein in both human and animal diets. It also ameliorates the soil through atmospheric nitrogen fixation. However, chickpea suffers from terminal drought in many of the areas that it is cultivated. This condition is exacerbated by the fact that climate change may cause an increase in intensity and frequency of droughts in the future. Supplementary irrigation may be used, however 80% of all allocable water is currently already used in agriculture and this option may not always be feasible. Growing chickpea genotypes that have high water use efficiency and can sustain yield under drought environments is a better option. However, the challenge still remains because water use efficiency is a complex trait and not an easy target for plant breeders. This breeding challenge be overcome by identifying secondary traits that are highly heritable and simple to work with as surrogates. A combination of improved genotypes and management options, including tillage practices, can help increase water use efficiency and sustain yields under water limited conditions.

This thesis investigated; i) water use, WUE and yield variation in chickpea genotypes, ii) the basis of chickpea yield under water limited field conditions, iii) effect of genotype by environment by management interactions on chickpea phenotypic stability and iv) development of a drought tolerant chickpea ideotype for the Australian grain belt (Figure 8.1).

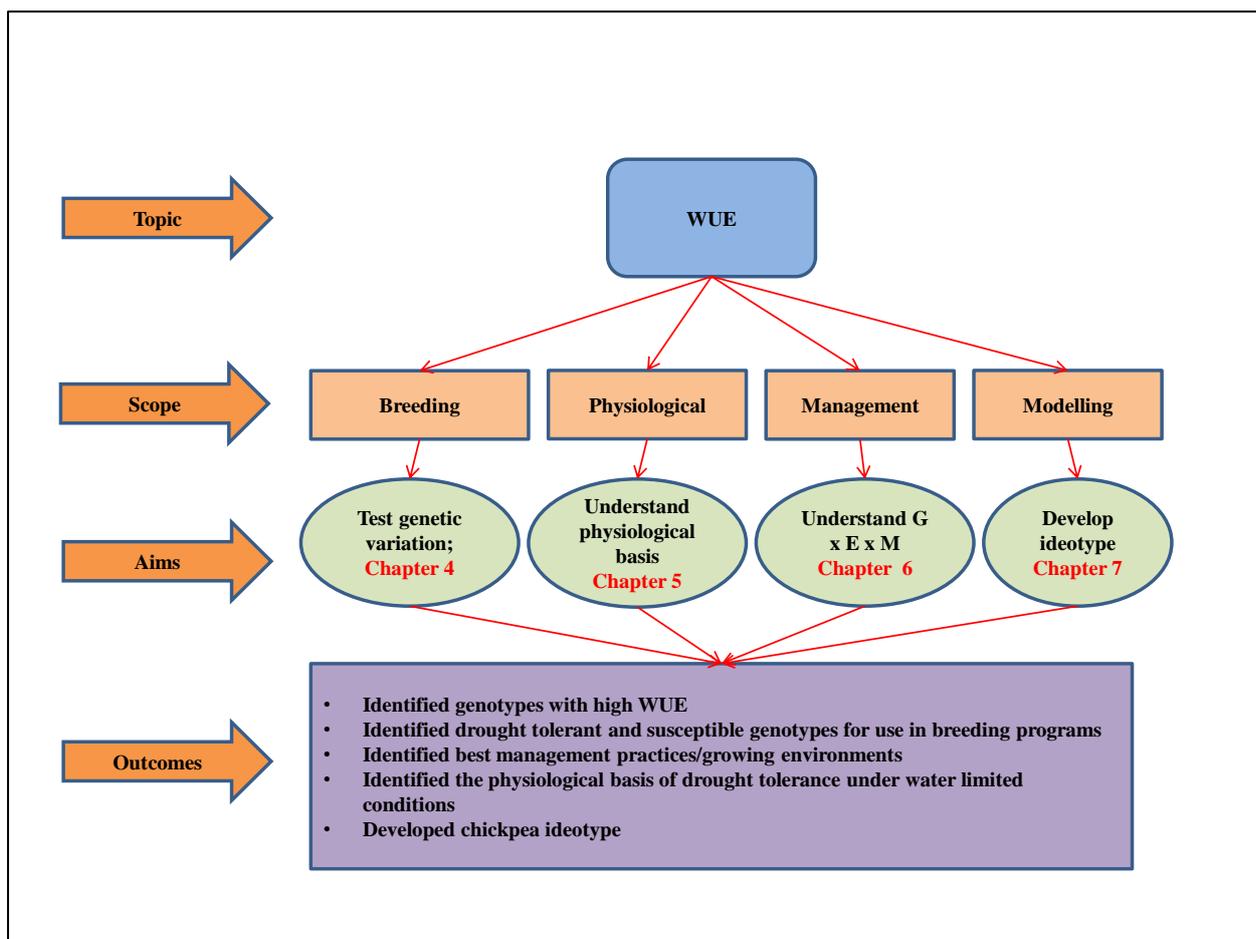


Figure 8.1: Schematic presentation of the scope, aims and findings of the present study

Table 8.1: Thesis summary with objectives, key findings and outcomes

Chapter	Objective	Key findings	Outcomes	Further enquiry
4	Elucidate differences in WU and WUE	No difference in WU in the tested chickpea genotypes but WUE was different	Better understanding of WU and WUE in chickpea genotypes	WUE efficiency results vary, more research is needed in a multi-factor level, using diverse soils and water regimes
	Discover the effect of tillage and irrigation on WUE	No till generally had higher WUE WUE efficiency was higher under irrigation	No till may be more beneficial than till due to increased WUE	
5	Identify drought tolerant and drought susceptible genotypes	Sonali, PBA Slasher and ICCV 96853 were drought tolerant and Genesis 079 and Amethyst are susceptible	Drought tolerant and susceptible chickpea types identified	Single drought indices may not always be the best predictors of drought tolerant genotypes. More indices should be evaluated under different drought intensities
	Identify traits associated with yield formation under water stressed conditions	A total of 21 phenological, morphological, physiological and yield component traits identified	Better understanding of chickpea yield formation under water stressed conditions	
	Identify field trait markers using drought indices	NDVI and chlorophyll content identified as good marker traits for drought tolerance	Relationship between marker traits and drought tolerance identified	

6	Measure extent of G x E interaction in chickpea	There was significant G x E interaction	G x E in different environments confirmed	More diverse environments need to be included to further test the extent of G x E in chickpea
	Identify possible mega-environments	Two mega-environments were identified	Discriminating ability and representativeness of environment identified	
	Identify stable and high yielding genotypes	The ideal genotype was Sonali, followed by ICCV 96853 and PBA Slasher	Ideal genotypes identified	
7	Develop chickpea ideotype	Chickpea ideotype outperformed commercial cultivars	Chickpea ideotype design and performance evaluated	Further research is needed to evaluate the performance of the ideotype under drought and irrigated conditions
	Characterise chickpea growing environments	Three major growing environments were identified	Drought patterns in growing areas identified	
	Identify critical growth stage for drought damage	Reproductive phase is the most critical stage in terms of sensitivity to drought	Critical stage identified	

8.2 Water use and water use efficiency in chickpea

Water use was not significantly different among the genotypes which is consistent with data reported by Brown et al. (1989). Chickpea yield was generally higher under no till compared with the tillage treatment. This may be attributed to the higher moisture levels evidenced in the no-till treatment resulting from soil moisture conservation and storage (Felton et al., 1995) and lower soil temperatures and evaporation due to higher plant residues on the soil surface (Hatfield et al., 2001). Genotypes that had high yield potential under water stressed conditions were drought tolerant with high WUE. Since chickpea is mostly grown on stored soil moisture, it is important to make management decisions that ensure moisture is conserved. No-till provides such an avenue for soil moisture conservation under receding moisture conditions and may be a helpful management option for chickpeas. WUE was higher under no-till than under till conditions with Sonali, ICCV 96853 and PBA having high WUE across all the treatments compared with the other test varieties. The most water efficient genotypes can be used as parents in a breeding program to increase WUE or grown directly by growers. The observed genotypic variation for WUE was generally low and there is a need to diversify the genetic base through germplasm introductions or hybridisation in efforts to breed for high WUE.

8.3 Chickpea yield under water limited conditions

Selection efforts for genotypes that are high yielding under both well-watered and water stressed conditions should be done carefully in order to obtain the best genotypes. In the present study, the use of drought indices has been shown to be a useful tool for identifying drought tolerant genotypes that have high yield potential under well-watered conditions and that can sustain yield under water limited conditions. Mean relative performance (MRP), relative efficiency index (REI) and stress tolerance index (STI) were the best of the indices used in this chickpea study for identifying drought tolerant genotypes with a high yield potential. These indices were highly correlated with yield under both well-watered and water stressed environments.

Several traits (21 in total) were identified as the main contributors (explained 91% of the total variation) to yield variation under water stressed environments. These traits included phenology (days to 50% flowering, days to last flower and flower duration), morphological (leaf characteristics and plant height), physiological (chlorophyll content and NDVI) and yield components (biomass, harvest index and seed weight). Water deficit conditions generally reduced the expression of these traits.

Trait association with drought indices can be used to identify select for drought tolerance in the field. NDVI and chlorophyll content were significantly and positively associated with mean relative performance, relative efficiency index and stress tolerance index. This means that NDVI and chlorophyll content can be used in the field to identify genotypes that are drought tolerant. By identifying such genotypes early in the field, the plant breeder can observe other traits during selection that are not necessarily related to yield but may be of importance to the end user.

8.4 Chickpea phenotypic stability

Total rainfall and rainfall distribution plays a key role in yield formation under water limited conditions. In the present study, there was less rainfall in 2014 during the vegetative phase than in 2015 but the yields were higher in 2014. This indicated that the vegetative phase may not be the critical stage for yield formation under rainfed conditions. There was a large seasonal effect (year) that caused much of the variation in yield.

In order to understand the effect of environment on yield stability, GGE biplots were used. They identified IRN14 and RFN14 as highly discriminating and representative environments. This indicates that genotype evaluation can be done in these two environments and representative information for the other environments under study will still be obtained. Evaluating phenotypic stability alone without yield potential is not sufficient. It is important to identify genotypes that have high yield potential and are stable across environments. In the present study, Sonali, PBA Slasher and ICCV 96853 were identified as relatively stable and possessing high yield potential.

8.5 Chickpea ideotype

Phenological, morphological, physiological and yield component traits were identified and used to construct a chickpea ideotype. Ideotype breeding helps the plant breeder focus selection on important traits and introgress them into the desired background. The constructed plant ideotype performed better than the commercially grown cultivars under a range of environments. Environmental characterisation delineated the Australian grain belt into three major clusters based on soil water deficit ratios. These environments varied in terms of drought and the timing of drought, with the high yielding environment having very little moisture deficit during the reproductive phase. The two other environments had different drought intensities towards the end of the growing season and affected the reproductive phase which was identified as the most sensitive to drought.

8.6 Summary of discussions

There is continued increase in incidence of drought in areas where chickpea is cultivated. This has called for concerted efforts in addressing this problem. An integrated approach was used in the present study whereby genotypes with high water use efficiency were identified in chickpea varieties commonly grown in farmers' fields and also used as parents in a breeding program. For the genotypes that are commonly grown under farmer field conditions, stability of yield was assessed under varying conditions to ensure sustainability of yield under diverse environmental conditions. Several physiological traits were also identified to help in the breeding program as well as key target traits in developing the chickpea ideotype.

8.7 Conclusions

There was genetic variation for WUE but not for water use. Chickpea genotypes that had high yield potential coupled with WUE performed well under both well-watered and water limited conditions.

There was a positive correlation between non stressed chickpea yield and stressed chickpea yield, and as such, selection performed under well-watered conditions should lead to high yields under water stressed conditions. Sonali, PBA Slasher and ICCV 96853 were identified as drought tolerant using three drought indices; namely mean relative performance, relative efficiency index and stress tolerance index. NDVI at early and late podding, as well as chlorophyll content at late podding, can be used as markers to select for drought tolerant genotypes in the field.

GGE biplot analysis grouped the growing environments into two mega environments with Sonali, ICCV 96853 and PBA Slasher showing a wider adaptation into the environments.

Water use was not different among the genotypes tested but hydraulic conductance was significantly different ($P < 0.05$) for whole plant, and root and stem. Water stress reduced expression of most morphological traits. Sonali, which is drought tolerant, had high hydraulic conductance for whole plant, root and stem, and leaves under water stressed conditions enabling it to quench the transpiration stream.

The developed chickpea ideotype outperformed the commercial genotypes tested *in silico* across a wide range of environments. Sonali was closer to the ideotype and had 76% similarity; hence it is a suitable target to introgress the preferred ideotype traits.

In general, chickpea productivity in water stressed environments can be increased by selecting genotypes with high yield potential and high WUE. These genotypes should show drought tolerance and be stable across environments. By targeting secondary traits that confer yield under water stressed environments, and using them to construct chickpea ideotypes which can be matched to the growing environment, yield may be increased.

8.7 Further research

- More research is needed to understand chickpea WUE in different tillage systems.
- Single drought indices may not be reliable in identification of drought tolerance in chickpea. A large combination of indices should be further tested under different drought intensities to identify the best combination for drought tolerant chickpea genotypes. These indices should also be tested to verify consistency of the identified physiological markers for drought tolerance.
- The genomic regions for the 21 identified traits that confer yield under water limited environments need to be identified using molecular tools for further testing and introgression.
- There was genotype by environment interaction under different soil and tillage environments. There is a need to test this interaction further by incorporating various sites with different soil types and moisture regimes to see if the interaction is repeatable and thus can be exploited by plant breeders.

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