PHYSIOLOGY OF YIELD DETERMINATION IN CHICKPEA (Cicer arietinum L.): CRITICAL PERIOD FOR YIELD DETERMINATION, PATTERNS OF ENVIRONMENTAL STRESS, COMPETITIVE ABILITY AND STRESS ADAPTATION

Lachlan Lake

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Contents

Abstract

Average global chickpea yields are low (< 1.0 t ha^{-1}), due mainly to a lack of adaptation, particularly to abiotic stresses such as water and temperature. To help address this we conducted five experiments to: (i) determine the critical period for yield determination as background for adaptation to stress; (ii) quantitatively characterise the Australian cropping environment for water and temperature stress and (iii, iv and v) evaluate the association of secondary traits with improved yield and reliability. Research used a set of 20 chickpea lines (fifteen Desi and five Kabuli) chosen for their variability. Experiments were conducted at Roseworthy (34∘52'S, 138∘69'E) and Turretfield (34∘33'S, 138∘49'E) South Australia from 2013 to 2015. All research uses cumulative thermal time or degree days (^{o}Cd) to quantify and measure phenology, based on the sum of mean diurnal temperature minus a species specific critical or base temperature.

(i)   The critical period for yield determination was determined using successive 14-day shade treatments to stress chickpea across the growing season and determine the period of greatest sensitivity. The critical period was found to be similar to field pea and lupin but later than cereals; it was 800 ^{o}Cd long with the most critical point being 100 – 200 ^{o}Cd after flowering where yield loss reached up to 70 percent (Chapter 2).

(ii)   Real yield, weather data, and modelled water stress were used to determine the major types, frequency and distribution of water and temperature stress patterns in the Australian chickpea growing regions (Chapter 3). Three dominant patterns of maximum and minimum temperature and four dominant patterns of water stress were identified. The most frequently occurring temperature environments were associated with the lowest yield, while the most frequently occurring

water stress environment types were associated with the second lowest yield.

(iii)   To determine the relationship between intragenotypic competitive ability and yield, comparisons were made between normal and relaxed density regions of the crop; the associated difference for trait values was considered the response to competition (Chapter 4). A significant negative association between competitive ability and yield was established. Wrights fixation index (Fst) genome scan revealed different genomic regions associated with yield under relaxed and normal competition and identified 14 regions that were implicated in response to competition of yield, seed number and biomass.

(iv)   We used normalised difference vegetative index (NDVI) with biomass calibration to measure crop growth rate and determine its association with yield. A significant linear relationship was established from 300 ^{o}Cd before until 200 ^{o}Cd after flowering (Chapter 5) indicating a tight coupling between crop growth and yield; the relationship was stronger under water stress.

(v)   To further investigate the drivers of crop growth, relationships between yield, radiation interception (PAR_{int}) and use efficiency (RUE) were established (Chapter 6). Yield was associated with seasonal, pre-flowering, post-flowering PAR_{int} across crops and with seasonal and after flowering PAR_{int} in the irrigated crops. Yield was positively associated with seasonal and after flowering RUE across crops, all stages in irrigated crops and with seasonal RUE in water stressed crops.

The knowledge on the critical period (Chapter 2), and quantitative environmental characterisation (Chapter 3) coupled with the association of yield with secondary

traits (Chapters 4 - 6) provide a platform for enhanced agronomy and breeding for the advancement of chickpea adaptation.

Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Publications

This thesis has been prepared in accordance with the specifications of the University of Adelaide's 'Thesis by publication' format. The thesis contains a collection of manuscripts, four of which have been published in refereed journals, and a fifth that has been accepted for publication in a refereed journal.

The thesis contains five manuscripts, each presented as a separate chapter (2 - 6) and are presented in the format required by the specific journal. References for the published manuscripts are detailed at the end of the manuscript while references for the introduction and general discussion sections are presented in a section at the end of the thesis. A statement of authorship precedes each published manuscript detailing individual contributions and signatures of authors.

Peer reviewed publications include:

Chapter 2. Lake, L., Sadras, V.O., 2014. The critical period for yield determination in chickpea (Cicer arietinum L.). Field Crops Research 168, 1-7.

Chapter 3. Lake, L., Chenu, K., Sadras, V.O., 2016. Patterns of water stress and temperature for Australian chickpea production. Crop and Pasture Science 67, 204-215.

Chapter 4. Lake, L., Li, Y., Casal, J.J., Sadras, V.O., 2016. Negative association between chickpea response to competition and crop yield: Phenotypic and genetic analysis. Field Crops Research 196, 409-417.

Chapter 5. Lake, L., Sadras, V.O., 2016. Screening chickpea for adaptation to water stress: Associations between yield and crop growth rate. European Journal of Agronomy 81, 86-91.

Chapter 6. Lake, L., Sadras, V.O., 2017. Associations between yield, intercepted radiation and radiation use efficiency in chickpea. Crop and Pasture Science 68, 140-147.

Acknowledgements

Chapter 1

Introduction and literature review

1.1 Introduction

In the next 30 years global agriculture needs to increase production to feed an extra 3 billion people in the face of increasing climate variability and a shrinking area of arable land (Vadez et al., 2012, Soltani et al., 2016, Cohen, 2003, Field et al., 2012). Cool season grain legumes are an integral part of a sustainable agriculture solution, particularly in arid and semi-arid regions. Cool season grain legumes have the ability to enhance soil health, fix biological nitrogen (reducing inputs and greenhouse emissions) and improve rotation and weed control options; pulses are also increasingly recognised for their role in human nutrition (Armstrong et al., 1997, Unkovich et al., 1995, Soltani and Sinclair, 2011, Soltani and Sinclair, 2012b, Foyer et al., 2016).

Chickpea is one of the most important cool season grain legumes in terms of both global and Australian production (Krishnamurthy et al., 2013, Berger et al., 2006, Farooq et al., 2016, Jumrani and Bhatia, 2014). In 2015 chickpea overtook lupin as the most widely produced grain legume in Australia with area harvested of ~ 600,000 hectares (FAO, 2015). However when compared to the annual Australian wheat area of 1,2616,000 ha in 2015, it is clear that there is opportunity to further integrate chickpea into the agricultural landscape. Wheat is a more reliable crop with better water and temperature stress adaptation, with the more vulnerable chickpea considered low yielding and unreliable in comparison (Kashiwagi et al., 2005, Kashiwagi et al., 2006, Zaman-Allah et al., 2011, Subbarao et al., 1995, Krishnamurthy et al., 2013, Devasirvatham et al., 2012, Singh, 1999, Singh and Virmani, 1996, Soltani and Sinclair, 2012a). The average Australian chickpea yield from 1983 - 1992 was 1.1 t ha^{-1} and despite breeding efforts since then, progress has been slow and in the last 10 years of poor rainfall and drought conditions, yield has averaged a mere 1.2 t ha^{-1} (FAO, 2015). In order to increase the adoption of chickpea in Australia and elsewhere, and to realise the potential benefits of grain legumes in rotations, progress must be made in improving yield and reliability particularly under water and heat stress.

1.2 Chickpea and the water and temperature stresses

Despite pulses being poorly adapted to water stress compared to cereals, chickpeas are considered one of the more drought tolerant of the cool season grain legumes (Leport et al., 1999, Berger et al., 2004) although the basis of this perceived drought tolerance and the effects of drought stress are not well understood (Singh, 1993). Possible reasons for this perceived drought tolerance among pulses include chickpea's ability to extract more soil water from the soil profile or perhaps due to a relatively smaller, slower developing canopy compared to other grain legumes or a combination of the two (Berger et al., 2004, Mwanamwenge et al., 1997). It has also been noted that chickpeas increase their rooting depth under water stress and are better adapted to dry conditions than field pea or soybean (Benjamin and Nielsen, 2006). Of particular relevance to chickpea adaptation is the domestication history. Unlike other current cool season grain legumes from the West Asian Neolithic Crop assemblage, chickpea was domesticated as a spring sown crop, meaning that yield was more reliant on stored soil moisture compared to autumn sown counterparts (Berger and Turner, 2007, Redden and Berger, 2007, Abbo et al., 2003).

Research strategies to increase the reliability of chickpeas in water limiting, Mediterranean type environments with hot terminal temperatures includes:

- Investigating short duration cultivars that will avoid late season water and heat stress (Kumar and Abbo, 2001, Kumar et al., 1985, Kashiwagi et al., 2006, Subbarao et al., 1995, Ludlow and Muchow, 1990, Abbo et al., 2003, Turner et al., 2001, Jagdish and Rao, 2001, Turner, 1997).
- Breeding for synchronous flowering (Krishnamurthy et al., 2013, Cohen, 1971).
- Breeding for deep profuse root systems (Krishnamurthy et al., 1998, Johansen et al., 1994, Kashiwagi et al., 2005, Kashiwagi et al., 2006, Ludlow and Muchow, 1990, Xuemei et al., 2010, Krishnamurthy et al., 2013, Turner et al., 2001, Subbarao et al., 1995).

- Conservation of soil moisture during the vegetative stages (Zaman-Allah et al., 2011, Mitchell et al., 2013).

To date these strategies have been largely unsuccessful due to the complex unpredictable nature of abiotic stress, a lack of understanding of the physiological underpinnings of yield and a lack of quantitative environmental characterisation. There has also been poor association between secondary traits and yield. Together these factors hinder quantification of tolerance and result in a lack of successful direct screening methods (Xuemei et al., 2010, Varshney et al., 2011).

1.3.0 Knowledge gaps

1.3.0.1 The critical period for yield determination

To better understand the effect of water and temperature stress on chickpea yield and identify potential methods to combat them, it is important to identify the species specific critical period for yield determination; exposure to stress during this period causes greatest yield loss. Much work has been done identifying the critical period for yield determination in cereals (Arisnabarreta and Miralles, 2008, Estrada-Campuzano et al., 2008, Early et al., 1967, Kiniry and Ritchie, 1985, Fischer and Stockman, 1980, Savin and Slafer, 1991, Mahadevan et al., 2016), quinoa (Bertero and Ruiz, 2008), soybean (Jiang and Egli, 1995, Board and Tan, 1995), lupin and fieldpea (Sandaña and Calderini, 2012, Guilioni et al., 2003), but as yet, no information is available in chickpea. Identification of the critical period will aid in management of the crop with emphasis on ensuring good growth and stress alleviation during the critical period; physiological status of crop plants in the critical period is tightly linked with grain number and yield (Andrade et al., 2005). Identification will also aid in (i) stress screening, with a greater ability to target stress exposure in the critical period and (ii) screening for secondary traits such as crop growth rate, which is reliant upon identification of physiologically meaningful windows (Tollenaar et al., 1992, Guilioni et al., 2003, Echarte et al., 2004, Zhang and Flottmann, 2016).

1.3.0.2 Quantitative environmental characterisation of the Australian chickpea regions

The largest component of crop yield variation in the short to medium term is the environment (Chenu, 2015, Sadras et al., 2012a); however quantification of this variance is traditionally limited with breeders relying on check varieties and multiple environments in an effort to disentangle the effects of environment on heritability and trait performance; the refined methods used to characterise genotypes are not employed to characterise environments (Sadras et al., 2009, Varshney et al., 2011). Recent research has used historical weather data and modelling to perform quantitative environmental characterisations of Australian water stress environments for crops such as sorghum, wheat and field pea (Chenu et al., 2011, Chenu et al., 2013, Sadras et al., 2012a, Muchow et al., 1996); these characterisations typically quantify the major types, frequency and distribution of water stress environments although little attention has been paid to temperature. Quantitative environmental characterisation for the major water and temperature stress environments has not been undertaken for the Australian chickpea production regions. The quantification and probability of the seasonal crop water and temperature stress types for a given location will aid breeding by enhancing the probability of successful site selection, reducing the number of sites needed, and reducing the likelihood of misrepresenting the target population of environments (Turner et al., 2001, Sadras et al., 2012a, Chenu, 2015). This information may also aid in agronomic decisions such as crop choice and sowing time.

1.3.0.3 Quantifying the relationship between yield and intragenotypic competitive ability

One of the largest increases in yield and stability in wheat occurred with the introduction of the less competitive semi dwarf or 'communal' plant types (Donald, 1981, Donald, 1963). This relationship between yield and competitive ability has been investigated in the cereals including rice, wheat and barley, and in sunflower (Jennings and Aquino, 1968, Jennings and Herrera, 1968, Jennings and Jesus,

1968, Khalifa and Qualset, 1975, Thomas and Schaalje, 1997, Sadras et al., 2000) but there has been no investigations into any of the grain legumes. Despite the volume of research on competitive ability, there has only been one study looking at the genetics of this relationship; Sukumaran et al. (2015) identified a major locus for adaptation to density using genome-wide association study method. A suitable method for genetic analysis will be to compare the trait variation using Wrights fixation index (Fst) genome scan method, which measures genetic variance among populations (Fumagalli et al., 2013). Quantifying the relationship between competitive ability and yield and exploring the genetic basis will aid in early generation selection methods and the breeding of higher yielding and more reliable chickpeas.

1.3.0.4 Quantifying the relationship between yield and crop growth rate

Crop growth rate within physiologically meaningful species-specific critical periods has been linked to yield in maize, wheat, sunflower, quinoa, canola, pea and soybean (Tollenaar et al., 1992, Andrade et al., 1999, Vega et al., 2001a, Vega et al., 2001b, Andrade et al., 2002, Guilioni et al., 2003, Echarte et al., 2004, Zhang and Flottmann, 2016, Bertero and Ruiz, 2008, Kantolic et al., 2013). It has been suggested that crop growth rate is a good indicator of yield under stress as it is directly affected by stress and integrates all environmental factors (Andrade et al., 2002, Wiegand and Richardson, 1990). The relationship between yield and crop growth rate within the species specific critical period is yet to be established within chickpea and may be useful for stress adaptation.

1.3.0.5 Quantifying the relationship between yield and radiation interception and use

One of the main determinants of crop growth and yield is the ability of the plant to intercept radiation and effectively convert this into biomass (Hao et al., 2016, Li et al., 2008). Growth, radiation interception (PAR_{int}) and radiation use efficiency (RUE) have all been shown to be reduced by water and temperature stress (Singh and Rama, 1989, Tesfaye et al., 2006); however research into the trends of RUE over the growth cycle and in response to stress is limited in chickpea. Some

research assumes a linear or constant RUE over the entire growth cycle (Soltani et al., 2006) however research in pea and lucerne demonstrates that RUE changes depending on the energy requirements of the growth stage (Lecoeur and Ney, 2003, Khaiti and Lemaire, 1992); in sunflower RUE reduces during the reproductive stage due to the higher energy cost of producing seeds compared to leaves and also due to senescence (Albrizio and Steduto, 2005, Trapani et al., 1992). In sorghum and maize Stockle and Kiniry (1990) and Kiniry et al. (1998) observed decreased RUE was associated with increased vapour pressure deficit (VPD) although Sinclair and Muchow (1999) dispute the conclusions reached by Kiniry et al. (1998). There is a gap in knowledge surrounding the variability of PAR_{int} and RUE at different phenological stages and how this relates to yield and stress adaptation in chickpea.

1.3.0.6 Overview

This review will summarise the current knowledge and status on: critical periods for crop yield determination, advances in environmental characterisation, the relationship between yield and competitive ability, crop growth rate, radiation interception and radiation use efficiency. This will develop our argument for the need to identify the critical period for yield determination and for quantitative environmental characterisation, to have a greater understanding of chickpea physiology in relation to competitive/communal traits and the benefit of identification of secondary traits associated with improved reliability under conditions of abiotic stress.

1.3.1 Critical period for yield determination

Understanding the physiological underpinnings of yield is critical for development of chickpea genotypes with greater yield and reliability in the Mediterranean environment. The critical period for yield determination is the most physiologically important period for yield development and the time when crops are most exposed to yield loss due to stress. There has been a significant amount of work

carried out on the critical period for yield determination in cereals, but significantly less in legumes, particularly cool season grain legumes (Sandaña and Calderini, 2012). Identification of the critical period for chickpea will assist breeders in selecting appropriate environments for stress screening and also assist in the identification of gene environment interactions (GE) (Sadras et al., 2012a, Chenu, 2015). Knowledge of the critical period will aid in modelling the effects of climate change on chickpea yield, specifically the change in length of phenological phases and associated yield effects (Vadez et al., 2012). There will also be implications for crop management, with identification of the most important physiological period to avoid or minimise exposure to stress.

In cereals the critical period has been determined in wheat, oat, barley, triticale and maize (Fischer, 1985, Fischer and Stockman, 1980, Savin and Slafer, 1991, Kiniry and Ritchie, 1985, Arisnabarreta and Miralles, 2008, Estrada-Campuzano et al., 2008, Cerrudo et al., 2013, Mahadevan et al., 2016); these critical periods are species specific with barley occurring before anthesis, wheat, oat and triticale around anthesis and maize extending into the post anthesis phase. In sunflower and quinoa the critical period has been determined to be after anthesis (Cantagallo et al., 1997, Bertero and Ruiz, 2008). The grain legumes soybean, pea and lupin have been shown to have later critical periods than the cereals (Ney et al., 1994, Board and Tan, 1995, Jiang and Egli, 1995, Guilioni et al., 2003, Sandaña and Calderini, 2012, Sandaña et al., 2009). In soybean the critical period has been identified as stretching from R1 to 12 days post R5 (beginning of bloom to 12 days after beginning seed) (Jiang and Egli, 1995, Board and Harville, 1993, Board and Tan, 1995, Torrion et al., 2012). In lupin and field pea the critical periods are 10 days before beginning of flowering up to 40 (lupin) and 50 (field pea) days post flowering (Sandaña and Calderini, 2012). A graph of the relative critical periods of barley, wheat, pea and lupin is presented in Sadras and Dreccer (2015). The differences between cereals and grain legumes may be attributed to the reproductive plasticity and the overlap of vegetative and reproductive growth

in grain legumes and the continuation of flowering after seed set (Slafer et al., 2009, Andrade et al., 2005, Guilioni et al., 2003).

In maize, plant growth rate was measured in the critical period and was shown to be a good indicator of yield under a range of environmental and management conditions (Andrade et al., 2002). In soybean the critical period has been utilised in research looking at the effects of environmental variation on seed number, with increased seed number relating to increased crop growth rate within the critical period (Kantolic et al., 2013). Investigations into reduced yield of field pea associated with heat and water stress showed that yield loss was caused by reduced crop growth rate in the critical period (Guilioni et al., 2003).

1.3.1.1 Method for determining the critical period for yield

One of the first methods that determined the critical period was via defoliation studies looking at density and physical damage in maize (Dungan, 1930, Hanway, 1969); it was observed that the greatest yield reductions were caused by treatments that were imposed around silking thus broadly identifying the critical period. Other early work in maize and one of the first trials to utilise shade as a controlled stress, was conducted by Early et al. (1967) who studied the effects of reduced sunlight on the grain yield and chemical composition of corn hybrids. This work was followed by Kiniry and Ritchie (1985) looking at the growth stage at which stress by shading had the most significant effect of kernels per ear in maize. Aluko and Fischer (1988) also used shading in experiments with maize to investigate the effect of assimilate supply changes during a critical period on final grain yield.

Early work to determine the sensitivity of wheat yield to stress at different physiological stages utilised artificial shading to reduce irradiance and simulate stress (Fischer, 1975, Early et al., 1967). Shading work described by Fischer (1975) and then Fischer and Stockman (1980) determined the most sensitive

point to yield reduction by using reduced radiation to reduce assimilates. More recently artificial shading has been successfully used as a stress to determine the critical period for yield determination in barley (Arisnabarreta and Miralles, 2008). Estrada-Campuzano et al. (2008) and Mahadevan et al. (2016) also investigated the critical period for triticale and oat using successive shading periods as a fast and repeatable stress.

Work in soybean looking indirectly at the critical period for yield determination was conducted by Schou et al. (1978) using different methods (reflectors, light absorbing black boards and shades) at different phenological stages to manipulate the amount of light received by a soybean canopy to determine the subsequent effect on yield and components. Egli and Yu (1991) and Jiang and Egli (1993) investigated the mechanisms responsible for seed yield per unit area by utilising shading as a source of assimilate reduction. An alternative approach to determine the critical period was developed using defoliation rather than shading to cause assimilate reduction (Board and Harville, 1993, Board and Tan, 1995). Kantolic and Slafer (2001) went further in their analysis of the critical period and conducted experiments to see if extending the natural photoperiod of field grown plants had an effect on the length of the critical period.

Recent work by Sandaña and Calderini (2012) looking at the critical period in field pea and lupin also utilised artificial shading over different periods to determine the most sensitive period to assimilate reduction.

The artificial shading commonly used by researchers ranged from 13% (Fischer, 1975) up to 80% (Early et al., 1967, Kiniry and Ritchie, 1985, Aluko and Fischer, 1988, Sandaña and Calderini, 2012). The shade height above the canopy for the different studies is commonly listed as 20cm above the plants, while the common reason to shade plants is to cause yield reduction based on reduced assimilate supply, mimicking the effects of stress (Fischer and Stockman, 1980). Experiments on drought tolerance of wheat found that the more drought tolerant

lines were characterised by an ability to maintain sink strength in the reproductive organs (Xuemei et al., 2010); the potential for shading to cause assimilate reduction to capture the effects of drought and other stresses is therefore high, although there is the potential for unintended effects on the length of phenological stages.

The defoliation method of source reduction adopted by Board and Harville (1993) and Board and Tan (1995) to reduce assimilate supply involved pruning the inter-row area between the rows to 12.5cm within the mid-row line until the desired growth stage was reached. This limited photosynthetic capacity and assimilate supply whilst pruning was maintained. Unintended or confounding consequences of this method may include unrecognised wounding responses, soil water differences between treatments caused by less above ground biomass (biomass), soil temperature differences due to sun exposure, as well as air movement differences, and would appear to make the calculation of harvest index (HI – the ratio of grain yield to harvest biomass) difficult. Defoliation may also have unintended effects associated with the removal of nitrogen from vegetative tissue (Lhuillier-Soundélé et al., 1999, Munier-Jolain et al., 1998).

On the weight of evidence, and considering the potential confounding effects of defoliation, the repeatability of shade and its association with crop growth rate, it is considered that shade is the most suitable method for stress imposition to determine the critical period for yield determination.

1.3.2 Environmental characterisation

One of the most important ways that physiologists can make contributions to breeding is by providing information on better choices of environments in which to conduct selection trials (Jackson et al., 1996). Physiologists via crop growth modelling can increase the efficiency of stress screening programs via environmental characterisation (Chapman, 2008, Subbarao et al., 1995, Chenu, 2015). Most breeding programs rely on multiple environment trials (METs) to

identify breeding material with trait performance that is superior to current genotypes in the target population of environments (TPEs) (Chapman, 2008, Cooper et al., 1996, Turner et al., 2001, Chapman et al., 2000a, Messina et al., 2011). Multi environment trials are costly and the complex interaction between genotype, location and season may lead to a misrepresentation of the intended or target population of environments, biased sampling and limited gain due to the large environmental variance effecting phenotype (Turner et al., 2001, Cooper et al., 2002, Chenu et al., 2013). To assess a genotype performance in a MET, the TPE (largest source of variation) must be characterised and the environments within the MET assessed to determine their suitability in representing the TPE; this will reduce bias and any unintended consequences of a mismatch between the MET and TPE (Chapman et al., 2000b).

The early work of Cooper et al. (1996) in wheat looked at long term GE for wheat in Queensland with the aim of maximising response to selection for yield within specific environments. Genotype location (GL) components were repeatable and through classification, Queensland was divided into regions and sub-regions. The increased knowledge of GL interactions in the sub regions allowed a more consistent application of selection pressure, and increased broad adaptation. Muchow et al. (1996) looked at three indicies of water deficit in sorghum in subtropical Australia in two locations over the period of 96 and 101 years for each environment. Within these locations they classified the water deficit environments and their frequency of occurrence. An index using soil water deficit and relative transpiration was the most useful in identifying groups of seasons with distinct patterns and frequency of occurrence.

This millennium has seen increased interest in environmental quantification, with most research investigating common water deficit patterns (Chapman, 2008, Chapman et al., 2002, Chapman et al., 2000a, Chapman et al., 2000b, Chenu et al., 2011, Chenu et al., 2013, DeLacy et al., 2010, Sadras et al., 2012a, Chauhan et al., 2008, Chauhan and Rachaputi, 2014, Chauhan et al., 2013). A recent

review by Chenu (2015) summarises the most common methods used. Most work to this point has taken place in the cereals wheat, sorghum and maize, however Chauhan et al. (2008) produced a study using phenology and yield data from Australian and Indian chickpea production environments to group environments into homoclimes based on simulated yields. This approach is not driven by specific stress but rather a combination of factors that affect yield; this approach also means that location classification is fixed, rather than probabilistic.

A superior alternative to this in regard to stress adaptation, is stress driven environmental characterisation which takes into account year to year variability at a single location, with multiple environment types possible for a single location. Stress driven environmental characterisation has been conducted in Australia for the cereals wheat, sorghum and maize and also field pea, in Brazil for wheat and rice, sorghum in India and maize in Europe and the United States (Loffler et al., 2005, Heinemann et al., 2008, Chenu et al., 2011, Chenu et al., 2013, Sadras et al., 2012a, Chauhan et al., 2013, Kholová et al., 2013, Harrison et al., 2014). These studies used location and weather data to run simulations to describe the common types of water stress. Chenu et al. (2011) identified three major water deficit patterns for wheat in northern Australia, while similar results were presented by Sadras et al. (2012a) with three major water deficit patterns for field pea in Australia. Most recently Chenu et al. (2013) carried out a large scale characterisation of drought patterns across the Australian wheat belt and defined four major environment types. There has been very little effort to emulate the water stress environmental characterisation for temperature stress.

1.3.3 Competitive ability, border effects and yield

"In the agronomic sense of the capacity to yield more grain as a crop, competitive success offers nothing" (Donald, 1981). Donald (1963) suggested that wheat lines with a higher grain yield under intergenotypic competition were likely to have poorer yield in pure stands when compared to less competitive lines. Donald

(1981) went on to describe the communal ideotype, which is adapted to existence within a pure stand and is of weak competitive ability so that it interferes with like neighbours to a minimum degree; this represents a trade-off between individual plant yield and communal yield (Asplen et al., 2012, Denison, 2015).

The majority of research on the association between competitive ability and yield has occurred in the cereals. In barley Hamblin and Donald (1974) observed that the yield of F_5 cross lines showed no correlation with F_3 single plant grain yield. They found that shorter plants were associated with lower single plant yield in the F_3 and higher stand yields in the F_5.

In wheat Khalifa and Qualset (1975) conducted a study on the competitive effects of tall and dwarf types. They sowed bulk populations with equal frequency of dwarf and tall type plants over four successive generations and witnessed the higher yielding dwarf type steadily decreasing in frequency caused by the competitive superiority of the tall type plants. More recently Reynolds et al. (1994) studied the difference in competitive ability between high and low yield potential wheat varieties and concluded that the high yield potential seemed to be associated with a less competitive phenotype. Thomas and Schaalje (1997) demonstrated that tall, low yielding varieties outperformed short, high yielding varieties when sown in a mixture, while Sadras and Lawson (2011) found that a decline in competitive ability associated with date of cultivar release was associated with higher yield. Sukumaran et al. (2015) showed that wheat genotypes that performed better under intense competition had a smaller response to reduced competition whilst generally being higher yielding. This was the first study to explore the genetic basis of response to competition and used genome wide association study method to detect a major locus associated with adaptation to density.

Research in rice includes a three part series (Jennings and Aquino, 1968, Jennings and Herrera, 1968, Jennings and Jesus, 1968) and a method for looking

at response to competition (Wang et al., 2013). The Jennings series demonstrated that segregating populations experienced intraspecific competition that resulted in a reduction in the proportion of desired individuals within the population (Jennings and Aquino, 1968). Wang et al. (2013) investigated the border effect of rice plots and the associated response to competition by comparing the yield in border rows and central rows of plots. The central rows experienced competition that is consistent with the crop environment, while border rows have low competition by virtue of the inter-plot spacing. The results showed a large difference in yield between the border rows and the central rows of experimental plots, the magnitude of which can be considered the response to competition.

Research in sunflower showed a negative association between the intraspecific competitive ability and yield, and a decreased sensitivity to competition at the population level as being associated with higher yield (Sadras et al., 2000, Andrade et al., 2005).

1.3.4 Crop growth rate and yield

Crop growth rate is one of the most important determinants of chickpea yield (Krishnamurthy et al., 1999, Williams and Saxena, 1991). It has been suggested that success in selecting for high yield in water limiting conditions requires selection for HI and crop growth rate (Krishnamurthy et al., 2013). Crop growth rate within the critical period for yield is able to account for seed number determination under environmental stress conditions with a lower threshold for reproductive partitioning leading to higher yields (Andrade et al., 2005). Relationships between crop growth rate during the critical period and yield have been established in maize, sorghum, wheat, barley, canola, sunflower, pea and soybean (Tollenaar et al., 1992, Andrade et al., 2002, Andrade et al., 2005, Guilioni et al., 2003, Zhang and Flottmann, 2016, Sadras et al., 2012b, Andrade and Ferreiro, 1996, Arisnabarreta and Miralles, 2008, Sadras and Lawson, 2011,

Oosterom and Hammer, 2008). There has also been a study in lupin and field pea that has identified a reduction in yield due to a slower crop growth caused by shading within the critical period (Sandaña and Calderini, 2012).

The models that describe the relationship between crop growth rate in the critical period and yield differ between species. Indeterminate species such as soybean and canola have a linear relationship while determinate maize and sunflower are hyperbolic (Egli and Yu, 1991, Jiang and Egli, 1993, Vega et al., 2001b, Andrade et al., 2005, Zhang and Flottmann, 2016, Vega et al., 2001a). Linear relationships indicate a tight coupling between vegetative and reproductive growth while hyperbolic indicates a decoupling. Pea has been reported to have linear (Guilioni et al., 2003) and non-linear (Sadras et al., 2013) relationships; the reasons for this discrepancy have not been resolved. The intercept of the model of yield and growth rate also differs with soybean and pea having zero intercept indicating no growth threshold for yield and maize and sunflower having non-zero intercepts, indicating a minimum growth threshold before crops yield.

Traditionally crop growth rate has been measured using biomass cuts or allometric methods (Sheehy and Cooper, 1973, Sandaña and Calderini, 2012, Tollenaar et al., 1992, Jiang and Egli, 1995, Vega et al., 2001a, Arisnabarreta and Miralles, 2008). However, a non-destructive strategy to measure crop growth rate is to estimate biomass using a GreenSeeker® as demonstrated by Sadras et al. (2013). The tool measures plant chlorophyll and returns a Normalised Difference Vegetative Index (NDVI) which is a ratio based on the reflectance of red light and near infrared light. The more chlorophyll present under the sensors of the device, the more red light absorbed, and the greater the NDVI returned. To determine biomass and crop growth rate from the NDVI, a species and morphology specific calibration equation must first be established by taking biomass cuts in conjunction with NDVI readings (Sadras et al., 2013).

1.3.5 Radiation interception, use efficiency and yield

Radiation interception (PAR_{int}) and radiation use efficiency (RUE – defined as the ratio of biomass produced and radiation intercepted) have been studied extensively in many crops for the purposes of crop growth analysis and modelling. Work has been conducted in the cereals (Muchow and Davis, 1988, Kiniry et al., 1989, Stockle and Kiniry, 1990, Albrizio and Steduto, 2005, Sadras and Lawson, 2011, George-Jaeggli et al., 2013, Schierenbeck et al., 2016), potato (Zhou et al., 2016) and grain legumes including chickpea, common bean, soybean, cowpea, fieldpea and faba bean (Singh and Sri Rama, 1989, Lecoeur and Ney, 2003, Albrizio and Steduto, 2005, Tesfaye et al., 2006, Jahansooz et al., 2007, Soltani et al., 2007, Giunta et al., 2009, Saha et al., 2015, Adeboye et al., 2016).

Several researchers working with chickpea have investigated either PAR_{int} and RUE or both. Li et al. (2008) investigated the effects of different leaf types and the associated PAR_{int} and RUE and found that fern-leaf cultivars achieved greater PAR_{int} but similar RUE than the unifoliate counterparts. Kang et al. (2008) studied the effects of irrigation on growth and yield of chickpea and found that increased yield was a direct result of increased PAR_{int} and that RUE was increased by both irrigation and nitrogen application. Soltani et al. (2007) determined that RUE changed with temperature and carbon dioxide concentration while Saha et al. (2015) studied the effect of elevated carbon dioxide on PAR_{int} and RUE and found a significant increase in leaf area index and RUE, but with no associated increase in PAR_{int}.

Specific research looking at RUE and water deficit by Singh and Sri Rama (1989) established that RUE is reduced after more than 30% of extractable soil moisture has been removed from the rooting zone; it was also observed that RUE was associated with VPD. More recently Soltani et al. (2006) found a temperature effect on RUE and also that RUE was constant over the chickpea crop cycle under non stressed conditions; this is simplistic, as demonstrated by changes in RUE with ontogeny in several crops (Ridao et al., 1996, Lecoeur and Sinclair, 1996,

Albrizio and Steduto, 2005). Tesfaye et al. (2006) also conducted research on RUE under three different water regimes, concluding that RUE was more sensitive to early stage rather than late stage reproductive water deficit.

1.4 Summary and aims of research

Chickpea is one of the most significant Australian grain legumes and will contribute to both a sustainable agronomic future and to human nutrition in an increasing capacity (Foyer et al., 2016, Berrada et al., 2007). However yield is constrained by a lack of adaptation to disease and abiotic stress, particularly water and heat; lack of adaptation has resulted in low and unreliable global yields that fall below 1.0 t ha^{-1} (Abbo et al., 2003). Current research and breeding for improved adaptation and reliability have to this point failed to realise significant yield gains. Increasing our understanding of the physiology of yield determination, the cropping environment, coupled with identification of secondary traits that are associated with improved yield and reliability are important steps to address this issue.

The objectives of this research are to:
- determine the critical period for yield determination;
- quantitatively characterise the Australian chickpea production environments for major temperature and water stress patterns;
- determine if an increased intraspecific competitive ability is related to lower crop yield;
- determine if crop growth rate in the critical period captures differences in yield in environments varying for stress; and
- determine if increased PAR interception or RUE at different physiological stages is related to increased yield and reliability in environments varying for stress.

1.5 Linking statement

The seven chapters presented in this dissertation include an introductory chapter with a review of current knowledge, research gaps and research objectives, four research chapters published in peer reviewed journals, one chapter accepted for publication in a peer reviewed journal and a final chapter with conclusions and future research. Journal chapters have been structured in accordance with the requirements of each specific journal, with each comprising an abstract, introduction, materials and methods, results and discussion. Some information is duplicated between the research chapters (2 - 6) and the literature review (1) and conclusions and future research (7) chapters. The content seeks to investigate the underpinnings of yield determination in chickpea, quantify the major thermal and water environment types for the Australian chickpea production regions and explore secondary adaptive traits associated with improved yield and reliability, particularly under water stress, in the Australian chickpea growing regions. The information presented will be useful for agronomy, breeding, modelling and growth analysis.

Chapter 1 presents a review of the topics of this dissertation, providing the justification for the research of chapters 2 – 6; this chapter also presents the objectives based on the identified research gaps.

Chapter 2 details the first important step in the research, exploring the physiological basis of chickpea yield determination and determining the critical period using two desi chickpea lines. Critical periods for yield determination have been identified in many species; this has relevance for stress screening as exposure within this period has the greatest impact on yield. This period has relevance for the measurement of other traits such as crop growth rate; crop growth rate has been shown to have the strongest relationship with yield when measured in the critical period. The critical period for yield determination is used in subsequent chapters to aid in experimental design and interpretation of results.

Chapter 3 presents a quantification of the major water stress and temperature environment types for the Australian chickpea production regions. This chapter builds on the second chapter by combining modelled and real data to determine the major chickpea water and temperature environment types and their associated yield, distribution and frequency of occurrence. This quantification provides a framework that can be combined with the information on the critical period and utilised by breeders and agronomists for purposes including environmental selection for stress screening, mitigation of stress within the critical period and increasing the accuracy of modelling.

Chapter 4 explores the relationship between yield and intragenotypic competitive ability and the associated genetic underpinnings of this relationship. A reduced competitive ability and introduction of communal traits in cereals resulted in large yield improvements; we test this hypothesis in chickpea. This chapter utilises the critical period from Chapter 2 and the environmental quantification presented in Chapter 3 to help interpret the G x E effects on response to competition. The analysis includes a genetic component where Fst genome scan is used to identify genomic regions under selection for a given trait by looking at large numbers of molecular markers to scan for regions with extreme differentiation between populations.

Chapter 5 explores the association between yield and crop growth rate within physiologically meaningful periods that are defined in Chapter 2 across environments contrasting for stress. The environmental quantification methods from Chapter 3 are also used to interpret GxE. This chapter also describes the use of NDVI as an alternative technique to measure crop growth rate. We show calibrated NDVI is a non-destructive, high throughput, cheap and repeatable method with advantages to conventional biomass cuts.

Chapter 6 builds on the work from Chapter 5, exploring the relationship between yield and two of the main components of crop growth rate: radiation interception

and radiation use efficiency. The relationship is explored in environments varying for stress, and in physiologically meaningful periods. Again, methods are used from Chapter 2 and 3 to help untangle the effects of GxE.

Chapter 7 summarises the research from Chapters 2 - 6 and presents conclusions with discussion of the impact of the research and future opportunities within the field.

Chapter 2

The critical period for yield determination in chickpea (*Cicer arietinum* L.)

Statement of Authorship

Title of Paper	The critical period for yield determination in chickpea (*Cicer arietinum* L.)
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Principal Author

Name of Principal Author (Candidate)	Lachlan Lake		
Contribution to the Paper	Lachlan Lake conducted the review of literature, designed and carried out experiments, performed analysis, interpreted data, wrote manuscript and acted as corresponding author.		
Overall percentage (%)	75%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	7/06/2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i.   the candidate's stated contribution to the publication is accurate (as detailed above);

ii.   permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Victor O Sadras		
Contribution to the Paper	Victor Sadras provided guidance in data analysis and interpretation and in constructing and developing the manuscript.		
Signature		Date	1/11/2016

The critical period for yield determination in chickpea (*Cicer arietinum* L.)

Lachlan Lake*, Victor O. Sadras

South Australian Research and Development Institute, Waite Campus, Australia

ABSTRACT

Chickpea seed yield is highly variable as a result of biotic, mostly fungal, and abiotic stresses including extreme temperatures and water stress. The effect of stress on yield depends on its intensity, timing and duration, hence the importance of knowing the critical window of yield formation and stress vulnerability. This window has not been determined in chickpea. To fill this gap, we compared the effect of sequential 14-d shading periods on the yield and yield components of two chickpea varieties, PBA Boundary and PBA Slasher, in three environments where unshaded controls yielded between 2880 and 3130 kg ha^{-1}. Unlike other species which do not respond to stress early in the season, shading reduced yield from emergence until the beginning of the critical period, 300 °Cd before flowering (base temperature = 0 °C). The critical period was found to be at least 800 °Cd long centred 100 °Cd after flowering. Seed number accounted for most of the variation in yield, which was unrelated to seed size. Pod number accounted for most of the variation in seed number prior to the critical period, while pod number and seeds per pod contributed to seed number within the critical period. After 400 °Cd post flowering, seeds per pod was the main variable affecting seed number. This information can be used in breeding and agronomy to improve stress adaptation.

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1. Introduction

Chickpea (*Cicer arietinum* L.) is one of the most important grain legumes worldwide (Berger et al., 2006; Krishnamurthy et al., 2013). It is grown predominantly in south Asian and Mediterranean environments; India is the largest producer with 7.7 million tonnes in 2012 (FAO, 2013). In Australia, production increased from 129,000 t in 2002 to 673,000 t in 2012 (FAO, 2013) making it the second largest world producer in 2012. Chickpea yield is constrained by biotic stresses, particularly fungal diseases such as *Ascochyta* blight (*Ascochyta rabiei*) (Knights and Siddique, 2003) and abiotic stresses such as water deficit and extreme temperatures (Knights and Siddique, 2003; Kashiwagi et al., 2006; Leport et al., 2006). As a result of poor adaptation to these stresses, chickpea can be perceived as relatively unstable and low yielding (Millan et al., 2006).

The effect of abiotic stresses on crop yield depends on the intensity, timing and duration of the stress, hence the effort to determine the critical period underpinning yield determination in major crops. Species specific critical periods have been determined

for cereals; wheat, barley, triticale and maize (Fischer, 1985; Kiniry and Ritchie, 1985; Savin and Slafer, 1991; Arisnabarreta and Miralles, 2008; Estrada-Campuzano et al., 2008; Cerrudo et al., 2013), sunflower (Cantagallo et al., 1997) and the grain legumes; soybean, peas and lupin (Board and Tan, 1995; Jiang and Egli, 1995; Guilioni et al., 2003; Sandaña et al., 2009; Sandaña and Calderini, 2012). Identification of critical periods aids in crop breeding and management, and ultimately improved yield and yield reliability (Sandaña and Calderini, 2012; Cerrudo et al., 2013).

In cereals the critical period has been commonly identified around the stage leading up to anthesis in barley (Arisnabarreta and Miralles, 2008), has extended into flowering for wheat and triticale (Fischer and Stockman, 1980; Fischer, 1985; Estrada-Campuzano et al., 2008), and even further post anthesis for maize (Cerrudo et al., 2013). In grain legumes, the majority of the critical period occurs further into seed filling with soybean identified as R1 (beginning of flowering) to R5 (beginning of seed set) and 10 days before R1–R5 for lupin and field pea (Board and Tan, 1995; Jiang and Egli, 1995; Sandaña and Calderini, 2012). The most likely reason for grain legume critical periods extending into seed filling is overlapping vegetative and reproductive stages and continuation of flowering after seed set (Slafer et al., 2009).

The most common method to determine the critical period is the application of shade to cause source reduction at different developmental stages (Fischer, 1985; Savin and Slafer, 1991; Jiang and Egli,

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* Corresponding author. Tel.: +61 400424942
E-mail addresses: lachlan.lake@sa.gov.au (L. Lake), victor.sadras@sa.gov.au (V.O. Sadras).

1993; Arisnabarreta and Miralles, 2008; Estrada-Campuzano et al., 2008; Sandaña et al., 2009; Sandaña and Calderini, 2012; Cerrudo et al., 2013). Shading is highly repeatable, and affects crop growth rate, which is correlated with seed set in the critical period (Fischer, 1985; Egli and Yu, 1991; Jiang and Egli, 1995; Andrade et al., 2005; Arisnabarreta and Miralles, 2008; Kantolic et al., 2013). Defoliation has also been used to cause source reduction (Board and Harville, 1993; Board and Tan, 1995) but may produce undesirable and confounded effects, such as soil temperature or moisture differences caused by reduced canopy. Defoliation is also likely to have effects associated with the removal of stored nitrogen from vegetative organs (Munier-Jolain et al., 1998; Lhuillier-Soundélé et al., 1999; Sandaña et al., 2009) and may also result in unintended and confounding competition effects. Munier-Jolain et al. (1998) reported no difference between the seed number of defoliated and control plants but a significant reduction in seed number of shaded plants compared to controls. Bertero and Ruiz (2008) used an indirect method to determine critical period in quinoa, looking at the association between crop growth rate in specific phenophases and seed number; however they recognise the need to enhance these results using shading.

In previous studies, sequential periods of shading have caused an increasing reduction in grain number as the critical period approaches, with little effect on grain weight (Fischer, 1985; Arisnabarreta and Miralles, 2008; Estrada-Campuzano et al., 2008; Sandaña and Calderini, 2012). The reductions in grain number generally resulted from less fertile florets per spike in cereals or reduced pod number in legumes.

Currently there is limited information on the critical period for yield determination in grain legumes and no information in chickpea. The aim of this study was to determine the critical period for yield determination in chickpea.

2. Methods

2.1. Plant material, environments and experimental design

Two chickpea varieties were grown in three environments. Varieties PBA Slasher and PBA Boundary were selected on the basis of reported phenotypic traits. PBA Slasher is adapted to Southern and Western Australian chickpea growing regions, is mid flowering and maturing, is Ascochyta blight resistant and is semi spreading. PBA Boundary is adapted to Northern New South Wales and Southern Queensland chickpea growing regions, is mid maturing, is Ascochyta blight resistant and has a tall erect plant type. Actual differences between varieties in key traits including development and yield were smaller than expected under our experimental conditions (Section 3). The three environments resulted from combinations of locations and sowing dates: Roseworthy (34°52′S, 138°69′E) sown on 7th June, Turretfield (34°33′S, 138°49′E) at recommended sowing date (14th June – TOS 1) and Turretfield late sown (9th of July – TOS 2). Roseworthy was supplied with 12 mm of supplemental irrigation at flowering. Daily weather data was obtained from the Roseworthy and Turretfield weather stations from the Queensland Government, Long Paddock website (http://www.longpaddock.qld.gov.au/silo/). Thermal time was calculated from daily mean temperature using a base temperature of 0°C (Berger et al., 2006).

Crops were sown after barley in a Calcic Luvisol (http://www.fao.org/fileadmin/user_upload/soils/docs/Soil_map_FAOUNESCO/new_maps/X_1_petit.jpg) at Roseworthy, and after canola into Calcic Luvisol at Turretfield. The target plant density was 50 plants m^{-2}. The seed was pre-treated with P – Pickel T fungicide to minimise the risk of seed borne _Ascochyta_ blight and inoculated with Group N rhizobia immediately before sowing. For all other seed treatments, fertiliser, insect, disease and weed management, agronomic practices were carried out in accordance with the protocols of the National Variety Trials (http://www.nvtonline.com.au/).

A split-plot design with four replicates was used where varieties were allocated to main plots and shading treatments, including unshaded controls, to randomised subplots. Plot size was 29 m^{-2}, comprised of 6 rows (spaced 24.2 cm) of 20 metres length. Shading treatments lasted for 14 days each, and were designated sequentially from 1 to 8, starting at 31 days (353 °Cd) after sowing at Roseworthy and 24 days (251 °Cd) after sowing at Turretfield TOS 1. Turretfield TOS 2 had a shorter growing season and had six shading treatments in sequence beginning 35 days (399 °Cd) after sowing. Owing to an error in shade placement, data from Turretfield TOS 1 shading treatment number 1 was discarded. Shading was ceased when plants within the experimental plots had ceased flowering, pods had yellowed and were perceived to have reached the final stage in seed abortion where no more yield loss was anticipated (Ney and Turc, 1993; Munier-Jolain et al., 1998). Plants were then harvested when completely desiccated several weeks later. The shades were constructed from black shade cloth that intercepted 90% of solar radiation and were maintained at a minimum of 10 cm from the top of the canopy at all times. The shade cloth was constructed into a frame using wire and wooden stakes so that plants were shaded from the top and the sides, with the southern side left open to allow for regular temperature variation and air movement. The size of the shaded area was 1.1 m × 1.1 m (1.21 m^2) with five of the six rows being shaded.

2.2. Traits

Weekly phenology observations were used to determine time of first flower (FF), fifty percent flowering (50F), pod emergence (PE), when 50% of plants showed visible pods, and end of flowering (EOF), when 50% of plants ceased flowering (Berger et al., 2004). Maturity was scored when 50% of pods in a plot had matured. Flowering duration was calculated as the time from 50% flowering to end of flowering. Phenological stages are expressed on a thermal time scale.

Yield and yield components were measured at maturity from samples taken from 3 m × 0.5 m length cuts of central rows of the shaded area; border rows were excluded (Rebetzke et al., 2014). Yield components included pod number, pod weight, seed size, seeds per pod, shoot biomass and the derived traits pod wall ratio (PWR = pod wall weight/whole pod weight (Lagunes-Espinoza et al., 1999; Clements et al., 2005; Sadras et al., 2013)) and harvest index (HI = seed yield/shoot biomass).

2.3. Data analyses

The effect of timing of shading, variety and the interaction was tested using analysis of variance separately for each environment as there was unequal numbers of shading treatments among environments. Fisher's PSLD test was used to determine differences between timing of shading treatment and unshaded controls.

Yield and yield components in shading treatments were normalised as a fraction of the control, and the trajectory of normalised traits was plotted against the phenology of controls (thermal time scale centred at flowering); curves were fitted by eye, as it has been done previously (Arisnabarreta and Miralles, 2008; Estrada-Campuzano et al., 2008; Sandaña and Calderini, 2012).

3. Results

3.1. Environmental conditions and crop development

Weather between sowing and flowering was very similar between environments with small differences reflecting the

sowing dates with increasing radiation and temperature corresponding to later sowing. For the later phenological stages Turretfield TOS 1 had cooler conditions. Between flowering and pod emergence, Turretfield TOS 1 had cooler maximums than the other environments with average maximum of 21.5 °C, compared with 22.2 °C and 22.9 °C for Roseworthy and Turretfield TOS 2. In this period the minimum temperatures were in the opposite order to expected with Roseworthy having the warmest, Turretfield TOS 1 intermediate and TOS 2 coolest (8.8, 7.8 °C and 6.1 °C). For the period pod emergence to end of flowering, Turretfield TOS 1 again had the coolest maximum and also minimums with 22.7/7.3 °C compared with Roseworthy (24.1/7.5 °C) and Turretfield TOS 2 (24.8/9.0 °C).

Rainfall matched or exceeded evaporation up to flowering at Roseworthy and past pod emergence for both Turretfield sites; stored soil water was not measured but might have contributed to the post-flowering period (Fig. 1). To test this further, we benchmarked our trials against the yield of chickpea in South Australian locations of the National Variety Trials (Section 3.2).

Phenological patterns of PBA Boundary and PBA Slasher were statistically similar (not shown). Shading treatment had a significant effect on phenological development with treatments imposed in the lead up to flowering causing a delay in flowering of between 230 and 420 °Cd compared to the controls.

3.2. Seed yield and components

Unshaded controls yielded 313 g m^{-2} at Roseworthy, 294 g m^{-2} at Turretfield TOS 1 and 288 g m^{-2} at Turretfield TOS 2 (Table 1).

This compares with National Variety Trials in the region, which averaged 197 g m^{-2}, with yearly averages ranging from 78 to 276 g m^{-2}, and single locations ranging from 23 to 408 g m^{-2} for 80 locations from 2005 to 2012 (http://www.nvtonline.com.au/).

Table 2 summarises the ANOVA of yield and its components. There was no significant difference between the yield and yield components of PBA Boundary and PBA Slasher in any of the environments with the exception of seed number and seed size at Turretfield. Shading affected yield and all yield components, with the exception of Turretfield TOS 1, where seed size and pod wall ratio where unaffected. There was no interaction between shade and variety on any trait, except seed size at Roseworthy and Turretfield TOS 2.

Table 3 presents the matrix of correlations between yield components. Yield had a strong positive correlation with both biomass and harvest index. The relationship between harvest index and biomass varied between environments, with a positive relationship at Turretfield and no relationship at Roseworthy. Yield was closely related to seed number and unrelated to seed size. Seed number was related with both pod number and seeds per pod, but the relationship was stronger with pod number, reflecting the greater plasticity of this trait.

3.3. Critical period

The effect of time of shading on yield and yield components was consistent for both varieties (i.e. shading by variety interaction largely not significant; Table 2) and was consistent across
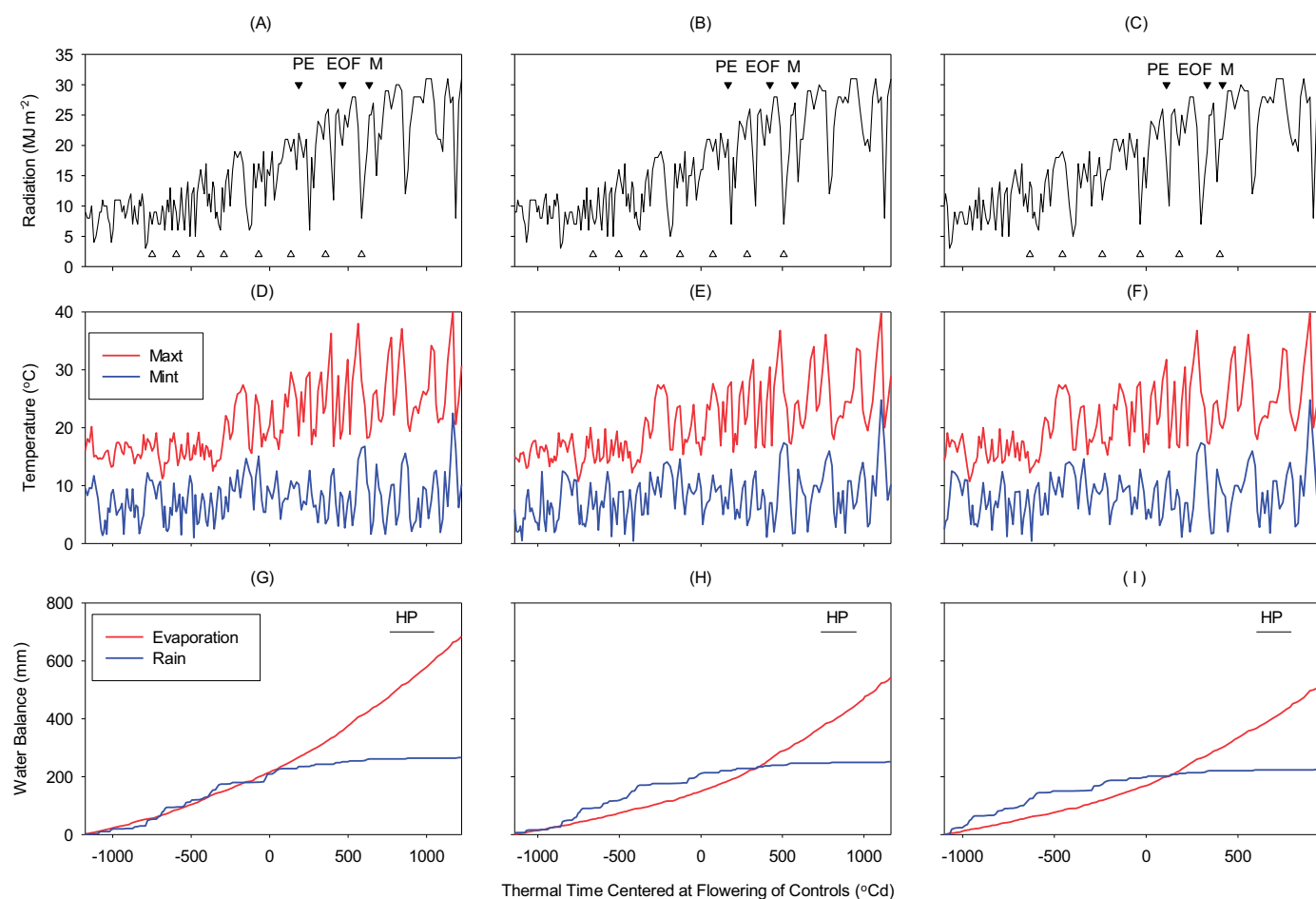
Fig. 1. Solar radiation, maximum and minimum temperature, and cumulative rainfall and evaporation during the growing season in three environments. (A, D, G) Roseworthy, (B, E, H) Turretfield TOS 1 and (C, F, I) Turretfield TOS 2. Closed triangles show time of pod emergence (PE), end of flowering (EOF) and maturity (M), while segments show the harvest period (HP). Open triangles show the midpoint of sequential shading periods. The phenological scale is for the unshaded controls.

Table 1
Average (SE) chickpea yield and yield components of untreated controls in three South Australian environments, Roseworthy, Turretfield TOS 1 and Turretfield TOS 2.

Environment	Yield (g/m^{-2})	Biomas (g/m^{-2})s	Pods (m^{-2})	Pod weight (g/m^{-2})	Seed size (g/100 seeds)	Seeds (m^{-2})	Harvest Index	Pod weight proportion	Seeds per pod
Roseworthy	313 (13.9)	786 (33.2)	1425 (57.4)	382 (16.9)	20.2 (0.276)	1547 (66.7)	0.40 (0.017)	0.18 (0.003)	1.09 (0.024)
Turretfield TOS 1	294 (14.8)	780 (30.1)	1515 (69.3)	358 (16.9)	19 (0.214)	1549 (73.5)	0.38 (0.012)	0.18 (0.005)	1.07 (0.072)
Turretfield TOS 2	288 11.4)	641 (19.7)	1285 (51.8)	352 (13.8)	20.1 (0.235)	1435 (57.4)	0.45 (0.007)	0.18 (0.004)	1.12 (0.024)

Table 2
P-values from analysis of variance for the effect of variety, timing of shade and their interaction on chickpea yield and yield components.

Environment	Source of variation	Yield	Biomass	Pods	Pod weight	Seed size	Seeds	HI	Pod weight proportion	Seeds per pod
Roseworthy	Variety	0.68	0.62	0.86	0.76	0.30	0.40	0.14	0.31	0.81
	Shade	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	Interaction	0.92	0.80	0.49	0.92	0.024	0.72	0.46	0.68	0.56
Turretfield TOS 1	Variety	0.33	0.57	0.62	0.35	0.014	0.0458	0.28	0.56	0.0541
	Shade	<0.0001	<0.0001	<0.0001	<0.0001	0.0815	<0.0001	<0.0001	0.1695	0.0075
	Interaction	0.63	0.33	0.77	0.67	0.28	0.37	0.44	0.26	0.35
Turretfield TOS 2	Variety	0.16	0.48	0.17	0.18	0.003	0.022	0.094	0.44	0.14
	Shade	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
	Interaction	0.77	0.94	0.84	0.79	0.0448	0.85	0.24	0.063	0.48

environments on a phenological scale (Figs. 2 and 3). Yield decreased for most shading treatments, with reductions in response to early shading of between 20 and 30% up to approximately 300 °Cd before flowering. The greatest reductions started approximately 300 °Cd before flowering and increased to 75% approximately 200 °Cd after flowering (Fig. 2A). After this critical point, yield increasingly recovered towards maturity. The most critical period for yield determination, with a reduction of at least 40%, spanned the window of 800 °Cd centred 100 °Cd after flowering. This represents a window of approximately 54 days centred 100 °Cd after flowering.

Reduction in yield was almost fully accounted for by reduction in seed number (Fig. 2A vs B). Seed size was largely unaffected by shading except for a ~20% increase when shade was imposed 200–300 °Cd after flowering and a ~20% decrease after this time (Fig. 2C). The slight increase in seed size for shading 200–300 °Cd after flowering is likely reflecting a favourable source:sink ratio for seed filling in correspondence with the severe reduction in seed number. It is therefore of interest to analyse the effect of shading on the components of seed number.

Seed number correlated with both pod number and seeds per pod, with no trade-off between the components of seed number (Table 3). Comparison of Figs. 2B and 3 shows that reduction in seed number was associated with (i) pod number from crop establishment until ~450 °Cd after flowering, (ii) both pod number and seeds per pod between ~300 °Cd before and ~450 °Cd after flowering,

Table 3
Correlation matrix of yield and its components. Correlations are based on averages of two varieties, split by environment (A) Roseworthy, (B) Turretfield TOS 1 and (C) Turretfield TOS 2. Significance is indicated as ***P < 0.0001 and *P < 0.05 according to Fisher's *r* to *Z* test.

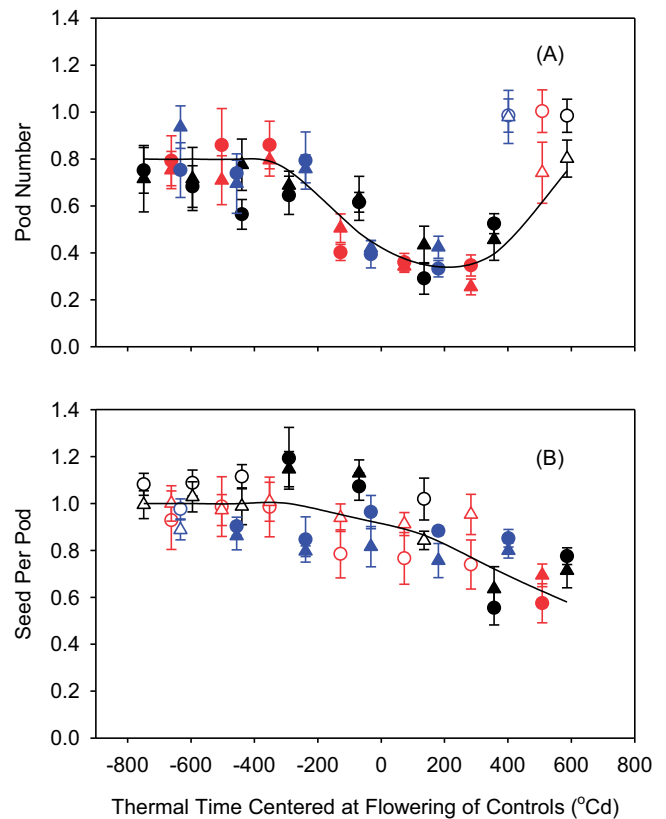|	Biomass (m^{-2})	Harvest index	Pods (m^{-2})	Pod weight (m^{-2})	Seeds (Pod^{-1})	Seeds (m^{-2})	Seed size	Pod wall ratio
(A)								
Yield	0.73***	0.68***	0.87***	1.00***	0.35*	0.97***	0.00	−0.46***
Biomass (m^{-2})		0.02	0.79***	0.75***	−0.06	0.72***	0.05	0.00
Harvest index			0.47***	0.65***	0.50***	0.65***	−0.03	−0.66***
Pods (m^{-2})				0.89***	−0.04	0.88***	−0.06	−0.19
Pod weight (m^{-2})					0.31*	0.97***	0.01	−0.40
Seeds (Pod^{-1})						0.41***	−0.48***	−0.64***
Seeds (m^{-2})							−0.20	−0.47***
Seed size								0.13
(B)								
Yield	0.80***	0.82***	0.88***	0.95***	0.41***	0.98***	0.08	−0.15
Biomass (m^{-2})		0.35***	0.75***	0.76***	0.27*	0.79***	0.06	−0.11
Harvest index			0.69***	0.79***	0.38*	0.80***	0.08	−0.15
Pods (m^{-2})				0.85***	−0.01	0.88***	−0.01	−0.06
Pod weight (m^{-2})					0.37*	0.94***	0.05	0.13
Seeds (Pod^{-1})						0.43***	−0.17	−0.19
Seeds (m^{-2})							−0.13	−0.13
Seed size								−0.12
(C)								
Yield	0.86***	0.79***	0.92***	1.00***	0.47***	0.98***	−0.04	−0.47***
Biomass (m^{-2})		0.38*	0.82***	0.87***	0.31*	0.86***	0.00	−0.28*
Harvest index			0.72***	0.78***	0.45***	0.77***	−0.05	−0.50***
Pods (m^{-2})				0.93***	0.17	0.94***	−0.18	−0.34*
Pod weight (m^{-2})					0.45*	0.98***	−0.04	−0.41*
Seeds (Pod^{-1})						0.49***	−0.20	−0.51***
Seeds (m^{-2})							−0.21	−0.46***
Seed size								0.11
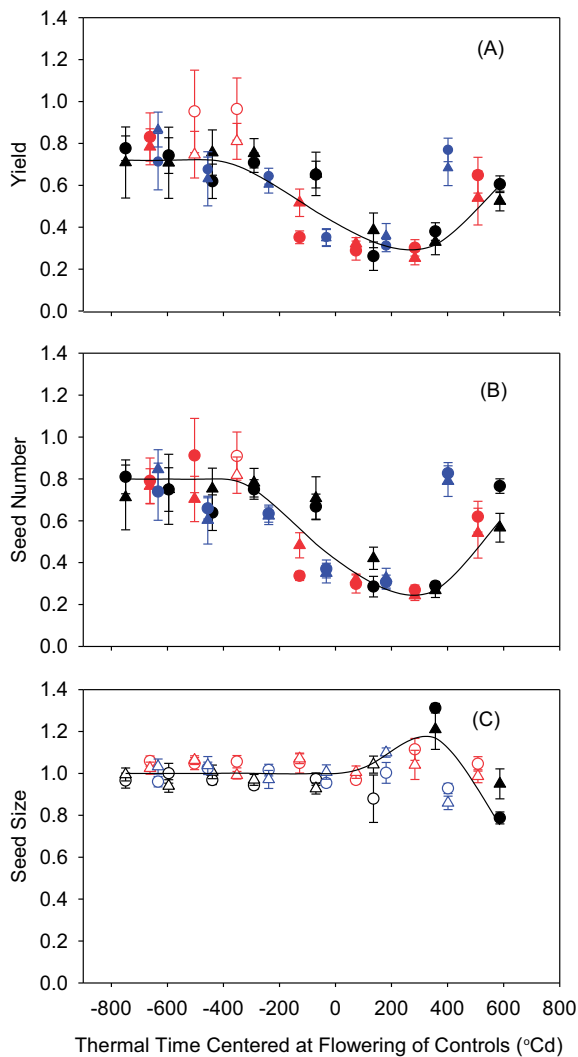
Fig. 2. Effect of timing of shading on (A) yield, (B) seed number and (C) grain size of chickpea PBA Boundary (circles) and PBA Slasher (triangles) compared to unshaded controls, at Roseworthy (black), Turretfield TOS 1 (red) and (C) Turretfield TOS 2 (blue). Open symbols are not significantly different from the control, while closed symbols are significantly different. The lines are spline curves fitted by eye. Error bars are ±SE and are not shown when smaller than symbol. The phenological scale is based on the unshaded controls. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Fig. 3. Effect of timing of shading on (A) pod number and (B) seeds per pod for chickpea PBA Boundary (circles) and PBA Slasher (triangles) compared to unshaded controls, at Roseworthy (black), Turretfield TOS 1 (red) and Turretfield TOS 2 (blue). Open symbols are not significantly different from the control, while closed symbols are significantly different. The lines are spline curves fitted by eye. Error bars are ±SE and are not shown when smaller than symbol. The phenological scale is based on the unshaded controls. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

and (iii) seeds per pod after ∼450 °Cd after flowering. Reductions in seed per pod were the result of both empty pods and fewer seed per pod.

4. Discussion

Southern Australia has a characteristic combination of low rainfall and poor soils leading to low seed yields (Fischer, 1985). Against these common conditions, the trial period was relatively favourable as shown in the weather patterns (Fig. 1) and the relatively high yield of controls compared to historical yield data (Section 3.2). The yield of controls, around 300 g m^{-2}, compares with yields of around 200–240 g m^{-2} in more favourable rainfed conditions worldwide (Krishnamurthy et al., 1999; Radicetti et al., 2012), and with 320 g m^{-2} in irrigated crops (Krishnamurthy et al., 2010).

The use of shade to determine the critical period is justified, and critical periods determined with this method can be extrapolated to other types of stress because (i) yield is a primary function of seed number, and (ii) seed number correlates with crop growth rate during the critical period irrespective of the driver of crop growth rate (Egli and Yu, 1991; Tollenaar et al., 1992; Guilioni et al., 2003; Andrade et al., 2005; Arisnabarreta and Miralles, 2008; Bertero and Ruiz, 2008; Sadras and Lawson, 2011; Sandaña and Calderini, 2012). Two examples reinforce this proposition. In wheat, the link between growth in the critical period and seed number is maintained irrespective of the source of variation in growth including radiation (Fischer, 1985; Savin and Slafer, 1991), nitrogen (Fischer, 1993; Prystupa et al., 2004) and lodging (Acreche and Slafer, 2011). In maize, the relationship between seed number and growth rate in the critical period is the same irrespective of whether the rate is reduced by shading, water or nitrogen stress (Andrade et al., 2005). A possible exception is extreme temperature (heat and frost), which might decouple seed set and crop growth rate.

The critical period for chickpea differed with other grain legumes such as lupin, field pea and soybean, where the majority of the critical period occurs after flowering (Board and Tan, 1995; Jiang and Egli, 1995; Sandaña and Calderini, 2012). The reasons for the broader critical period in chickpea are unknown, and deserve further research.

The response of seed number and seed size to shading was in accordance with empirical evidence (Arisnabarreta and Miralles, 2008) and current theory of crop yield determination (Andrade et al., 2005; Sadras, 2007; Sadras and Denison, 2009; Sadras and Slafer, 2012). A significant increase in seed size was associated with shading around pod emergence. This may be due to preferential carbohydrate partitioning to developing seeds that have passed the

final stage in seed abortion (Munier-Jolain et al., 1998), rather than younger flowers and embryos.

Pod number contributed more to the variation in seed number than seeds per pod. This is expected from the relatively low variation in seeds per pod in chickpeas compared to other legumes. However, Sandaña and Calderini (2012) also found seed number to be closely related to pod number in lupin and field pea.

This research has identified the critical period for yield determination and the associated critical periods for yield components. This knowledge will allow for more targeted stress mitigation practices, e.g. combining sowing date and cultivar phenology to reduce the likelihood of severe stress in the critical window. Increased knowledge of the critical period will also enhance the ability of breeders to screen for stress tolerance with more targeted stress impositions. Both agronomic and breeding adaptations require quantitative environmental characterisations (Chapman, 2008; Chenu et al., 2011, 2013; Sadras et al., 2012) including the timing of water stress and probability of occurrence of different stress types.

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Chapter 3

Patterns of water stress and temperature for Australian chickpea production

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Principal Author

Name of Principal Author (Candidate)	Lachlan Lake
Contribution to the Paper	Lachlan Lake conducted the review of literature, designed and carried out experimental simulations, performed analysis, interpreted data, wrote manuscript and acted as corresponding author.
Overall percentage (%)	70%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.
Signature	Date 7/06/2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

    i.   the candidate's stated contribution to the publication is accurate (as detailed above);

    ii.   permission is granted for the candidate in include the publication in the thesis; and

    iii.   the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Victor O Sadras
Contribution to the Paper	Victor Sadras provided guidance in data analysis and interpretation and in constructing and developing the manuscript.
Signature	Date 1/11/16

Name of Co-Author	Karine Chenu

Contribution to the Paper	Karine Chenu contributed to the data analysis and interpretation (principal component analysis and cluster analysis) provided guidance in data analysis and interpretation and in constructing and developing the manuscript.			
Signature			Date	6/7/16

Patterns of water stress and temperature for Australian chickpea production

Lachlan Lake[A,C], *Karine Chenu*[B], *and Victor O. Sadras*[A]

[A]South Australian Research and Development Institute, Waite Campus, GPO Box 397, Adelaide,
  SA 5001, Australia.
[B]The University of Queensland, Queensland Alliance for Agriculture and Food Innovation (QAAFI),
  203 Tor Street, Toowoomba, Qld 4350, Australia.
[C]Corresponding author. Email: Lachlan.Lake@sa.gov.au

Abstract. The environment is the largest component of the phenotypic variance of crop yield, hence the importance of its quantitative characterisation. Many studies focussed on the patterns of water deficit for specific crops and regions, but concurrent water and thermal characterisations have not been reported. To quantify the types, spatial patterns, frequency and distribution of both water stress and thermal regimes for chickpea in Australia, we combined trial and modelled data. Data from National Variety Trials including sowing time, yield and weather from 295 production environments were entered into simulations. Associations between actual yield, in a range from 0.2 to 5.2 t/ha, actual temperature and modelled crop water stress were explored. Yield correlated positively with minimum temperature in the 800 degree-days window bracketing flowering and the correlation shifted to negative after flowering. A negative correlation between maximum temperature over 30°C and yield was found from flowering through to 1000 degree-days after flowering. Yield was negatively correlated with simulated water stress from flowering until 800 degree-days after flowering.

Cluster analysis from 3905 environments (71 locations × 55 years between 1958 and 2013) identified three dominant patterns for both maximum and minimum temperature accounting for 77% and 61% of the overall variation, and four dominant patterns for water stress accounting for 87% of total variation. The most frequent environments for minimum and maximum temperature were associated with low actual yield (1.5–1.8 t/ha) whereas the most frequent water-stress environment was associated with the second lowest actual yield (1.75 t/ha). For all temperature and water-stress types, we found significant spatial variation that is relevant to the allocation of effort in breeding programs.

Additional keywords: environment, heat stress, modelling.

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Introduction

Chickpea (*Cicer arietinum* L.) is a major grain legume crop in terms of both production and human consumption (Singh 1997; Abbo *et al*. 2003; Kashiwagi *et al*. 2006). Its domestication stems from the crop assemblage process in the early days of agriculture in the Fertile Crescent (Abbo *et al*. 2003; Kerem *et al*. 2007). Chickpea transitioned from winter to spring sowing early in its domestication (Abbo *et al*. 2008); this may have shifted the thermal requirements of chickpea compared with other winter-sown crops such as field pea that was also domesticated in the Near East (Sadras and Dreccer 2015). Climate change is predicted to increase the frequency and intensity of extreme temperature and drought in environments where these factors already limit chickpea yield (Singh 1999; Battisti and Naylor 2009; Devasirvatham *et al*. 2012; IPCC 2012; Krishnamurthy *et al*. 2013; Awasthi *et al*. 2014; Thudi *et al*. 2014; Devasirvatham *et al*. 2015). Screening for adaptation to stress has historically relied on yield performance in multi-environment trials (Chapman *et al*. 2000*b*; Turner *et al*. 2001; Messina *et al*. 2011; Chenu *et al*.

2013). This approach is costly, can lead to biased sampling, misrepresent the target population of environments and produce limited genetic gain due to the large environmental variance affecting phenotype and heritability (Chapman *et al*. 2000*b*; Turner *et al*. 2001; Cooper *et al*. 2002; Chapman 2008; Chenu *et al*. 2013). Chapman *et al*. (2000*a*) suggested that temporal and spatial variability of stress could cause a mismatch between the target environments and multi-environment trials. The mismatch may be large enough to reverse genetic gain, as in the case of drought-affected trials favouring early flowering genotypes that yield poorly in more favourable environments (Chapman *et al*. 2000*b*).

Characterisation of the target population of environments, the largest source of yield variation (Chenu 2015), and the different environment types within a multi-environment trial is critical to extrapolate the relationship between abiotic stress and yield. Environmental quantification can assist to reduce bias and increase genetic gain in breeding trials. A comprehensive review by Chenu (2015) has summarised methods to characterise the target population of environments with emphasis on water

stress. Little effort has yet been placed on the quantification of thermal environments as background for breeding and agronomy.

Australian chickpea is produced in three main regions (Fig. 1*a*). These regions vary in management, soil and climate, hence the large and diverse target population of environments. Chauhan *et al*. (2008) used phenology and yield data to characterise Australian and Indian chickpea production environments, grouping them into homoclimes based on their similarity in simulated yield. This grouping of environments is driven by many combined factors but does not specifically account for individual stresses and is fixed for a given location. Stress-driven environmental characterisation takes into account year-to-year variation and is able to classify one geographic location with multiple environment types with their associated frequency of occurrence. Examples of stress-driven environmental characterisation include field pea, sorghum, wheat and maize in Australia, wheat and rice in Brazil, maize in the United States and Europe and sorghum in India (Löffler *et al*. 2005; Heinemann *et al*. 2008; Chenu *et al*. 2011, 2013; Sadras *et al*. 2012; Chauhan *et al*. 2013; Kholová *et al*. 2013; Harrison *et al*. 2014). All of these studies used simulations to describe the common types of water stress but none of them has described the thermal environments. This paper aims to (i) quantify the timing, duration, intensity and frequency of the patterns of water stress, (ii) develop new methods for quantification of thermal regimes, (iii) determine the

associations between actual yield, water stress and thermal regime, and (iv) compare chickpea and field pea water-stress patterns to determine if there are differences arising from ancient cultivation as a summer or a winter crop.

Methods

Actual yield and climate data

The National Variety Trials online database (www.nvtonline.com.au) was used to source yield and sowing date for 295 chickpea crop trials resulting from combinations of location and year within the three Australian chickpea-growing regions (Fig. 1*a*) from 2005 to 2013; locations are mapped in Figs 7 and 9. The Northern region had 102 crops, the Southern region 166 and the Western region had 27 crops. All locations-seasons included numerous varieties with no single variety common to all trials. Thus, we used the average yield for all varieties in each trial for the analysis (average number of check varieties was 6 with a range of 1–12). This is justified because variation between locations and seasons is much larger than variation among varieties in a given trial (Sadras and Slafer 2012). The bias associated with this approach was tested by comparison of yield between regionally adapted check varieties and environmental mean yield resulting from the pooling of all varieties in each trial. Climate data were obtained from SILO on the Queensland Government, Long Paddock website (www.longpaddock.qld.gov.au/silo/).
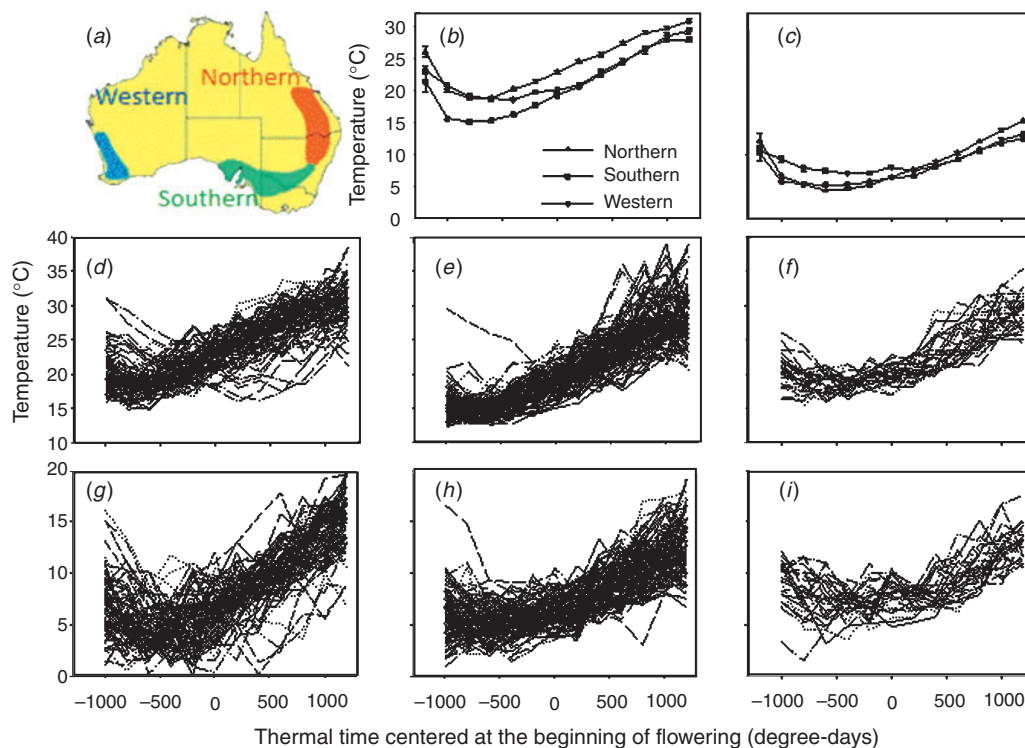
Fig. 1. (*a*) Australian chickpea-growing regions, average (*b*) maximum and (*c*) minimum temperature during the growing season of chickpea crops for the three growing regions in National Variety Trials; (*d–f*) maximum temperature during the growing season for individual crops within the (*d*) Northern (*e*) Southern (*f*) and the Western growing region; (*g–i*) minimum temperature for individual crops in the (*g*) Northern, (*h*) Southern and (*i*) Western region.

Associations between actual yield, temperature and modelled water stress

We investigated the association between actual yield in the 295 National Variety Trials, actual temperature and modelled water stress. For each crop, we simulated flowering date and water stress with the chickpea module of APSIM (Robertson *et al.* 2002; Holzworth *et al.* 2014). The performance of this model has been tested in independent experiments with varying cultivars, sowing dates and agronomy returning $r^2 = 0.70$ for the comparison of actual and modelled grain yield (Robertson *et al.* 2002) and $r^2 = 0.74$ for the comparison of actual and modelled flowering date (Carberry 1996). The water-stress index was calculated as the ratio of potential water supply (based on soil and root parameters) and water demand of the crop (based on canopy size and weather). The water stress index ranges from 1 corresponding to no stress to 0 indicating that leaf expansion has ceased. Average maximum temperature, maximum temperature over 30°C (Devasirvatham *et al.* 2012), minimum temperature and water-stress index were calculated for 200 degree-days brackets centred at the simulated time of flowering and associations with yield were explored using correlation analysis as in Sadras *et al.* (2012). A base temperature = 0°C was used (Singh and Virmani 1996; Robertson *et al.* 2002; Berger *et al.* 2006).

Characterisation of water stress and thermal patterns

To characterise the patterns of water stress and thermal regimes, long-term simulations were performed with APSIM for 71 locations and 55 years (1958–2013), totalling 3905 combinations. Locations were the same as in the National Variety Trials. Sowing date was established with a minimum rainfall of 20 mm over 2 days as sowing rule.

All simulations used the 'desi' variety Tyson that was grown nationally and has been extensively used as a parent in the production of newer varieties. We sourced soil parameters from the soil module of APSIM that best represented each location. Soils from the Northern region were from black vertisol, to red sodosol, with maximum plant-available water ranging from 91 to 287 mm. Soils from the Southern region were from sandy loams to black vertisol with maximum plant-available water ranging from 54 to 163 mm. Soils from the Western region were from loamy sand to red clay with maximum plant-available water ranging from 66 to 244 mm. As each year × location was treated as a separate environment, the starting soil water was reset on 1 January each year at 15% of maximum plant-available water (Sadras *et al.* 2012).

For each of the 3905 combinations, we divided the growing season into 200 degree-days segments centred at the simulated time of the beginning of flowering (section *Associations between actual yield, temperature and modelled water stress*) and for each interval we calculated the average daily maximum temperature, maximum temperature over 30°C, minimum temperature and water-stress index. Cluster analysis was performed using the partitioning clustering function (*Clara*) from the R statistical package (R Core Team 2014) (Chenu *et al.* 2011; Sadras *et al.* 2012). The major environment types were then defined by the cluster average of the water-stress pattern or thermal regime. The frequency of each major

environment type was calculated for each region and for the whole country.

Results

Actual yield and modelled flowering time in National Variety Trials

Actual mean yield in the National Variety Trials ranged from 0.2 to 5.2 t/ha demonstrating the range of environments over the Australian production regions. The Northern region
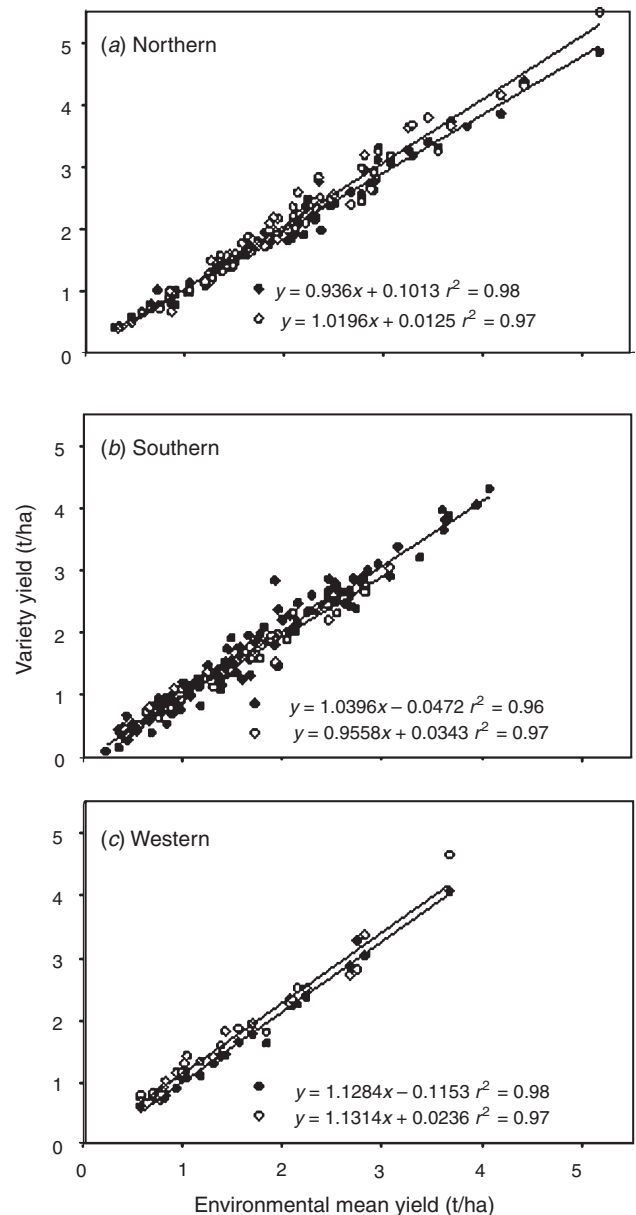
Fig. 2. Environmental mean yield of National Variety Trials for the (*a*) Northern region plotted against yield of varieties PBA HatTrick (closed circles) and PBA Boundary (open circles), (*b*) Southern region plotted against Genesis 090 (closed circles) and PBA HatTrick (open circles), (*c*) Western region plotted against PBA Slasher (closed circles) and PBA Striker (open circles). All r^2 are significant at $P < 0.0001$.

averaged 2 t/ha with a range from 0.3 to 5.2/ha, the Southern region averaged 1.7 t/ha with a range from 0.2 to 4.1 t/ha, whereas the Western region averaged 1.5 t/ha with a range from 0.6 to 3.7 t/ha. Trial mean yields responded to environmental variation similarly to check varieties (Fig. 2). This reinforces the robustness of our approach based on the average yield across varieties for a given location and season as a means to capture environmental drivers of yield.

Modelled flowering date ranged from 64 to 100 days after sowing for the Northern region, from 62 to 117 days after sowing in the Southern region and from 74 to 92 days after sowing in the Western region.

Thermal regimes and associations with actual grain yield

Maximum temperature declined from sowing up to 500, 750 and 450 degree-days before flowering in the Northern, Southern and Western regions, respectively (Fig. 1b). Afterwards, maximum temperature increased steadily up to maturity. The Northern region had the warmest maximum temperature throughout the season, whereas the Southern region had the coolest maxima up to flowering. The Western

region was similar to the Northern early in the season and then transitioned towards temperatures similar to the Southern region in the period before flowering.

A similar pattern was observed for minimum temperature (Fig. 1c). It decreased up to 600 degree-days before flowering in the Northern and Southern regions and up to 400 degree-days before flowering in the Western region. The Western region had the warmest minimum until flowering, and the Northern region became warmer afterwards.

Figure 1d–i shows the thermal regimes for each of the 295 National Variety Trials crops; it highlights the larger variability in temperature in the Northern region (Fig. 1d, g), particularly for minimum temperature.

Figure 3a–c shows the relationships between yield and temperature at particular developmental windows. In the Northern region, yield was not associated with minimum temperature. In the Southern region, yield was associated with minimum temperature positively early in the season up to 400 degree-days after flowering and negatively at 1000 degree-days after flowering. In the Western region, the association of yield with minimum temperature was stronger but only in specific windows with a positive association 200 degree-days before
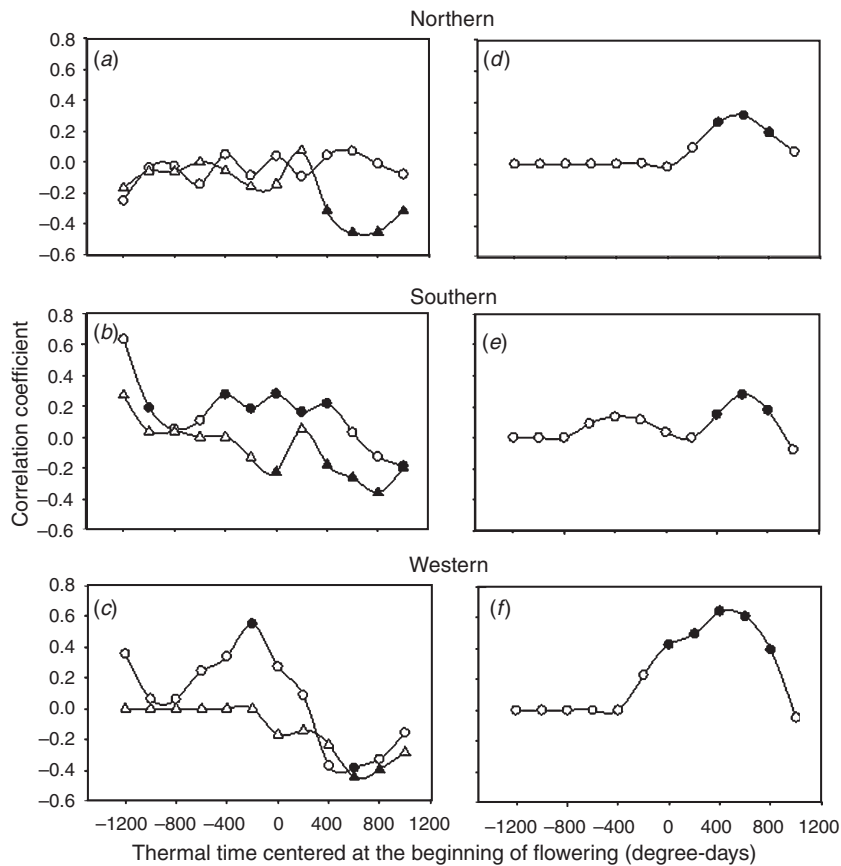
Fig. 3. Coefficient of correlation between actual mean yield of chickpea crops in National Variety Trials and minimum temperature (*a–c* circles), number of days with maximum temperature over 30°C (*a–c* triangles) and simulated water supply : demand ratio (*d–f*) during the growing season. Open symbols indicate correlations that are not significantly different from zero ($P > 0.05$) whereas closed symbols indicate a significant correlation ($P < 0.05$).

flowering, and a negative association 600 degree-days after flowering. In all regions, yield had a negative association with maximum temperature over 30°C after flowering, particularly in the period 600–800 degree-days after flowering. Maximum temperature over 30°C showed stronger correlations with yield than maximum temperature (data not shown).

Water-stress patterns and associations with actual grain yield

The development of water stress tended to begin around the onset of flowering in all regions with little or no stress during
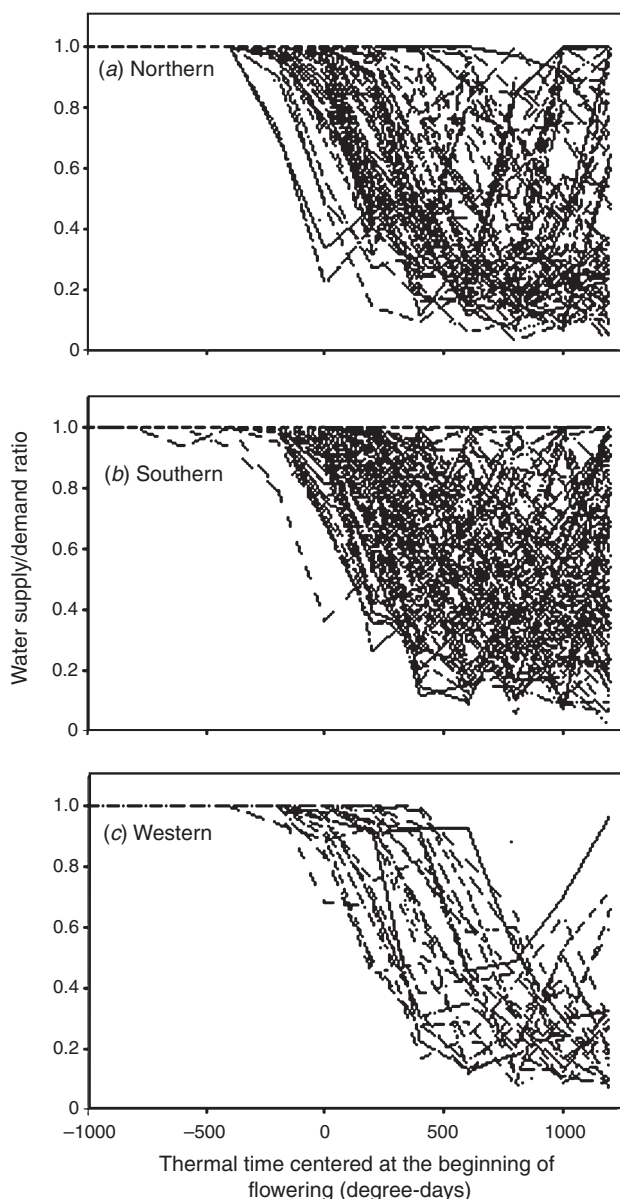
Fig. 4. Modelled patterns of water stress during the growing season of National Variety Trials. The water stress index is the ratio between the potential water supply (based on soil and root characteristics) and water demand of the canopy (based on canopy size and weather). A stress index of 1 indicates no stress whereas 0 indicates no growth.

crop establishment and early vegetative growth (Fig. 4). Although the patterns of water stress are all unique, water stress generally increased over the season, with some environments showing recovery and some environments having increasingly severe water stress. Accordingly, yield was unrelated with water stress before flowering, whereas associations emerged after flowering (Fig. 3*d–f*). The Northern and Southern regions were similar and had significant associations between yield and water-stress index from 400 to 800 degree-days after flowering, whereas the Western region had a stronger association from flowering until 800 degree-days after flowering.

### Associations of temperature and water stress

It has been noted previously that the correlations between yield, temperature and water stress are not independent because temperature and water stress are not independent (Rodriguez and Sadras 2007; Sadras *et al.* 2012). Fig. 5 illustrates the negative association between water stress and maximum temperature in the window 500–700 degree-days after flowering. Analysis of residuals highlights regional differences; positive residuals for the Northern region and negative residuals for the Western region indicate more severe and lesser water stress at the same maximum temperature, respectively.

### Spatial patterns of minimum and maximum temperature

Cluster analysis revealed three dominant patterns for maximum and minimum temperature (Fig. 6). All thermal patterns showed a common trend of cooling from sowing to ~600–400 degree-days before flowering, and increasing temperatures afterwards. The three dominant patterns for maximum temperature (Fig. 6*a*) accounted for 77% of the total variation. MAX1 had the highest associated yield (2.3 t/ha) and represented 23% of total environments, whereas MAX2 and MAX3 had lower average yields of 1.6 and 1.8 t/ha, and occurred with a frequency of 27% and 50%, respectively (Fig. 6*b*). The patterns of MAX1 and MAX3 were almost parallel over the season with an offset of 4−5°C. MAX2 was characterised by maximum temperature similar to MAX1 at the beginning of the season and transitioning towards MAX3 shortly before flowering.

Figure 7*a* depicts the spatial variation of environment types for maximum temperature. MAX1 dominated in the Southern region, MAX2 was mainly distributed across the Southern and Western region, whereas MAX3 was common across the Northern region with some occurrence in the northern part of the Western region.

The three dominant patterns for minimum temperature (Fig. 6*a*) accounted for 61% of total variation. MIN1 was characterised by low minimum temperature, despite a mild beginning with temperature between MIN3 (warmest) and MIN2 (coolest). MIN1 was the coolest environment from 600 degree-days before flowering onwards, and was ~4°C cooler than MIN3 400 degree-days before flowering, when the three environment types were the most contrasting. The three environments converged at the end of the season. Overall, MIN3 had the warmest minimum temperature during the whole season.
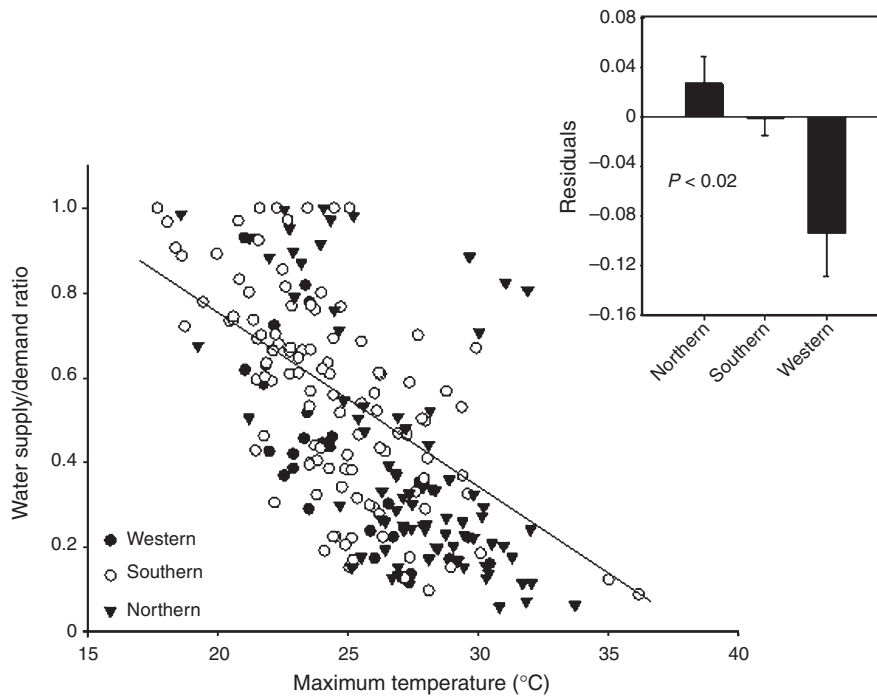
Fig. 5. Negative relationship between simulated water supply : demand ratio and maximum temperature in the period from 400 to 600 degree-days after flowering. The line is least square regression fitted across all regions ($r = -0.66$; $P < 0.001$). The inset shows the mean (and standard error) of residuals for each of the three regions.
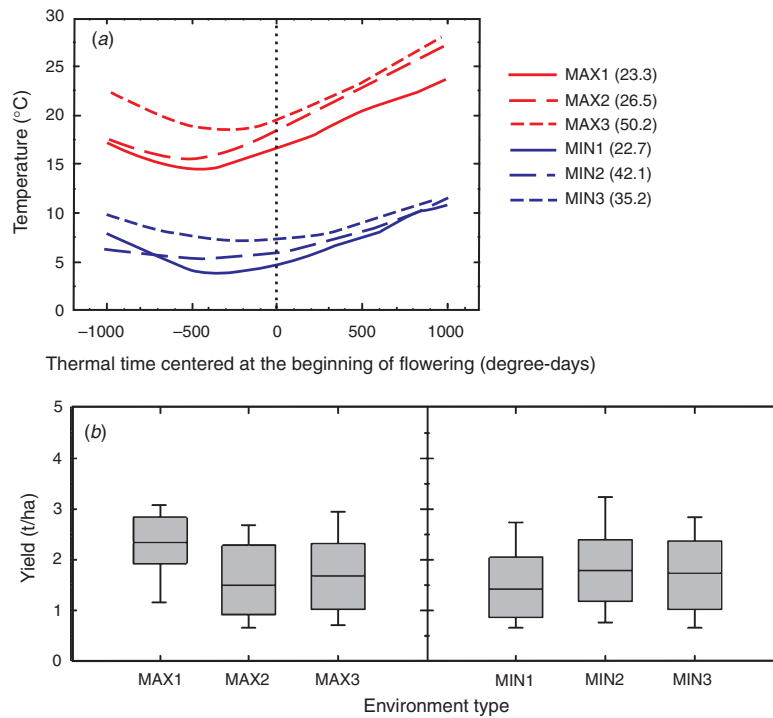
Fig. 6. (*a*) Major temperature environment types for maximum and minimum temperature over long-term for the Australian chickpea-growing region (55 years × 71 locations; i.e. 3905 simulations). Numbers between brackets indicate frequency of occurrence (%). (*b*) Frequency distribution of actual yield for each environment. Boxplots are: 25–50–75th percentile, top and bottom tails: 90–10th percentile.

MIN1, the coolest minimum temperature and most common minimum thermal type (occurring in almost half of the environments) was associated with the lowest yields (average yield of 1.5 t/ha) whereas MIN2 and MIN3 had similar average yield (1.9 t/ha and 1.8 t/ha). The frequency of occurrence was 47% for MIN1, 27% for MIN2 and 25% for MIN3.

Figure 7b depicts the spatial variation of types of environments for minimum temperature. MIN1 was prevalent on the east coast of Australia, with some minor representation in South and Western Australia. MIN2 was distributed evenly over the three growing regions, with a relatively low variation in frequency across locations. MIN3 was common in the northern

part of the Northern region, as well as the northern part of the Western region and also in part of southern Australia. However, MIN3 was absent from parts of south-eastern and eastern Australia.

Spatial patterns of water stress

Four dominant patterns of water stress were identified that accounted for 87% of total variation (Fig. 8a). Patterns varied mostly in onset and intensity of water stress. The two extreme patterns were WS4 and WS1; WS4 represented the worst condition, with an early onset of water stress, and association
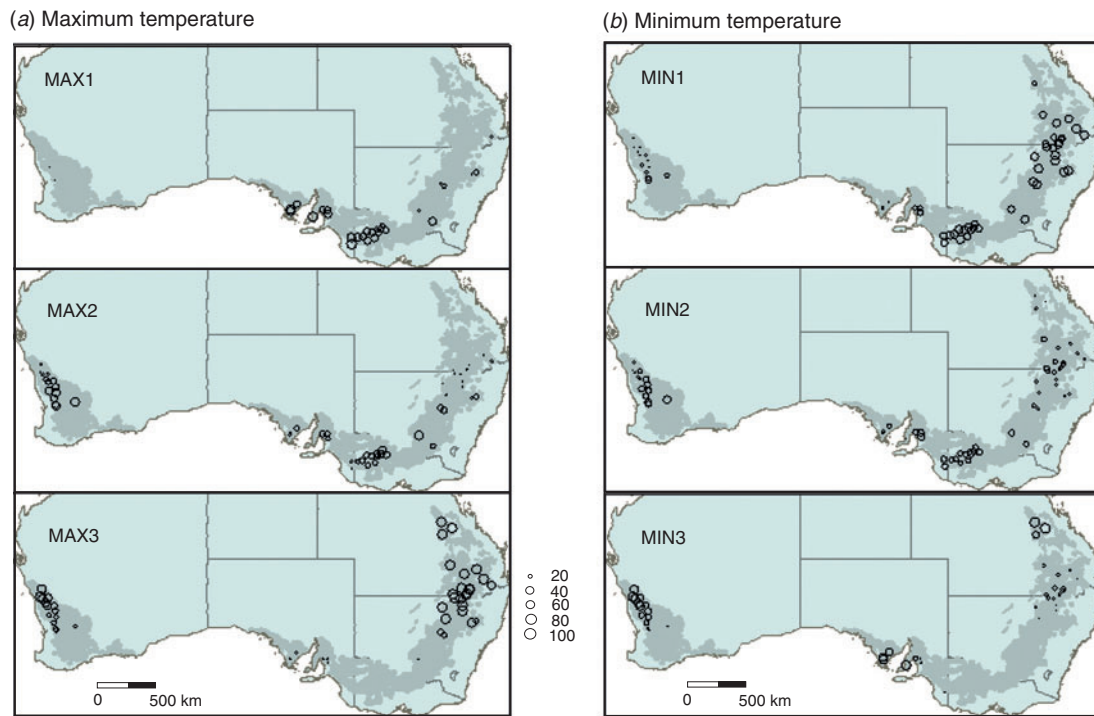
Fig. 7. Spatial distribution of (a) maximum and (b) minimum temperature environment types for Australian chickpea production (55 years – 71 locations; i.e. 3905 simulations). The size of the circles indicates the frequency of the environment types described in Fig. 5, with larger circles indicating a higher frequency of occurrence.
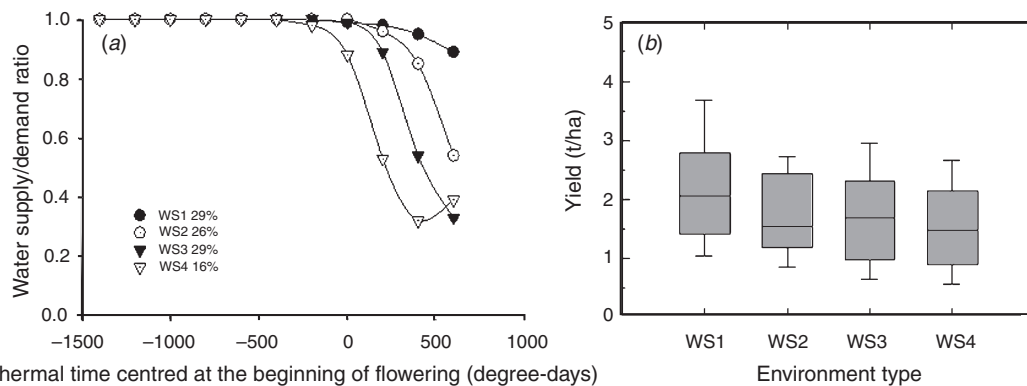
Fig. 8. (a) The four dominant water-stress environment types identified for chickpea in Australia (55 years – 71 locations; i.e. 3905 simulations), and their frequency of occurrence. (b) Frequency distribution of actual yield for each environment. Boxplots are: 25–50–75th percentile, top and bottom tails: 90–10th percentile.

with low yield but a low frequency (16%) in comparison to WS1, which was the more favourable environment with a late onset of stress, highest yield and a frequency of 29%. Patterns W2 and W3 were in between these extremes.

All the water-stress types occurred in most locations, with some differences in frequency (Fig. 9). The frequency of WS1 was higher in eastern Australia, i.e. in both the Northern and Southern regions, and rear in the Western region. WS2 and WS3 frequencies had a similar spatial distribution, and were more frequent in the Western region compared with the Northern or the Southern regions. WS3 was slightly more common in the Western region than WS2, but little difference was observed between WS2 and WS3 in either the Northern or Southern regions. The more severe water-stress type WS4 increased in frequency northwards and inland in both the Western and Northern regions, with little occurrence in the Southern region.

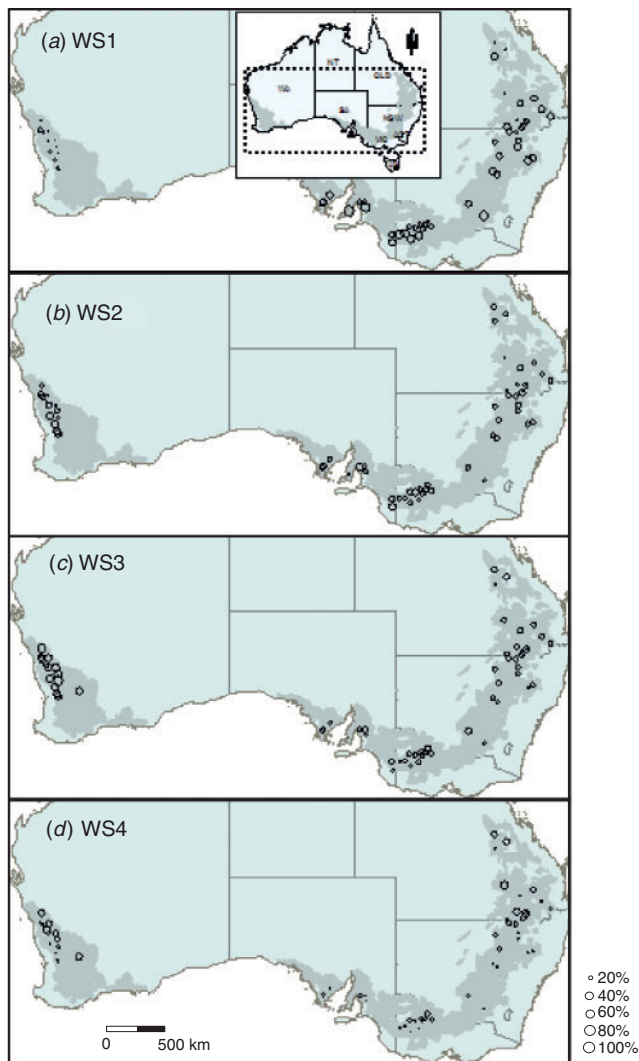**Fig. 9.** Spatial distribution of water-stress environment types for Australian chickpea production (55 years – 71 locations; i.e. 3905 simulations). The size of the circles indicates the frequency of the environment types described in Fig. 8*a*, with larger circles indicating a higher frequency of occurrence.

Discussion

Assumptions and limitations

To interpret the results of this study we need to consider the assumptions and limitations of the methods including both the yield database and the modelling component (Sadras *et al.* 2012; Turner *et al.* 2014). We simplified the influence of variety in two ways. First, we simulated crop phenology using the parameters for cultivar Tyson, which may be different to current varieties (Chenu *et al.* 2013). The patterns of water stress and thermal regimes could therefore involve some bias if extrapolated to early or late varieties compared with Tyson. Second, we considered environmental mean yield to explore associations with water stress and temperature. The strong correlations between check varieties and environmental mean yield (Fig. 2) justify this approach and reinforce the proposition that the environment was the dominant source of variation in yield; this was indeed what we need for environmental characterisation.

Correlations between yield and meteorological variables involve confounded effects, for example between temperature and water stress (Fig. 5). Our approach thus provides useful but inconclusive evidence; manipulative experiments are needed to separate the effects of water stress, minimum and maximum temperature and related variables such as vapour pressure deficit on yield (Bonada and Sadras 2015).

Grain yield and temperature

Quantification of thermal regimes has received less attention than quantification of water stress (Chenu 2015; Sadras *et al.* 2015). Herein, the common thermal patterns for Australian chickpea production were quantified, mapped relative to their frequency of occurrence, and analysed in terms of their putative impact on yield. The negative association between maximum temperature after flowering and yield may be a direct effect of stress, particularly above 30°C, on reproductive processes (Summerfield *et al.* 1984; Devasirvatham *et al.* 2012), an indirect effect of reduced soil water (Wahid *et al.* 2007; Upadhyaya *et al.* 2011; Dogan *et al.* 2013; Jumrani and Bhatia 2014), or indirect effect through increased vapour pressure deficit causing stomatal closure, reduction in transpiration, photosynthesis and radiation-use efficiency (Rodriguez and Sadras 2007; Zaman-Allah *et al.* 2011; Lobell *et al.* 2013; Sadras *et al.* 2015). Non-stressful high temperatures also have a developmental effect with direct implications for yield (Sadras *et al.* 2015).

The lack of association between yield and minimum temperature in the Northern region may be due to the warmer maximum temperatures compared with the Southern and Western regions, negating the benefits of slightly warmer minimum. This lack of association has been reported previously for field pea in New South Wales (Sadras *et al.* 2012). The negative association of yield with minimum temperature after flowering is consistent with low temperatures (<15°C) inhibiting pollen growth and pod set (Srinivasan *et al.* 1999; Berger *et al.* 2004, 2006; Chauhan *et al.* 2008).

The thermal patterns and frequencies identified can be used to aid breeding and agronomic decision making. The yield correlation with warmer early season minima indicates that

breeding for tolerance to colder temperatures during this phase may be beneficial. The negative correlations associated with high temperatures and yield later in the season indicate that breeding for high temperature tolerance later in the growth cycle should also have benefit. Agronomically, sowing earlier or selecting a short season variety would reduce the likelihood of exposing plants to higher terminal temperatures that are a characteristic of MAX3. Where MAX1 with lower maximum temperature is more likely, more options are available including later sowing or longer season varieties. When considering minimum temperature, MIN3 environments would allow for more options when sowing as minimum temperatures are consistently warmer. Where MIN1 environments are more likely (almost half of all environments), sowing later would be beneficial so as to shift the flowering period into warmer temperatures, minimising the risk of yield losses due to cold temperatures.

Grain yield and water stress

Water stress before flowering was not common; the dominant patterns of stress demonstrated low yield was associated with stress at or after the start of flowering. This absence of stress before flowering is distinct compared with other crops such as field pea, sorghum and wheat (Chapman *et al*. 2000*a*; Sadras *et al*. 2012; Chenu *et al*. 2013). In Australian field pea, the most severe stress occurred as early as 500 degree-days before flowering (Sadras *et al*. 2012). In specific Australian sorghum environments, stress can begin ~600–200 degree-days before flowering (Chapman *et al*. 2000*a*, 2000*b*), whereas in wheat some environments showed stress 600–400 degree-days before flowering (Chenu *et al*. 2013).

The contrast between the dominant post-flowering stress patterns in chickpea and environments where substantial pre-flowering stress develops for field pea (Sadras *et al*. 2012) can be explained in terms of morphological, physiological and thermal adaptation of these species. Berger *et al*. (2004), Siddique *et al*. (2001) and Zhang *et al*. (2000) showed chickpea is able to extract more soil water than other grain legumes, which would contribute to a reduced stress and later onset. Berger *et al*. (2004) highlighted chickpea's poor early vigour and late phenology compared with field pea, leading to lower water use early in the season. The greater canopy size of field pea compared with chickpea may also lead to a greater requirement of soil water (Neugschwandtner *et al*. 2013, 2014). Figure 10 highlights chickpea's lower shoot and higher root biomass compared with field pea of the same age and inset of Fig. 10 shows that APSIM captures the difference in shoot growth between these species. Benjamin and Nielsen (2006) found that chickpea roots responded better to water stress than field peas, a result supported by Gan *et al*. (2010). Miller *et al*. (2003) found chickpea used more soil water when compared with field pea, which was attributed to the shallow rooting habit of field pea. There is also some evidence that chickpea proteins denature at higher temperatures than field pea proteins (Withana-Gamage *et al*. 2011). All these observations are consistent with the effects of summer domestication of chickpea compared with the winter domestication of fieldpea (Abbo *et al*. 2008).

Comparing the distribution and frequency of modelled water-stress types in our study to the yield-based homoclines identified by Chauhan *et al*. (2008), we find some similarities and differences. Where the lower yielding homoclines are dominant (e.g. north of Western grainbelt), we also find that
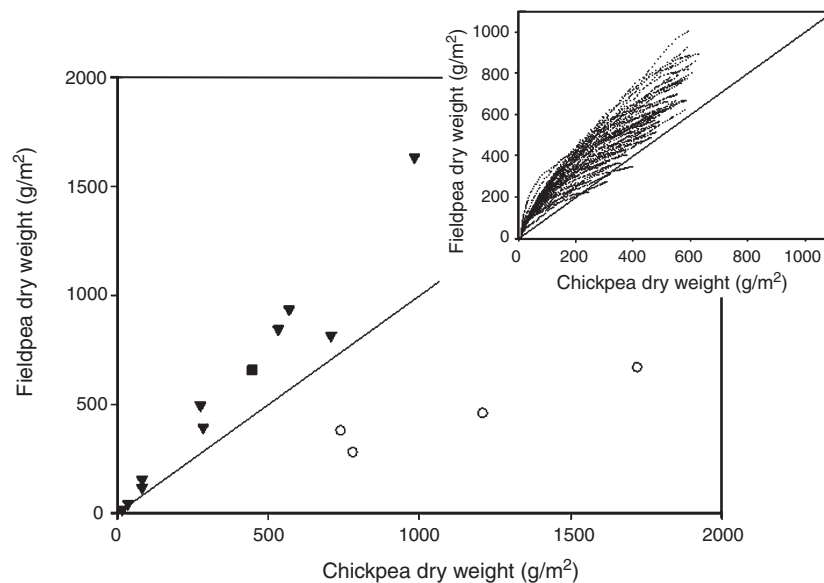
Fig. 10. Comparison of field pea and chickpea biomass. Data sources for root dry matter: Benjamin and Nielsen (2006), open circles. Sources for shoot dry matter: Siddique *et al*. (2001), square; and Neugschwandtner *et al*. (2014), triangles. The inset shows results of an APSIM simulation run from 1957 to 2012 for dry weight accumulation for field pea and chickpea at Roseworthy (−34.5267, 138.6883).

the frequency of low-yielding water-stress types are higher. Despite the partial agreement between our results and those of Chauhan *et al.* (2008), it must be emphasised that with the approach of homoclimes, locations cannot be grouped into more than one category, where in reality, environments change from year to year; this can be captured with stress environment types which are not limited to a location or year (Chapman *et al.* 2000*b*).

The patterns and frequencies for water stress can aid breeding and agronomic decision making. The correlations of water stress with yield indicate that water stress before flowering is unlikely to affect yield, and that water-stress tolerance after flowering needs to be addressed. However, enhancement of early vigour might change this pattern. Agronomically, it would be advantageous to sow early or use short season varieties in regions more likely to experience severe terminal drought (WS3 and WS4) whereas the less stressful environments could benefit from longer season varieties and have the option of later sowing.

Conclusion

For Australian chickpea production, this paper has identified relationships between temperature and yield, water stress and yield and the major thermal and water stress environment types, which were mapped according to their frequency of occurrence. We have also identified that chickpea experiences water stress at a later phenological stage than field pea, wheat and sorghum, which has implications for crop and cultivar selection.

These results will assist breeders to improve the efficiency of multi-environment trials by allowing for appropriate weighting of environments, minimising duplication of similar environment types and allowing for more targeted stress screening (Chenu 2015). Agronomists and producers will also benefit via enhanced knowledge of the environment and selection of varieties with better suited phenology and adaptation (Berger *et al.* 2004, 2006; Vadez *et al.* 2012).

Acknowledgements

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Chapter 4

Negative association between chickpea response to competition and crop yield: Phenotypic and genetic analysis

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Principal Author

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Signature		Date	24/08/2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

   i.   the candidate's stated contribution to the publication is accurate (as detailed above);
   ii.   permission is granted for the candidate in include the publication in the thesis; and
   iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Yongle Li		
Contribution to the Paper	Yongle Li contributed to data analysis and interpretation (specifically the Fst genome scan) and in constructing and developing the manuscript.		
Signature		Date	06/09/2016

Name of Co-Author	Jorge J Casal

Contribution to the Paper	Jorge Casal provided guidance and expertise in genomic analysis and interpretation of Fst genome scan and in constructing and developing the manuscript.		
Signature		Date	05/09/2016

Name of Co-Author	Victor O Sadras		
Contribution to the Paper	Victor Sadras provided guidance in experimental design, data analysis and interpretation and in constructing and developing the manuscript.		
Signature		Date	24/08/2016

Negative association between chickpea response to competition and crop yield: Phenotypic and genetic analysis

Lachlan Lake [a,*], Yongle Li [b], Jorge J. Casal [c], Victor O. Sadras [a]

[a] *South Australian Research and Development Institute, Waite Campus, GPO Box 391, Adelaide 5001, Australia*
[b] *School of Agriculture, Food and Wine, University of Adelaide, Australia*
[c] *IFEVA, Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Av. San Martın 4453, 1417 Buenos Aires, Argentina*

ABSTRACT

Donald's ideotype and empirical evidence in cereal and oilseed crops indicate high yield is associated with less competitive plants. In this study we grew 20 chickpea lines in six environments to investigate the association between yield and intra-specific competitive ability and its genetic underpinnings using Fst genome scan based on whole genome resequencing data. We measured yield and its components and calculated response to competition (RC) as the ratio between the trait in outer rows (relaxed competition) and the trait in inner rows (higher competition). Crop yield correlated negatively with RC for yield, biomass, harvest index, seed number, and pod number. Fst genome scan revealed 14 genomic regions under selection for response to competition of yield, seed number or biomass, and 6 genomic regions under selection for yield in inner or outer canopy rows. Candidate genes in these regions include members of the nitrate-transporter 1 family, patatin and hormone-related genes. The top genomic regions found to be under selection for yield in inner rows and outer rows did not coincide. This genetic architecture provides a mechanistic basis for the observation that phenotypes that are adequate for relaxed competition often perform poorly in dense stands.

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1. Introduction

Plant-plant interactions include interactions between neighbours arising from utilisation of a common resource or through interference that is not mediated by resources, such as light or chemical signals (Aphalo and Ballare, 1995; Gillet, 2008; Schmidt et al., 2009; Karban, 2015). Donald (1968) postulated that a successful crop plant will be a weak competitor and suggested a breeding strategy targeting the 'communal ideotype' which is based on introgressing traits for weak competitive ability that confer adaptation to monocultures. This involves a trade-off between individual plant yield and communal yield, which has been recently reviewed by Asplen et al. (2012) and Denison (2015).

The negative association between competitive ability and yield has been particularly tested in cereals. In rice (Jennings and Aquino, 1968; Jennings and Herrera, 1968; Jennings and Jesus, 1968) and wheat (Khalifa and Qualset, 1975; Thomas and Schaalje, 1997) mixed line populations were sown, and the composition studied

over generations. Natural selection favoured the more competitive types, increasing their frequency, with a corresponding decrease in total yield per unit area. Hamblin and Donald (1974) observed that shorter barley plants with a lower single-plant yield in the F_3, corresponded to higher plant stand yields in the F_5. In wheat, barley and sunflower, high yield was associated with a less competitive phenotype (Romani et al., 1993; Reynolds et al., 1994; Sadras et al., 2000; Andrade et al., 2005; Sadras et al., 2012). Nasseer et al. (2016) assessed intraspecific competition, and found that high tillering in wheat showed a yield advantage under relaxed competition, but not in a normal cropping community. Duggan et al. (2005) also observed higher yield in reduced tillering lines under high intraspecific competition.

Sukumaran et al. (2015a) found that wheat genotypes that yielded more in high density stands responded less to reduced competition and used genome-wide association (GWAS) to identify markers for early stage selection in low density breeding trials. Similar to GWAS, Fst genome scan identifies genomic regions under selection using a large amount of molecular markers to scan for regions with extreme genetic differentiation between populations. It has been widely used to detect selection signatures in human and livestock genomes (Weir et al., 2005; Holsinger and Weir, 2009; Qanbari and Simianer, 2014). In crops, Fst scan has been

used to explore the genetics of powdery mildew resistance in wheat (Jordan et al., 2015) development in sorghum (Mace et al., 2013), and carbon isotope discrimination and nitrogen fixation in chickpea (Sadras et al., 2016). One of the advantages of Fst is that it returns robust information with relatively small number of genotypes. In the study of Sadras et al. (2016) for example, Fst scan identified genomic regions associated with agronomic traits in a collection of 20 chickpea lines.

Donald's hypothesis remains largely untested in pulses where the indeterminate growth habit (Cohen, 1971; Loomis and Connor, 1992) and symbiotic nitrogen fixation (Kiers et al., 2013) might influence plant–plant interactions and their impact in crop-level yield. In this paper, we tested the hypothesis of an inverse relationship between competitive ability and crop yield in chickpea and used Fst genome scan to explore the genetic basis of this relationship. Chickpea is a suitable crop for this study for three reasons: it is widely grown as a source of protein worldwide (Berger et al., 2006; Krishnamurthy et al., 2013; Farooq et al., 2016), its draft genome sequence has been published (Varshney et al., 2013), and it has been tested in Fst genome scan studies (Sadras et al., 2016).

2. Methods

2.1. Plant material, crop husbandry and experimental design

We used 20 chickpea lines that represent a broad range in agronomic adaptation, yield, phenology, and seed type (Table 1). This is the same set used in previous Fst scan studies (Sadras et al., 2016). Lines were compared in six environments in South Australia that were a combination of locations, seasons and sowing dates. The six environments were Turretfield (34°33′S, 138°49′E) at recommended sowing time (TOS 1; 8th June 2013 and 6th June 2014) and late sowing (TOS 2; 9th of July 2013 and 15th of July 2014), and Roseworthy (34°52′S, 138°69′E) at recommended sowing time (TOS 1 on 10th June 2014) and late sowing (TOS 2 on 15th July 2014).

The trials were sown after canola (2013) and barley (2014), into Calcic Luvisol at Turretfield and after barley, into Calcic Luvisol at Roseworthy. The seed was pre-treated with P − Pickel T fungicide to minimise the risk of *Aschochyta* blight and inoculated with Group N rhizobia immediately before sowing. To account for differences in plant vigour, the target plant density was 55 plants m^{-2} for Desi and 30 plants m^{-2} for Kabuli types. Crops were fertilised with 80 kg ha^{-1} mono ammonium phosphate at sowing. Before sowing weeds were controlled with an initial spray of Paraquat (135 g/L) and Diquat (115 g/L) mix, with follow up grass sprays (mixture of Butroxydim (250 g/kg) and Clethodim (240 g/L) and complementary hand weeding. We monitored crops for fungal symptoms on a weekly basis and applied preventative sprays (Chlorothalonil, 720 g/L) around flowering and podding or whenever symptoms were seen. Crops were treated with insecticide (Omethoate, 290 g/L) to prevent damage from *Helicoverpa spp.* around early podding.

The experiment was set in a randomised design with three replicates. Plot size was 7.25 m^2, comprised of standard six rows (spaced 24 cm in accordance with the design of the seeding machine) of five meters length. Plots were spaced 55 cm apart from each other for decreased competition in outer rows (Rebetzke et al., 2014).

2.2. Crop traits

Phenology was scored weekly to establish the time to 50% of plants in each plot reaching flowering, pod emergence (developing pods of 2–4 mm in length), end of flowering and maturity (yellowing pods) (Berger et al., 2004; Lake and Sadras, 2014). Phenology

was expressed on a thermal time scale, calculated from daily mean temperature and base temperature of 0 °C (Berger et al., 2006).

Yield and components were measured in two 50-cm samples taken from outer and inner rows (Bustos et al., 2013; Wang et al., 2013; Rotundo et al., 2014; Assefa et al., 2015). We determined shoot biomass, seed weight, seed number, pod number, seed size, seeds per pod and the derived traits harvest index (seed yield/shoot biomass) and pod wall ratio (pod wall weight/whole pod weight) (Lagunes-Espinoza et al., 1999; Clements et al., 2005; Lake and Sadras, 2014). Response to competition (RC, unitless) was calculated using the ratio of the trait in the outer row and the trait in the inner row, as in previous studies (Reynolds et al., 1994; Sadras et al., 2000; Sadras and Lawson, 2011; Sukumaran et al., 2015b).

2.3. DNA sequencing and F_{st} genome scan

DNA of each of the 20 lines was extracted from young leaf tissue from a single plant using Qiagen DNeasy Plant Mini Kit. Using TruSeq library kit, pair-end sequencing libraries were constructed for each cultivar with insert sizes of ∼500 base pairs (bp) according to the Illumina manufacturer's instruction. About 40 million 100 bp pair-end reads for each cultivar were generated using Illumina HiSeq 2000 platform.

Pair-end reads for each cultivar were trimmed, filtered and mapped to the Kabuli reference genome 2.6.2 using SOAP2 (Li et al., 2009). The BAM files containing sequence alignment information of each cultivar were separated into two contrasting groups (10 cultivars in each group) according to adjusted entry means of phenotypes. Fst was estimated in 100 kilobase pair (kb) non-overlapping windows based on the BAM files of two contrasting phenotypic groups using software ngsPopGen (Fumagalli et al., 2013). The Wright's Fst is a descriptive statistic that measures genetic variance among populations in population genetics (Fumagalli et al., 2013). Large Fst means the allele frequencies within each population are different; small Fst means the allele frequencies within each population are similar. he whole genome was scanned to identify regions with extreme population genetic differentiation (large Fst value compared to the surrounding region) which could serve as an indicator of selection signature; the Fst method has been used previously on the same 20 chickpea lines to explore the genetic basis of yield and traits related to nitrogen assimilation and water use efficiency (Sadras et al., 2016). The rationale is that genetic differentiation between groups at a given neutral locus (not under selection pressure) is determined by stochastic random factors such as random genetic drift. If a locus is under natural or artificial selection, the pattern of genetic differentiation may change. For example, regions showing uncommonly large amounts of genetic differentiation (different alleles are fixed in different groups) may have undergone diversifying selection. To avoid high error rate of next-generation sequencing data resulting in biased estimate of allele frequency, site frequency spectrum (SFS), the distribution of sample allele frequencies jointly for all sites (single nucleotide polymorphism in this case) and all cultivars, is incorporated into estimation of Fst (Fumagalli et al., 2013). This is a Bayesian framework where Fst is estimated from posterior probabilities of sample allele frequencies at each locus without genotype calling. To minimise the effect of sampling error, the Fst value for each single nucleotide polymorphism (SNP) within a window of 100 kb was averaged. We define regions with the top 0.1% Fst as genomic regions under selection. We do not intend to seek statistical significance, however, this serves to pinpoint regions where Fst values are extremely different from those in the rest of the genome. Different traits have different thresholds due to different Fst distribution (Supplementary Fig. 1).The adjacent genomic regions under selection are binned together and treated as one region.

Table 1
Selected features of 20 chickpea lines used in the study of competition. Yield response to competition (RC) is unitless; beginning of flowering and maturity are thermal time from sowing. Data are averages across all six environments, with range in parenthesis.

Line	Type	Yield (g m^{-2})	Yield RC	Flowering (Cd$^\circ$)	Maturity (Cd$^\circ$)
Sonali	Desi	285 (168–399)	1.55 (0.68–2.10)	947 (782–1087)	1695 (1542–1885)
CICA1229	Desi	302 (216–420)	1.58 (0.95–2.50)	992 (822–1201)	1651 (1438–1851)
PBA Striker	Desi	354 (213–500)	1.48 (0.90–2.23)	995 (782–228)	1656 (1438–1851)
Genesis079	Kabuli	380 (236–520)	1.48 (0.91–2.95)	1021 (811–1171)	1757 (1607–1885)
Genesis836	Kabuli	300 (170–465)	1.34 (1.00–1.84)	1028 (844–1201)	1724 (1571–1916)
Howzat	Desi	330 (243–479)	1.59 (1.11–2.32)	1033 (834–1216)	1716 (1557–1885)
PBA Slasher	Desi	342 (216–428)	1.55 (1.12–2.12)	1034 (834–1216)	1726 (1557–1902)
Genesis509	Desi	333 (168–463)	1.31 (0.82–1.74)	1035 (799–1228)	1672 (1504–1851)
PBA Boundary	Desi	305 (138–430)	1.66 (0.79–4.28)	1042 (834–1228)	1705 (1542–1902)
PBA Monarch	Kabuli	392 (226–627)	1.42 (1.12–1.97)	1045 (844–1239)	1727 (1495–1989)
CICA1016	Desi	302 (174–502)	1.76 (1.13–2.56)	1049 (844–1228)	1700 (1542–1865)
PBA HatTrick	Desi	281 (173–454)	1.55 (0.90–2.15)	1050 (868–1228)	1718 (1542–1902)
CICA1007	Desi	322 (194–398)	1.63 (1.16–2.12)	1054 (899–1228)	1724 (1557–1902)
PBA Pistol	Desi	320 (173–537)	1.68 (1.10–2.95)	1054 (868–1251)	1727 (1542–1902)
CICA0912	Desi	278 (192–392)	1.58 (1.14–2.50)	1056 (868–1282)	1697 (1521–1865)
Jimbour	Desi	323 (221–463)	1.51 (0.76–2.21)	1081 (899–1364)	1716 (1557–1906)
Almaz	Kabuli	321 (182–545)	1.50 (1.00–2.39)	1106 (907–1239)	1916 (1715–2150)
Kyabra	Desi	303 (185–391)	1.53 (1.13–2.32)	1106 (899–1364)	1721 (1557–1902)
Genesis090	Kabuli	336 (164–528)	1.55 (0.75–2.63)	1114 (855–1364)	1841 (1667–2020)
GenesisKalkee	Kabuli	360 (199–562)	1.39 (0.89–2.20)	1224 (999–1426)	1953 (1715–2150)

2.4. Environmental characterisation

Environmental characterisation lags behind phenotyping and genotyping efforts, hence our interest in quantitative, rather than nominal (e.g. location/season), environmental indices (Sadras et al., 2013). Two daily indices were used to quantify the water and photothermal environments, shown to be related to crop yield (Sadras et al., 2015; Lake et al., 2016). They were based on daily rainfall, temperature, radiation, vapour pressure and humidity from the nearest available weather station (https://www.longpaddock.qld.gov.au/silo/).

Daily water stress index was simulated using the chickpea module of Agricultural Production Systems Simulator (APSIM) software and actual weather data (Keating et al., 2003; Holzworth et al., 2014). Water stress index is the ratio between water supply (soil and root characteristics) and demand, driven by radiation, temperature and humidity. The range of the stress index is 1 (no stress) to 0 (maximum stress − growth has ceased). Details are in Lake et al. (2016).

Daily photothermal quotient corrected by vapour pressure deficit (PTQ$_{vpd}$) relates to non-stressful thermal effects on canopy size and yield (Sadras et al., 2015). It was calculated as PTQ$_{vpd}$ = radiation/(average temperature−vapour pressure deficit); we assumed a base temperature of 0 °C. For both water stress index and photothermal quotient, we divided the season into 200°-day intervals and calculated the average index for each interval centred at the flowering date for each environment across lines.

3. Results

3.1. Environmental conditions

The driest environments were the late-sown 2014 crops where seasonal rainfall was 100 mm for Roseworthy and 146 mm for Turretfield compared to 251 mm in the wettest environment, i.e. Turretfield, normal sowing in 2013. The normal-sown crops experienced an average of 2.1 °C cooler maxima and 0.82 °C cooler minima than the late-sown crops and received 2.8 MJ m^{-2} less radiation per day; vapour pressure deficit averaged 1.42 kPa for normal-sown crops and 1.62 kPa for late-sown crops.

Fig. 1 aggregates individual weather factors in physiologically meaningful indices: water stress index (Fig. 1a) and PTQ$_{vpd}$ (Fig. 1c).

At pod set (100–200 °Cd after flowering, there was a 19% difference in the water stress index between the least and most stressful environments, and a difference of ~0.6 MJm^{-2} °C^{-1}kPa^{-1} for the highest and lowest PTQ$_{vpd}$.

3.2. Phenology

Flowering time across environments ranged from 947 °Cd from sowing for Sonali to 1224 °Cd for Genesis Kalkee (Table 1). Time to pod emergence ranged from 1110 °Cd for Sonali to 1325 °Cd for Genesis Kalkee, and end of flowering ranged from 1356 °Cd for PBA Striker to 1510 °Cd for Genesis Kalkee (Table 1). The earliest maturing variety was CICA 1229 while the latest was Genesis Kalkee. The environment with the shortest average season was Roseworthy late-sown in 2014, with 874 °Cd to flowering, 979 °Cd to pod emergence, 1233 °Cd to end of flowering and 1571 °Cd to maturity. Turretfield normal sowing in 2013 was the longest season with 1235 °Cd to flowering, 1422 °Cd to pod emergence and 1625 °Cd to end of flowering; maturity was not scored for this environment.

3.3. Yield and its association with phenology

Across environments and varieties yield ranged from 138 to 627 g m^{-2} (Table 1). Across environments there was a positive relationship between yield and time to maturity (r = 0.60, $P < 0.0001$); relationships were also significant but weaker for other phenophases. However, sowing time was the driver of this relationship as normal-sown crops were higher yielding and had longer phenophases. To remove this effect we split the data by time of sowing; this revealed (i) no association of phenology and yield in late-sown crops and (ii) yield associations with time to pod emergence (r = −0.26, $P < 0.05$), end of flowering (r = −0.27, $P < 0.05$) and maturity (r = 0.42, P 0.01) in normal-sown crops.

3.4. Response to competition

Averaged across lines, yield response to competition ranged from 1.40 to 1.87 and was larger in environments with higher water supply/demand ratio and higher PTQ$_{vpd}$ (Fig. 1b,d). The response to competition of yield and its components varied among lines and environments (Table 1, Fig. 2); yield response to competition was associated with low crop yield across all environments. Fig. 2 illustrates the response to competition of yield, and its components
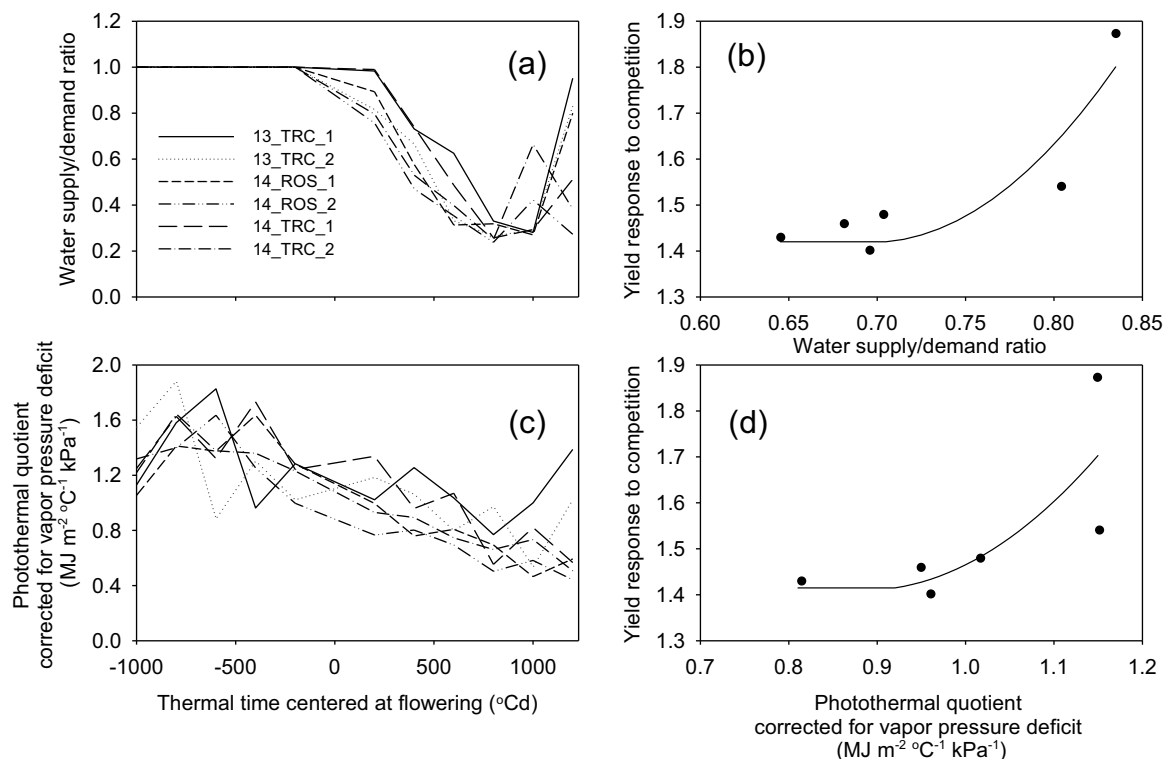
Fig. 1. (a) Patterns of water stress during the growing season (1 indicates no stress while 0 indicates maximum stress). (b) Relationship between the average water stress within the critical period for yield determination and yield response to competition for the six environments. (c) Patterns of photothermal quotient corrected for vapour pressure deficit during the growing season. (d) Relationship between average photothermal quotient corrected for vapour pressure deficit within the critical period for yield determination and yield response to competition for the six environments. The critical period was 200Cd° before flowering to 600Cd° post flowering.

seed number and seed size, using the approach of Sukumaran et al. (2015b). This demonstrates the association of yield (O+I) with a lesser difference between yield in the inner (I) and outer (O) rows. The same applies for grain number, whereas seed size was largely unresponsive to competition.

A principal component analysis visualises the relationships between crop yield (g m^{-2}, measured in inner rows) and response to competition of different traits for all lines across environments (Fig. 3). Crop yield had a strong, negative correlation with response to competition of yield, seed number, pod number, biomass and harvest index ($P < 0.0001$) and was unrelated to response to competition of seeds per pod, seed size and pod wall ratio.

We used a ratio to describe response to competition, with subsequent analysis of the form $Y_{(I)}$ vs $Y_{(O)}/Y_{(I)}$, where Y is yield, I is inner row and O is outer row. The common term $Y_{(I)}$ may give rise to spurious correlations (Brett, 2004). However, the likelihood of spurious correlations is low for two reasons. Firstly, spurious correlations are more likely when the variation in the shared term $Y_{(I)}$ is >1.5 times larger than the non-shared term $Y_{(o)}$ (Brett, 2004) whereas the shared term in our data had a coefficient of variation (0.26) that was almost equal to the non-shared term (0.25). Secondly the coefficient of variation for the sampled population was less than 0.4 which also reduces the chances of spurious correlations (Brett, 2004). Furthermore, response to competition of yield correlated with response of competition of other traits such as biomass, for which there is no common term in the calculations (Fig. 3).

3.5. Genomic regions under selection for yield in inner and outer rows

Fig. 4 compares the selection signature for yield in inner and outer rows. Four genomic regions with exceptionally large Fst values (top 0.1%) have been identified to be under selection for yield in

inner rows, whereas only two genomic regions with exceptionally large Fst values have been identified for yield in outer rows. The genomic regions under selection for yield in inner rows and outer rows did not overlap. Genes are listed in Supplementary Table 1.

3.6. Genomic regions under selection for response to competition

The distribution of Fst was highly skewed toward zero with average Fst of 0.0444 for yield (RC), 0.0854 for seed number (RC) and 0.0974 for biomass (RC) (Supplementary Fig. 1). Five genomic regions have been identified with exceptionally large values for yield (RC) and biomass (RC), and four genomic regions for seed number (RC) (Fig. 5). Some genomic regions have been identified to be under selection for different traits. For example, a genomic region in Ca4 (Ca4:2,401,618.Ca4:2,501,618) is identified as under selection for yield (RC), seed number (RC), and biomass (RC). Another genomic region in Ca4 (Ca4:1,901,618.Ca4:2,001,618) is identified as under selection for both yield (RC) and biomass (RC). Supplementary Table 1 shows the complete list of genes present in the regions under selection for yield response to competition.

4. Discussion

4.1. Response to competition, yield components and environment

Previous studies in cereals and sunflower conform with the theory of Donald's ideotype with more competitive lines producing a lower yield in pure stand (Jennings and Aquino, 1968; Jennings and Herrera, 1968; Hamblin and Donald, 1974; Khalifa and Qualset, 1975). This is the first study that investigates grain legumes. Our finding also conforms to theory: lines that are more responsive to competition have a lower yield than their less responsive counterparts.
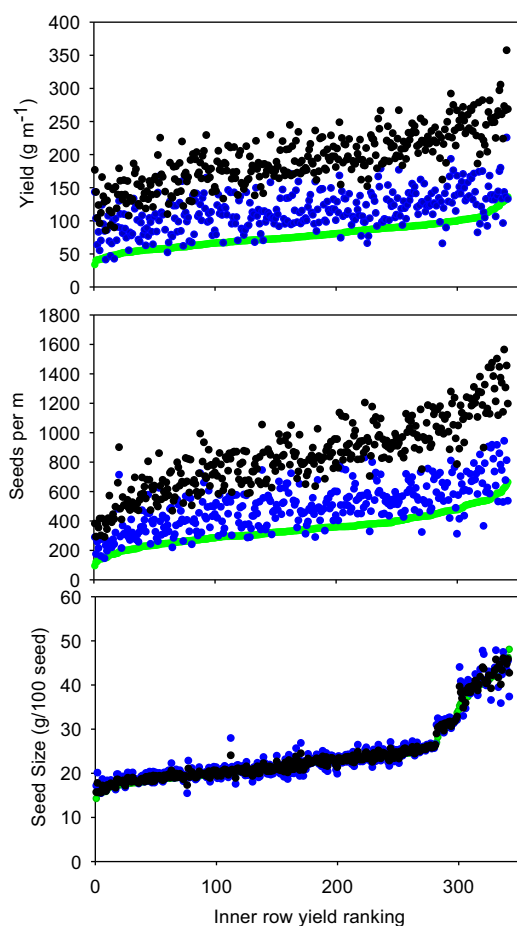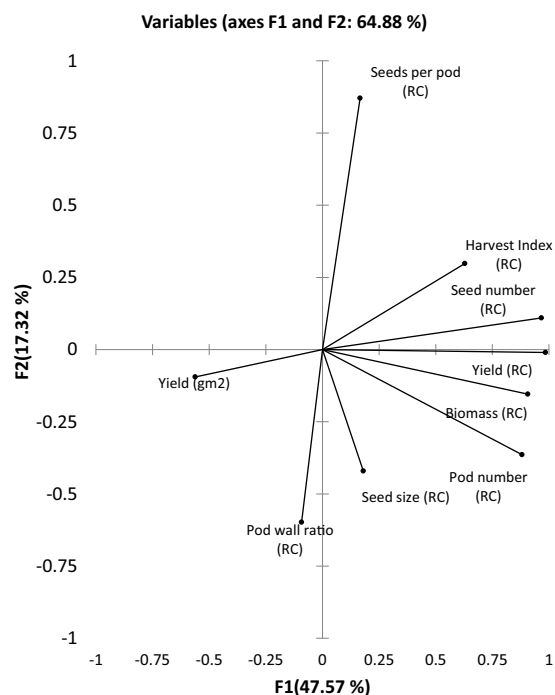
Fig. 2. Comparison of (a) grain yield, (b) seed number and (c) seed size measured in the inner rows (I, green), outer rows (O, blue), and the total (I+O, black). Data is based on all lines from all environments (n = 360). The x-axis was sorted by the inner row value. For seed size, the average of O and I was used. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)


Fig. 3. PCA of crop yield (yield g m^{-2}) and response to competition (RC) of yield and yield components. Data is from all lines and environments.

Yield response to competition has been reported as 5–84% in sunflower Sadras et al. (2000), from 6 to 90% in wheat (Fischer and Laing, 1976; Austin and Blackwell, 1980; Reynolds et al., 1994; Sadras and Lawson, 2011; Sukumaran et al., 2015b) and 41–45% in barley (Romani et al., 1993). This compares with our responses from 31 to 76%. Response to competition of yield was mediated by response of competition of seed number. This is in agreement with both yield response to competition in other species (Khalifa and Qualset, 1975; Reynolds et al., 1994; Sadras and Lawson, 2011; Sukumaran et al., 2015b) and current models of crop yield assuming that crops accommodate environmental variation through seed number, and a conserved seed size (Sadras, 2007; Sadras and Slafer, 2012; Slafer et al., 2014).

The response to competition was larger in favourable environments (lower water stress and higher PTQ$_{vpd}$), as found in other studies. In wheat, Sadras and Lawson (2011) reported a range of response to competition from 79% in a favourable environment to only 27% under stress. In *Chenopodium acuminatum* and *Abutilon theophrasti* a larger response to competition occurred in the fertilised treatments (Sugiyama and Bazzaz, 1997; Wang et al., 2014). In sunflower, hybrids that were tolerant of disease showed larger response to reduced competition (Sadras et al., 2000), while in wheat, high tillering plants only showed yield gain at low competition or in high resource environments (Nasseer et al., 2016).

For the normal time of sowing, the negative relationship between yield and time to flowering, pod emergence and end of flowering, coupled with the positive relationship between maturity and yield, conforms to physiological principles surrounding indeterminate species; earlier flowering and later maturity mean a longer reproductive window and higher yield in favourable conditions. Normal sowing also means less likely stress during the critical period for yield formation despite the longer flowering duration (Lake and Sadras, 2014).

4.2. Genomic regions under selection for yield and response to competition

Theory (Donald, 1963; Donald, 1968; Donald, 1981; Denison, 2011; Denison, 2015) and empirical evidence (Pedró et al., 2012) show that the phenotype that favours yield under competition (i.e. crop yield) and the phenotype that favours seed production in isolated plants or under relaxed competition are different. Here we show a genetic architecture that accounts for these earlier conclusions based on phenotypes. By using stringent criteria (top 0.1% Fst threshold for each trait) we have identified five genomic regions under selection for yield response to competition, four for yield in inner rows and two for yield in outer rows. The top genomic regions under selection for yield in crop conditions are different from the top genomic regions under selection for yield of plants under relaxed competition. Although each one of these regions could have a contribution in the opposite condition, the magnitude of this contribution is different. Furthermore, the top regions for yield RC are also different from those identified for yield in inner and outer rows. These regions could have minor but opposite effects in inner and outer rows, which would place them beneath the Fst threshold in each case but emerging when RC is calculated. In other words, neither the phenotypes nor the genotypes that favour yield under relaxed competition are necessarily superior in dense stands. This genetic architecture justifies the search for and focus on communal traits as suggested by Donald and highlights the caution needed in extrapolating from individual plants or single rows to normal crop configurations, where plant–plant interference is significant.
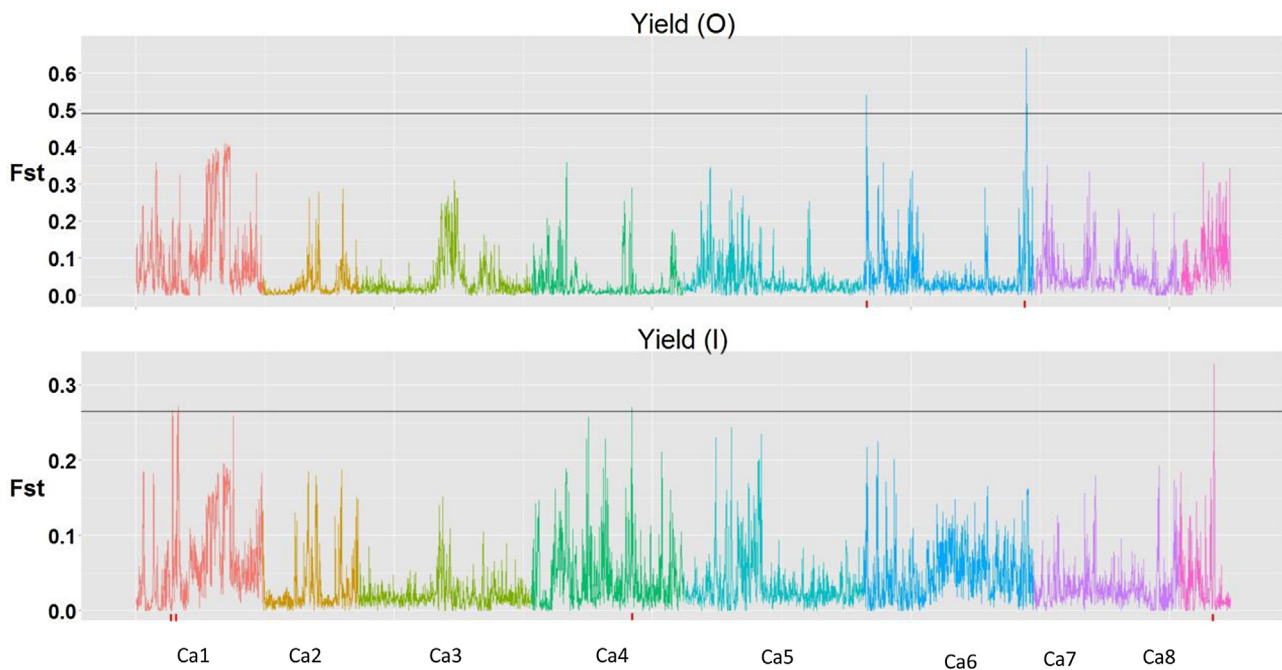
Fig. 4. Fst genome scan of yield of inner (I) and outer (O) rows. Fst value (see method) above the black lines (top 0.1% of Fst) indicate genomic regions with extreme population genetic differentiation (regions under selection). Ca1-8 represent chromosome1-8.
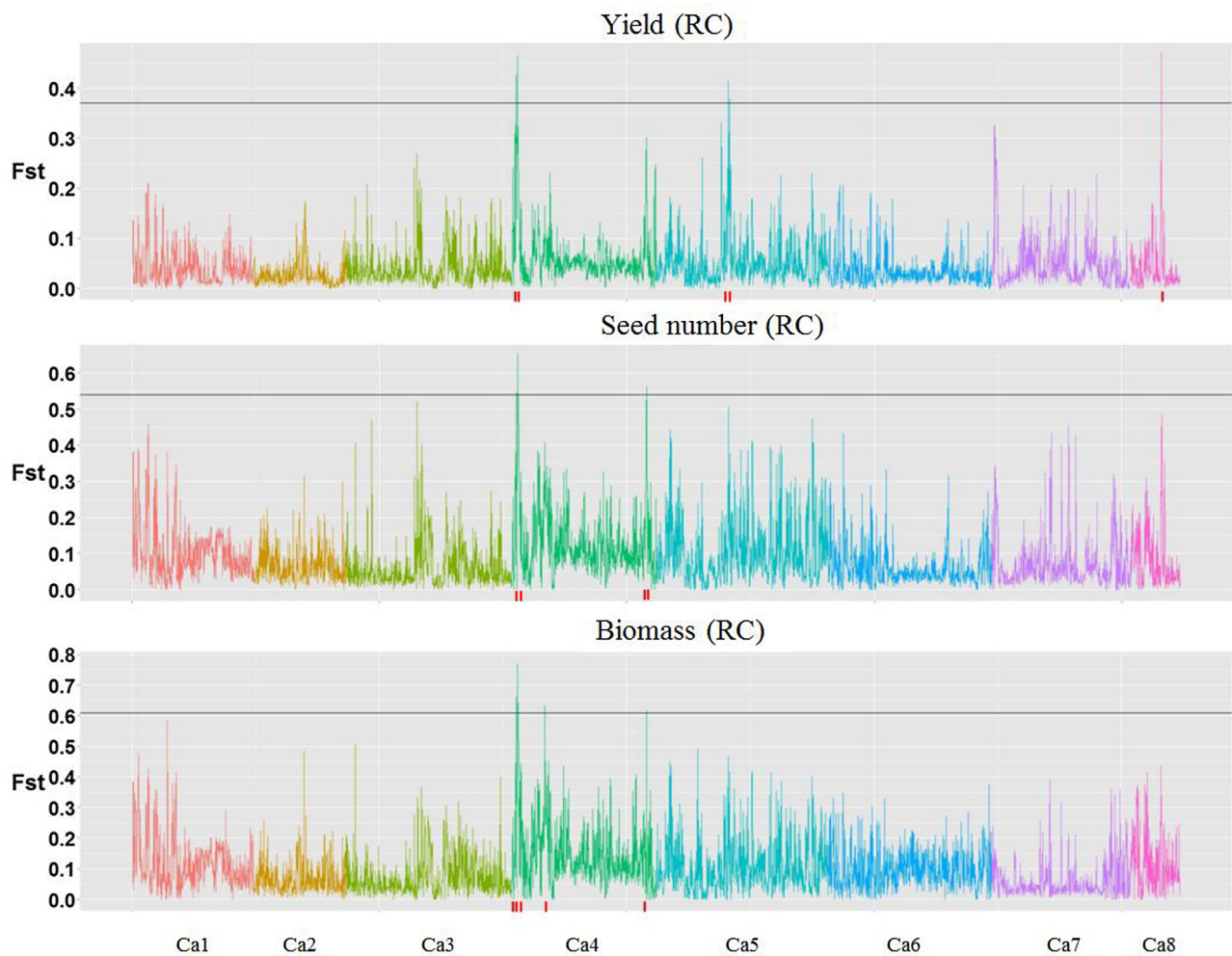
Fig. 5. Fst genome scan of yield (RC), seed number (RC), and biomass (RC). Fst value (see method) above the black lines (top 0.1% of Fst) indicate genomic regions with extreme population genetic differentiation (regions under selection). Ca1-8 represent chromosome1-8.

Within the regions identified here there are many candidate genes that could theoretically contribute to yield. However, it is interesting to focus on some of them for which there is direct evidence for associations with yield. For instance, the region Yield-Outer-1 in chromosome 6 includes a gene (Ca6:1267008, Ca6:1283051, Ca6:1282482) that bears similarity to the AT2G02040 locus in *Arabidopsis thaliana* (Table S1), which encodes the *PEPTIDE TRANSPORTER 2 (PTR2)* gene belonging to the *NITRATE TRANSPORTER 1 (NRT1)*. Anti-sense expression of *PTR2* causes reduced seed number due to impaired seed formation in Arabidopsis (Song et al., 1997). The *OsPTR9* gene of *Oryza sativa* (LOC_06g49250) is also closely related to the *PTR2* gene of Arabidopsis. Elevated expression of *OsPTR9* in transgenic rice plants enhances ammonium uptake, lateral root formation and grain yield, whereas the loss-of function mutation causes the opposite effects (Fang et al., 2013). Of interest, grain yield was related to uptake of mineral nitrogen and unrelated to nitrogen fixation in field experiments including the same collection of lines in similar environments (Sadras et al., 2016).

There are other examples of members of the NRT1 family affecting embryo development and controlling abortion (Almagro et al., 2008). Noteworthy, another region in chromosome 6, the Yield-outer-2 region, contains a gene (Ca6:62849772) with high similarity to the AT1G69850 gene of Arabidopsis, which encodes another member of the NRT1family.

The Yield-RC-1 region in chromosome four contains a gene (Ca4:1996068) with similarity to the Arabidopsis AT3G63200 locus that encodes the *PATATIN-LIKE PROTEIN 9* gene involved in lipid metabolic processes. Overexpression of a patatin-like protein in *Camelina sativa* (Li et al., 2015) or in Arabidopsis (Li et al., 2013) reduced growth and overall seed production but increased seed oil content. There are also two WRKY transcriptional factors in these genomic regions: WRKY13 and WRKY51. The former is a transcriptional factor that responds to drought stress via suppressing transcriptional factor SNAC1, which mediates drought tolerance by promoting stomatal closure (Xiao et al., 2013). The latter is involved in regulating gene expression involved in phytohormone ABA and GA signalling crosstalk in rice (Xie et al., 2006). In addition, a predicted gene encoding ovate family protein OFPs, is also under selection in Yield (RC). This gene family functions as transcriptional repressors and regulate multiple aspects of plant growth and development in Arabidopsis such as cell elongation and secondary cell wall formation (Wang et al., 2011).

Two seed number (SN)-RC regions, contained genes related to the metabolism of the plant hormone cytokinin which plays an important role in various phases of plant growth and grain development in maize and barley (Powell et al., 2013). The SN-RC-2 region in chromosome 4 contains a gene (Ca4:2446117) with similarity to AT3G63110, which encodes a cytokinin biosynthetic enzyme called *ISOPENTENIL TRANSFERASE 3 (IPT3)* in Arabidopsis. Another region in chromosome 4, SN-RC-3 contains a gene (Ca4:54666172) with similarity to AT5G21482, which encodes the *CYTOKININ OXIDASE 7 (CKX7)* gene. The rice Gn1a gene encoding cytokinin oxidase/dehydrogenase (*OsCKX2*) has been found to increase grain number (Ashikari et al., 2005). Additionally, two Arabidopsis mutants of cytokinin oxidase/dehydrogenase were found to increase total number of seed by 55% compared with the wild type (Bartrina et al., 2011). The SN-RC-2 region in chromosome 4 also contains a gene (Ca4:2560130) with similarity to AT3G23150, which encodes one of the ethylene receptors in Arabidopsis (*ETR2*). ETR2 has been found to be associated with a reduction in effective panicles and seed-setting rate, and delayed flowering in rice (Wuriyanghan et al., 2009).

Evidence from other species suggests that genes within these regions under selection are likely to be involved in different phenotypic responses to competition (Djakovic-Petrovic et al., 2007; Schmidt et al., 2009; Wang et al., 2011; Xiao et al., 2013); however, further research is needed to validate the functions of these candidate genes/SNPs on response to competition in chickpea.

5. Conclusion

This research has demonstrated that a less competitive chickpea phenotype is associated with higher yield and conforms to the idea of the 'communal ideotype'. A corollary of this finding is the caution needed to extrapolate yield-related traits from single plants or single rows to crops. Early generation selection for yield will favour traits that are conducive to individual rather than communal performance. We have identified genetic regions under selection for response to competition and associated candidate genes that offer insight into these processes. Further research on communal traits in pulses is warranted. Molecular markers associated with less competitive types might be useful in breeding, provided they return higher rates of yield improvement than direct selection for yield, or similar rates at lower cost.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2016.07.021.

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Chapter 5

**Screening chickpea for adaptation to water stress:
Associations between yield and crop growth rate**

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Overall percentage (%)	75%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.
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By signing the Statement of Authorship, each author certifies that:

iv. the candidate's stated contribution to the publication is accurate (as detailed above);

v. permission is granted for the candidate in include the publication in the thesis; and

vi. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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Contribution to the Paper	Victor Sadras provided guidance in data analysis and interpretation and in constructing and developing the manuscript.
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Screening chickpea for adaptation to water stress: Associations between yield and crop growth rate

Lachlan Lake*, Victor O. Sadras

South Australian Research and Development Institute, Waite Campus, G.P.O. Box 391, Adelaide 5001, Australia

A B S T R A C T

Robust associations between yield and crop growth rate in a species-specific critical developmental window have been demonstrated in many crops. In this study we focus on genotype-driven variation in crop growth rate and its association with chickpea yield under drought. We measured crop growth rate using Normalised Difference Vegetative Index (NDVI) in 20 diverse chickpea lines, after calibration of NDVI against biomass accounting for morphological differences between Kabuli and Desi types. Crops were grown in eight environments resulting from the combination of seasons, sowing dates and water supply, returning a yield range from 152 to 366 g m^{-2}. For both sources of variation – environment and genotype – yield correlated with crop growth rate in the window 300 °Cd before flowering to 200 °Cd after flowering. In the range of crop growth rate from 0.07 to 0.91 g m^{-2} °Cd^{-1}, the relationship was linear with zero intercept, as with other indeterminate grain legumes. Genotype-driven associations between yield and crop growth rate were stronger under water stress than under favourable conditions. Despite this general trend, lines were identified with high crop growth rate in both favourable and stress conditions. We demonstrate that calibrated NDVI is a rapid, inexpensive screening tool to capture a physiologically meaningful link between yield and crop growth rate in chickpea.

1. Introduction

Chickpea is one of the most important pulse crops grown in over 50 countries with an aggregated annual production of 14 million tonnes in 2014 (Jumrani and Bhatia, 2014; FAO, 2015). It is an important source of affordable protein, which is being increasingly recognised for its health benefits, and contributes nitrogen fixation in rotations with cereals (Venn and Mann, 2004; Duc et al., 2014; Arnoldi et al., 2015; Rubiales and Mikic, 2015). However, chickpea yield remains unstable and unreliable and in many countries averages less than 1 t ha^{-1} mainly as a result of abiotic and biotic stress (FAO, 2015; Rubiales et al., 2015; Rubiales and Mikic, 2015).

Yield is associated with crop growth rate in a species-specific critical window in maize, wheat, canola, sunflower, pea and soybean (Tollenaar et al., 1992; Andrade et al., 2002, 2005; Guilioni et al., 2003; Sadras et al., 2012b; Zhang and Flottmann, 2016). Crop growth rate integrates environmental and genotypic sources of variation, and is thus a trait often used in modelling and with potential applications in breeding (Wiegand and Richardson, 1990).

Guilioni et al. (2003) for example, found a single linear relationship between yield and crop growth rate of field pea regardless of stress type (drought or heat), while Echarte et al. (2004) demonstrated that growth rate in a critical period was useful in quantifying yield differences in maize hybrids grown in contrasting environments.

Both the timing of the critical period and the models describing the relationship between yield and crop growth rate differ among species. The most critical period is before flowering in small grain cereals, and after flowering in pulses (Sadras and Dreccer, 2015); Fig. 1c outlines the critical period of chickpea. Indeterminate soybean has a linear relationship with zero intercept, canola also has a linear relationship with undefined intercept, while determinate maize and sunflower are non-linear (hyperbolic) with a non-zero intercept indicating a minimum crop growth rate for reproduction (Egli and Yu, 1991; Egli, 1993; Vega et al., 2001a; Guilioni et al., 2003; Andrade et al., 2005; Zhang and Flottmann, 2016). Linear (Guilioni et al., 2003) and non-linear relationships (Sadras et al., 2013) have been reported for field pea. The shape of the model is important because a linear relationship indicates a tight coupling between vegetative and reproductive growth, whereas non-linearity indicates decoupling. The decoupling can be morphological as in maize and sunflower where strong apical dominance constrains seed set under high availability of resources, or physio-

* Corresponding author.
E-mail addresses: lachlan.lake@sa.gov.au (L. Lake), victor.sadras@sa.gov.au (V.O. Sadras).
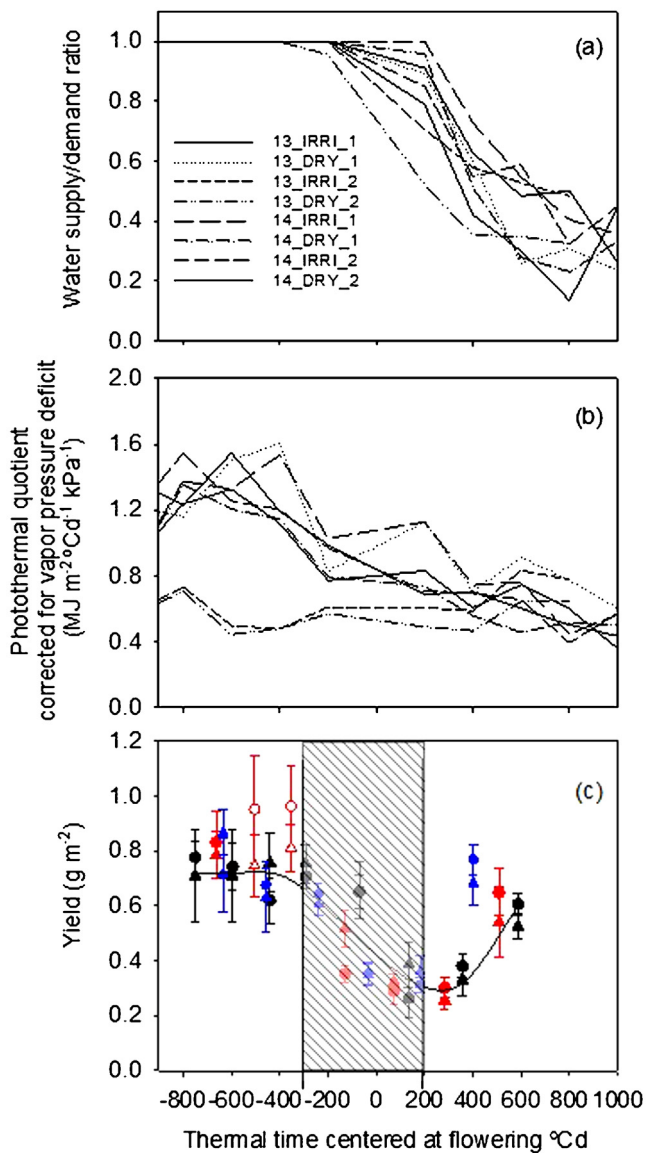
Fig. 1. Seasonal patterns of (a) water stress index (1 indicates no stress while 0 indicates maximum stress) and (b) photothermal quotient corrected for vapour pressure deficit in eight environments. As a reference, (c) shows the critical period for yield determination (adapted from Lake and Sadras (2014)) where the shaded area represents the time when we measured crop growth rate. Key to environments: Year_Water Regime_sowing time; for example 13_IRRI_1 indicates 2013, irrigated, 1st sowing.

Few studies investigated the association between yield and crop growth in chickpea. Krishnamurthy et al. (1999) and Ramamoorthy et al. (2016) reported relationships between crop growth rate and yield in chickpea but their growth rates were derived from harvest biomass and duration of growth; this is in reality a primary measure of maturity biomass and does not allow for specific insights into the relationship between yield and crop growth rate in physiologically meaningful periods. There is scarce information in chickpea about the association of yield and crop growth rate within physiologically meaningful critical periods (Lake and Sadras, 2014), the nature of the association (linear/non-linear) or the consistency of the relationship for different varieties and environments. This research aims to test the association between growth rate within the critical period and yield in a collection of chickpea lines grown in an environmental range from nearly yield potential to agronomically meaningful water stress (Passioura, 1996, 2007).

2. Materials and methods

The experimental details have been presented in Sadras et al. (2016) who also reported yield and phenology. In this section we summarise general methods, and provide detail on the approach to measure crop growth rate and its association with yield.

2.1. Plant material and experimental design

Fifteen Desi and five Kabuli chickpea lines (Table 1) that represent a broad range in agronomic adaptation, yield, morphology and phenology were evaluated. Crops were grown at Roseworthy (34°52′S, 138°69′E) in South Australia; eight environments resulted from a combination of two seasons (2013 and 2014), two sowing dates and two water regimes.

The first sowing date was 7th June 2013 and 10th June 2014 and the second was 9th July 2013 and 15th July 2014. Late-sown crops were expected to have lower yields caused by elevated temperatures and lower photothermal quotient (Fig. 1b) (Sadras and Dreccer, 2015).

The two water regimes were either sprinkler irrigated or rainout shelter canopy for the first sowing date (installed on the 3rd August in 2013 and 23rd July in 2014) and sprinkler irrigated and rainfed for the late sowing (from here on we will refer to the rainfed and rainout shelter environments as "dry"). Irrigation was applied to match evaporative demand and begun 41–76 days after sowing. Water regimes were intended to provide conditions suitable for high yield, and water deficit around the critical period for yield determination (Fig. 1a and c).

Treatments were laid out in a split-split-plot design of three replicates with sowing date as main plot, water regime as secondary plot, and varieties randomised within each plot. Plot size was 7.25 m², comprised of six rows (spaced 24 cm) of five meters length. For further details of crop management see Sadras et al. (2016).

2.2. Measurements

2.2.1. Phenology

We scored phenology weekly to establish time to: 50% of plants in each plot reaching flowering, pod emergence (developing pods of 2–4 mm in length), end of flowering and maturity (yellowing pods) (Berger et al., 2004; Lake and Sadras, 2014). Flowering duration was calculated as the time between 50% flowering and the end of flowering. We used a thermal time scale to express phenology, calculated from daily mean temperature and base temperature of 0 °C (Berger et al., 2006).

logical as speculated for field pea (Andrade et al., 2005; Sadras et al., 2013).

Crop growth rate can be derived from destructive measurements of biomass (Tollenaar et al., 1992; Andrade et al., 1999; Guilioni et al., 2003; Zhang and Flottmann, 2016) or with morphometric measurements based on allometric relationships (Vega et al., 2001b). Both methods are time consuming. A non-destructive option is spectral reflectance, which can provide high throughput alternatives (Ma et al., 1996, 2001; Sadras et al., 2013). There has been limited work in grain legumes which have a more challenging architecture as illustrated by Sadras et al. (2013) who used Normalised Difference Vegetative Index (NDVI) to measure crop growth rate in field pea where separate calibrations were required for different morphological types (semi-leafless and conventional leaf types).

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Table 1
The 10th, 50th and 90th percentile yield and crop growth rate (CGR) of 20 chickpea lines grown in eight environments.

Line	Seed type	10th percentile		50th percentile		90th percentile	
		Yield($g\,m^{-2}$)	CGR($g\,m^{-2}\,°Cd$)	Yield($g\,m^{-2}$)	CGR($g\,m^{-2}\,°Cd$)	Yield($g\,m^{-2}$)	CGR($g\,m^{-2}\,°Cd$)
Almaz	Kabuli	121	0.09	218	0.50	325	0.75
PBA Monarch	Kabuli	166	0.16	291	0.53	558	0.66
CICA0912	Desi	152	0.26	257	0.53	336	0.65
CICA1007	Desi	156	0.21	284	0.51	451	0.61
CICA1016	Desi	183	0.26	290	0.53	400	0.64
CICA1229	Desi	135	0.28	283	0.52	475	0.73
GenesisKalkee	Kabuli	145	0.13	255	0.53	398	0.72
Genesis079	Kabuli	183	0.28	269	0.60	492	0.76
Genesis090	Kabuli	143	0.27	308	0.52	449	0.84
Genesis509	Desi	155	0.24	265	0.51	464	0.65
Genesis836	Desi	154	0.24	238	0.45	402	0.63
Howzat	Desi	158	0.25	277	0.49	392	0.62
Jimbour	Desi	128	0.19	251	0.48	416	0.63
Kyabra	Desi	148	0.18	300	0.51	400	0.80
PBA Boundary	Desi	182	0.34	288	0.47	430	0.63
PBA HatTrick	Desi	121	0.23	245	0.47	411	0.70
PBA Pistol	Desi	176	0.26	256	0.51	531	0.72
PBA Slasher	Desi	184	0.26	315	0.48	446	0.69
PBA Striker	Desi	169	0.31	271	0.50	415	0.65
Sonali	Desi	149	0.27	278	0.51	409	0.77

2.2.2. NDVI – biomass calibration

Our approach included two steps. In step 1, we derived a NDVI-biomass calibration, and in step 2, we tested the calibration with an independent data set.

2.2.2.1. Step 1.
Two Kabuli (Genesis Kalkee, Genesis 090) and four Desi (CICA 1229, PBA Slasher, PBA Boundary, Sonali) lines were grown in three environments: Turretfield (34°33′S, 138°49′E), where crops were sown on 14th June and 9th July 2013, and Roseworthy where crops were sown on 10th June 2014. We collected NDVI (Greenseeker NTech Industries Inc, California, USA) and shoot biomass data once every 7–10 days throughout the growing season. NDVI was measured by passing the Greenseeker over the four central rows at a height of 40 cm ensuring to keep within the border rows. We also measured NDVI of the bare soil to verify the similarity of soil spectral properties in the three environments (Baret and Guyot, 1991). Immediately after measuring NDVI, we sampled shoot biomass (4×1 lineal meter cuts $\sim 1\,m^2$). We fit exponential curves to relate NDVI and biomass.

2.2.2.2. Step 2.
One Kabuli (PBA Monarch) and six Desi (CICA1229, PBA HatTrick, PBA Striker, PBA Pistol, Genesis 836, PBA Boundary) lines were grown under four conditions (early and late sowing, irrigated and dry) in 2015 using the same experimental design as in Section 2.1. Every 10–15 days, we measured NDVI and shoot biomass as in step 1. We compared crop growth rate derived from NDVI using the calibration in step 1, and crop growth rate derived from biomass.

2.2.3. Crop growth rate and yield

Yield was measured from 2×1 lineal m cuts taken from inner rows of plots; see Sadras et al. (2016) for details. We estimated crop growth rate using weekly measurements of NDVI after the crops reached a minimum threshold of canopy cover (no more than 50% of the soil visible through canopy) until maturity. A minimum canopy cover is required for meaningful NDVI as a large soil: vegetation ratio distorts readings (Baret and Guyot, 1991). We fitted polynomials to plot the progression of NDVI with time and used the calibration equations (Section 2.2.2) to convert NDVI to biomass and calculate crop growth rate (Sadras et al., 2012a). We used three criteria to define the time-window for the calculation of crop growth rate; it had to be consistent with the physiology of the species (Lake and Sadras, 2014), relate to yield, and fit within

the confines of the NDVI ability to detect biomass changes before saturation (Fig. 2a). These criteria returned a window from 300 °Cd before to 200 °Cd after flowering (Fig. 1c). Hereafter, crop growth rate refers to this window.

2.3. Environmental characterisation and data analysis

We used physiologically relevant indices to quantify our environments. Water stress index and photothermal quotient corrected for vapour pressure deficit were calculated daily using daily rainfall, temperature, radiation, and vapour pressure from Roseworthy's weather station (https://www.longpaddock.qld.gov.au/silo/).

We used the chickpea module of Agricultural Production Systems Simulator (APSIM) software and actual weather data to simulate daily water stress index (Keating et al., 2003; Holzworth et al., 2014). Water stress index ranges from 1 (no stress) and 0 (maximum stress where growth ceases). The index is driven by radiation, temperature and humidity and is calculated as the ratio between water supply (soil and root characteristics) and demand.

Daily photothermal quotient corrected by vapour pressure deficit (PTQ_{vpd}) was calculated as PTQ_{vpd} = radiation/(average temperature × vapour pressure deficit) (Rodriguez and Sadras, 2007).

The effect of environment, line and the interaction was tested using analysis of variance. Linear and non-linear models were fitted to explore the associations between crop traits and between crop traits and environmental variables. As the x and the y variables were subject to error, we used linear regression Modell II (Ludbrook, 2012).

3. Results

3.1. Environmental conditions

The modelled water supply/demand ratios for each of the environments are presented in Fig. 1a. The trajectories of water supply/demand were bounded by the late sown, rainfed crop of 2013 with a water-stress onset at about 400 °Cd before flowering, and the late sown irrigated crop of 2014 with an onset 200 °Cd after flowering. Around the critical point of 200 °Cd after flowering (Lake and Sadras, 2014) there was a 48% difference in water stress between the most and least stressed crops.

Throughout the season the early-sown crops experienced an average 1.4 °C cooler maxima and 0.4 °C cooler minima than the
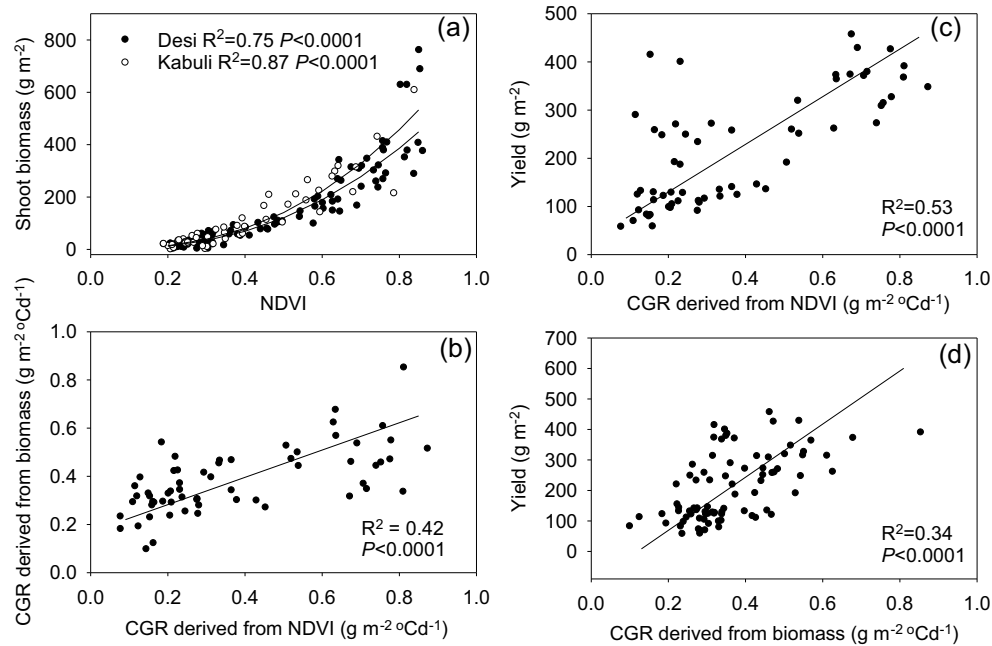
Fig. 2. (a) Relationship between shoot biomass and NDVI for four Desi and two Kabuli chickpeas grown in three environments in 2013 and 2014. The fitted curves are $y = a\,e^{xb}$ with parameters $a = 671.57$, $b = 2.478$ for Desi and $a = 800.65$, $b = 2.509$ for Kabuli. (b) Comparison between the crop growth rate derived from biomass and crop growth rate derived from NDVI. (c) Relationship between yield and crop growth rate derived from NDVI. (d) Relationship between yield and crop growth rate derived from biomass. In (b, c, d) data are from 7 lines and 4 environments in 2015, and crop growth rate is for the window from $300\,°Cd$ before flowering to $200\,°Cd$ after flowering.

late-sown crops, while radiation was $4.5\,MJ\,m^{-2}$ less per day; vapour pressure deficit averaged 1.73 kPa for early-sown crops and 2.08 kPa for late-sown crops. Fig. 1b shows the PTQ_{vpd} for each environment, highlighting the low values for the late sown crops in 2013. Around the critical point of $200\,°Cd$ after flowering (Lake and Sadras, 2014) there was 57% difference in PTQ_{vpd}.

3.2. Yield and phenology

Yield and phenology were analysed in Sadras et al. (2016). Variation of yield was 4.6-fold, from $1.1\,t\,ha^{-1}$ (PBA HatTrick in 2013, first sowing, dry treatment) to $5.1\,t\,ha^{-1}$ (PBA Monarch in 2014, first sowing, irrigated treatment); it was affected by line, season, water regime ($P < 0.0001$), sowing date ($P = 0.005$), the interaction between season and sowing date ($P < 0.0001$), and the interactions between water regime with line ($P = 0.001$) and season ($P = 0.0003$). Yield variation between lines is presented in Table 1.

Across environments the earliest line flowered in $962\,°Cd$ from sowing (Sonali) and the latest took $1180\,°Cd$ (Genesis Kalkee), while the earliest environment flowered in $860\,°Cd$ and the latest took $1263\,°Cd$. Longer phenological stages had a positive association with yield although this was largely driven by environmental differences with less stressful environments having longer phenophases and higher yield.

3.3. NDVI-biomass calibration

The relationship between NDVI and shoot biomass was strong across the three environments and lines, with an upper NDVI limit of ~0.9 when the canopy had closed. Separate curves were fitted to Desi and Kabuli lines (Fig. 2a) as the curve fitted to the pooled data returned different residuals for the two types ($P = 0.052$). Using the independent data set (step 2 in methods), we found a significant but scattered association between crop growth rate derived from biomass and crop growth rate derived from NDVI (Fig. 2b). We then compared the association of yield to crop growth rate derived from each of the two methods (Fig. 2c and d). The relationship

was stronger with NDVI-derived crop growth rate. This is possibly related to NDVI being measured over a larger area ($\sim4.5\,m^2$) than biomass ($\sim0.25\,m^2$) and with greater frequency.
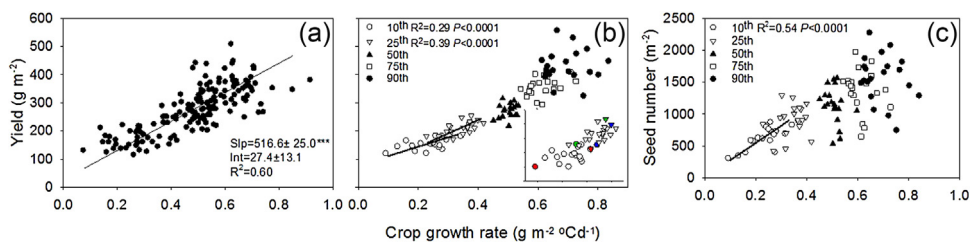
3.4. Crop growth rate and its relationship with yield

The analysis of variance revealed a significant effect of environment, line and their interaction on crop growth rate (all $P < 0.0001$). There was a positive relationship between crop growth rate and phenology for all phenological stages ($P < 0.0001$); however the primary driver of this relationship was environment and the relationship became non-significant when the effect of environment was removed. Water stress index (Fig. 1) was the dominant driver of environmental variation with a significant positive relationship with crop growth rate ($R^2 = 0.68$, $P < 0.011$).

Fig. 3 shows the relationship between yield, seed number and crop growth rate. Across lines and environments, yield was closely related to crop growth rate (Fig. 3a). The association between yield and crop growth rate for lines averaged across environments was significant but more scattered ($R^2 = 0.22$, $P = 0.0374$). We further analysed this association calculating yield and growth rate for the 10th, 25th, 50th, 75th and 90th percentiles for each line, thus accounting for the environmental variation from more stressful (10th percentile) to more favourable (90th) (Fig. 3b). The association between yield and crop growth rate was stronger under stress (10th and 25th percentiles), and this is reinforced by the association between seed number and crop growth rate in the 10th percentile (Fig. 3c). Among the 20 lines investigated, there were lines such as CICA 1016 and PBA Boundary which had relatively high crop growth rate in both the 10th and the 25th percentile environments with no significant difference to other lines in the 90th percentile (Fig. 3b inset and Table 1).

In all cases, the relationships between yield and crop growth rate were linear (i.e. quadratic term not significant, $P = 0.14$) and intercept not different from zero ($P > 0.9$).

Fig. 3. (a) Relationship between yield and crop growth rate derived with NDVI for the combination of 20 lines and 8 environments. Relationship between NDVI derived crop growth rate and (b) yield and (c) seed number. In both (b) and (c), the 10th, 25th, 50th, 75th and 90th percentiles are presented to represent a range from more stressful to more favourable conditions. Lines are Model II (Reduced Major Axis) regressions accounting for error in both variables (Ludbrook, 2012), and are not plotted when not significant ($P > 0.05$). Inset in 3(b) zooms in on the 10th (circles) and 25th (triangles) percentiles for yield and crop growth rate and highlights three contrasting lines. Red is Almaz, blue is PBA Boundary and green is CICA 1016.Crop growth rate is for the window from 300 °Cd before flowering to 200 °Cd after flowering. Note the difference in the x-scale among panels, reflecting the difference in range of crop growth rate depending on source of variation. Lines are Model II (Reduced Major Axis) regressions accounting for error in both variables (Ludbrook, 2012). Slope (Slp) and intercept (Int) are shown with standard errors. Significance is denoted as $P < 0.0001$***, $P < 0.01$** and $P < 0.05$*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Limitations of using NDVI to estimate crop growth rate

NDVI has been used in this study to calculate crop growth rate as it is rapid, repeatable, non-destructive, inexpensive and has been used successfully in the past in grain legumes to calculate crop growth rate (field pea) and to predict yield (soybean) (Ma et al., 2001; Sadras et al., 2013). The exponential curves fitted to our NDVI biomass calibrations are characteristic of other spectral indices approaching saturation asymptotically for biomass or leaf area index (Wiegand and Richardson, 1990; Baret and Guyot, 1991). Our calibrations revealed that NDVI-derived crop growth rate correlates with biomass-derived crop growth rate, and more importantly, has superior correlation with yield. A limitation to this method is the saturation of the NDVI to biomass relationship once the canopy closes. For this study, the upper limit occurred on average 290 °Cd after flowering meaning that our defined period for crop growth rate 300 °Cd before flowering to 200 °Cd after flowering fits within these limits. It also means we could capture a significant portion of the critical period (Fig. 1c).

4.2. Crop growth rate and yield

The crop growth rates reported here fit well with expectations based on the adaptation of the varieties used (K Hobson Pers. Comm.). Genesis 090 is considered widely adapted and was one of the best performing lines across environments, while the slow growing Jimbour is specifically adapted to warmer Northern regions and may not be well suited to the cooler conditions of southern Australia. Water was the most important environmental source of yield variation thus making this work relevant for drought adaptation. This is especially evident when considering the significant association between yield and crop growth rate in the stressful conditions.

Positive relationships between yield and crop growth rate have been demonstrated previously in other species, with key differences in the models describing the relationships. Maize and sunflower follow a non-linear trajectory, pea has been reported to follow linear (Guilioni et al., 2003) or curvilinear trajectory (Sadras et al., 2013) while soybean and canola follow a linear trajectory (Egli and Yu, 1991; Egli, 1993; Vega et al., 2001a; Guilioni et al., 2003; Andrade et al., 2005; Zhang and Flottmann, 2016). We have found that chickpea conforms with soybean and canola having a linear relationship between yield and crop growth rate. Physiologically this grouping of the determinate species maize and sunflower and the indeterminate species soybean, canola and chickpea reflects the reproductive plasticity of the pulses and brassicas allowing them to adjust their seed number to the environment, while maize and sunflower respond linearly only up to a ceiling determined by the number of inflorescences (Vega et al., 2000, 2001b; Guilioni et al., 2003).

Our linear models have intercepts that were not significantly different from zero indicating that there is no minimum threshold for yield, a result also reported in soybean and pea (Egli and Yu, 1991; Jiang and Egli, 1995; Guilioni et al., 2003). NDVI-derived growth rate correlated with biomass-derived growth rate, and returned better relations with yield. Our range in crop growth rate derived using spectral reflectance of 0.021–1.05 g m^{-2} °Cd^{-1} compares with Krishnamurthy et al. (1999) who reported biomass derived range of 0.083 and 0.34 g m^{-2} °Cd^{-1} for rainfed and irrigated chickpea; the smaller upper value in their study compared to ours is likely due to their calculation over the whole season which captures slow-growth periods during establishment and close to maturity. Field pea crop growth rate in a critical period ranged from 0.01 to 1.95 g m^{-2} °Cd^{-1} using NDVI and 0.135–2.12 g m^{-2} °Cd^{-1} using biomass (Guilioni et al., 2003; Sadras et al., 2013).

4.3. Implications for breeding

In contrast to the more generalised relations between yield and NDVI (as a surrogate for crop biomass), here we used NDVI to calculate a physiologically relevant trait, namely crop growth rate in a critical window. We have demonstrated that NDVI is suitable for high-throughput phenotyping of chickpea which could be applied within breeding programs. We have also demonstrated the link between yield and crop growth rate under water stress and provided information on lines contrasting for ability to grow fast under stress and non-stress conditions. With careful selection aiming at lines such as Genesis090 it should be possible to produce chickpeas with increased crop growth rate in water stress environments without suffering a yield penalty in favourable environments.

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Chapter 6

Associations between yield, intercepted radiation and radiation use efficiency in chickpea

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Signature		Date	7/12/2016

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By signing the Statement of Authorship, each author certifies that:

 i. the candidate's stated contribution to the publication is accurate (as detailed above);

 ii. permission is granted for the candidate in include the publication in the thesis; and

 iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

Name of Co-Author	Victor O Sadras		
Contribution to the Paper	Victor Sadras provided guidance in experimental design, data analysis and interpretation and in constructing and developing the manuscript.		
Signature		Date	1/11/16

Associations between yield, intercepted radiation and radiation-use efficiency in chickpea

Lachlan Lake[A,B] *and Victor Sadras*[A]

[A]South Australian Research and Development Institute, SA, Australia.
[B]Corresponding author. Email: Lachlan.Lake@sa.gov.au

Abstract. Relationships between yield, biomass, radiation interception (PAR_{int}) and radiation-use efficiency (RUE) have been studied in many crops for use in growth analysis and modelling. Research in chickpea (*Cicer arietinum* L.) is limited, with variation caused by environment and phenological stage not adequately described. This study aims to characterise the variation in chickpea PAR_{int} and RUE with phenological stage, line and environment and their interactions, and the impact of this variation on yield. Chickpea lines (six desi and one kabuli) previously identified as varying for yield, competitive ability, crop growth rate and phenology were compared in four environments resulting from a combination of two sowing dates and dry and irrigated water regimes. Yield varied from 0.7 to 3.7 t ha^{-1}. Line, environment, phenological stage and the interactions line (G) × environment (E) and environment × stage affected both RUE and PAR_{int}. Line × stage interaction also affected RUE. High PAR_{int} and RUE were associated with high yield, but the interaction between environment and phenological stage dictated this relationship; higher PAR_{int} and RUE were observed in irrigated environments. Some environment × phenological stage combinations resulted in no significant associations, particularly before flowering in dry environments. These results emphasise the importance of understanding the effects of G × E on capture and efficiency in the use of radiation and have implications for growth analysis, modelling and breeding.

Additional keywords: abiotic stress, breeding chickpea, radiation, yield.

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Introduction

Chickpea (*Cicer arietinum* L.) is being grown over an increasing range of environments to satisfy increased demand as a human food and as a part of sustainable cropping systems (Wani *et al*. 1995; Giunta *et al*. 2009; Foyer *et al*. 2016). The yield of chickpea is unreliable and can be considered low in most major producer countries; water deficit is identified as a major cause (Soltani and Sinclair 2012; Kashiwagi *et al*. 2015; Foyer *et al*. 2016).

Research investigating stress adaptation in chickpea has identified a linear relationship between crop growth rate within the critical period and yield, particularly under water stress (Lake and Sadras 2016). The main determinants of crop growth rate are the ability of the crop to intercept photosynthetically active radiation (PAR_{int} 400–700 nm) and radiation use efficiency (RUE) (Li *et al*. 2008; Giunta *et al*. 2009; Hao *et al*. 2016). In the Early Bronze Age, chickpea was changed from an autumn-sown to a spring-sown crop, which shifted the vernalisation and thermal requirements of the crop (Berger *et al*. 2005; Abbo *et al*. 2008; Sadras and Dreccer 2015; Pinhasi van-Oss *et al*. 2016). As a consequence, chickpea grows slowly during winter compared with cereals and other pulses such as field pea (Armstrong *et al*. 1997; Lake *et al*. 2016*a*), and PAR_{int} is naturally relatively low (Mwanamwenge *et al*. 1997). Further, water stress reduces both PAR_{int} and RUE (Muchow 1985; Singh and Rama 1989; Stöckle

and Kemanian 2009). Improvements in chickpea PAR_{int} and RUE are likely to increase yield and reliability (Li *et al*. 2010).

Both PAR_{int} and RUE have been studied extensively in many crop species for use in modelling and crop-growth analysis (Muchow 1985; Ridao *et al*. 1996; Sinclair and Muchow 1999; Lecoeur and Ney 2003; Tesfaye *et al*. 2006; Giunta *et al*. 2009; Stöckle and Kemanian 2009). Specific research on PAR_{int} and RUE in chickpea includes studies of Li *et al*. (2008) who studied the effects of different leaf types, Kang *et al*. (2008) who investigated the effects of irrigation, and Soltani *et al*. (2007) and Saha *et al*. (2015) characterising the effect of elevated carbon dioxide on RUE. Singh and Sri Rama (1989) established that RUE is reduced after >30% of extractable soil moisture has been removed from the rooting zone. Tesfaye *et al*. (2006) showed that RUE was more sensitive to early-stage rather than late-stage reproductive water deficit. Soltani *et al*. (2006) investigated biomass accumulation and partitioning in chickpea and assumed that RUE was constant over the crop cycle under non-stressed conditions; this is simplistic, as demonstrated by changes in RUE with ontogeny in several crops (Ridao *et al*. 1996; Lecoeur and Ney 2003; Albrizio and Steduto 2005).

For growth analysis, modelling and breeding for enhanced yield and reliability, it is necessary to understand how radiation capture and use efficiency vary in response to stress and non-stress

environments, phenological stage (before and after flowering), genotype and all associated interactions. This study aims to characterise the variation in chickpea PAR_{int} and RUE with phenological stage, line, environment and their interactions, and the impact of this variation on yield.

Methods

Plant material, crop husbandry and experimental design

A factorial experiment was established combining seven lines and four growing conditions in a Calcic Luvisol (FAO Soils Portal, www.fao.org/soils-portal/soil-survey/soil-classification/fao-legend/key-to-the-fao-soil-units/en/) at Roseworthy, South Australia (34°52′S, 138°69′E) in 2015. We compared six desi (PBA HatTrick, Genesis 836, PBA Pistol, PBA Striker, PBA Boundary, CICA 1229) and one kabuli (PBA Monarch) chickpea lines showing variation in yield and components, competitive ability, crop growth rate, and phenology when previously evaluated in environments varying for water stress (Lake and Sadras 2016; Lake *et al.* 2016*b*; Sadras *et al.* 2016). The four environments were selected to give a range of water-stress and growing conditions, particularly around flowering, and resulted from a combination of two sowing dates and dry and irrigated water regimes. In each environment, the seven lines were laid out in a randomised complete block design of three replicates. Each replicate had an area of 7.25 m², comprising six rows (spaced 24 cm) of 5 m length.

Crops were sown after barley. The first sowing date was 9 June (early) and the second (late) 7 July. Late-sown crops were expected to have lower yields caused by elevated temperature and lower photothermal quotient (Sadras and Dreccer 2015). For the early-sown crops, the water regimes were sprinkler-irrigated and rainout-shelter canopy (installed 6 August), and for the late crops, sprinkler-irrigated and rainfed. Rainfed and rainout-shelter environments are hereafter referred to as 'dry'. Overhead sprinklers were used as needed to match evaporative demand (estimated from temperature and plant size); the first watering date was 16 July for the first sown crop and 28 August for the late-sown crop. We intended to provide well-watered conditions that were conducive to high yield and water deficit around the critical period for yield determination (Fig. 1*a*).

To minimise the risk of Ascochyta blight, seed was pre-treated with P-Pickel T fungicide (Crop Care, Brisbane, Qld) and, for effective nodulation, was inoculated with Group N rhizobia immediately before sowing. Crops were fertilised with 80 kg ha⁻¹ mono-ammonium phosphate at sowing with a target plant density of 55 plants m⁻² for desi and 30 plants m⁻² for kabuli types to account for differences in plant size and vigour. Weeds were controlled with an initial spray of paraquat (135 g L⁻¹) and diquat (115 g L⁻¹) mix before sowing, and then with follow-up grass sprays (mixture of butroxydim at 250 g kg⁻¹ and clethodim at 240 g L⁻¹) and hand weeding. Crops were monitored weekly for fungal symptoms, with application of preventative sprays (chlorothalonil, 720 g L⁻¹) around flowering and podding, or when symptoms were seen. Insecticide (omethoate, 290 g L⁻¹)
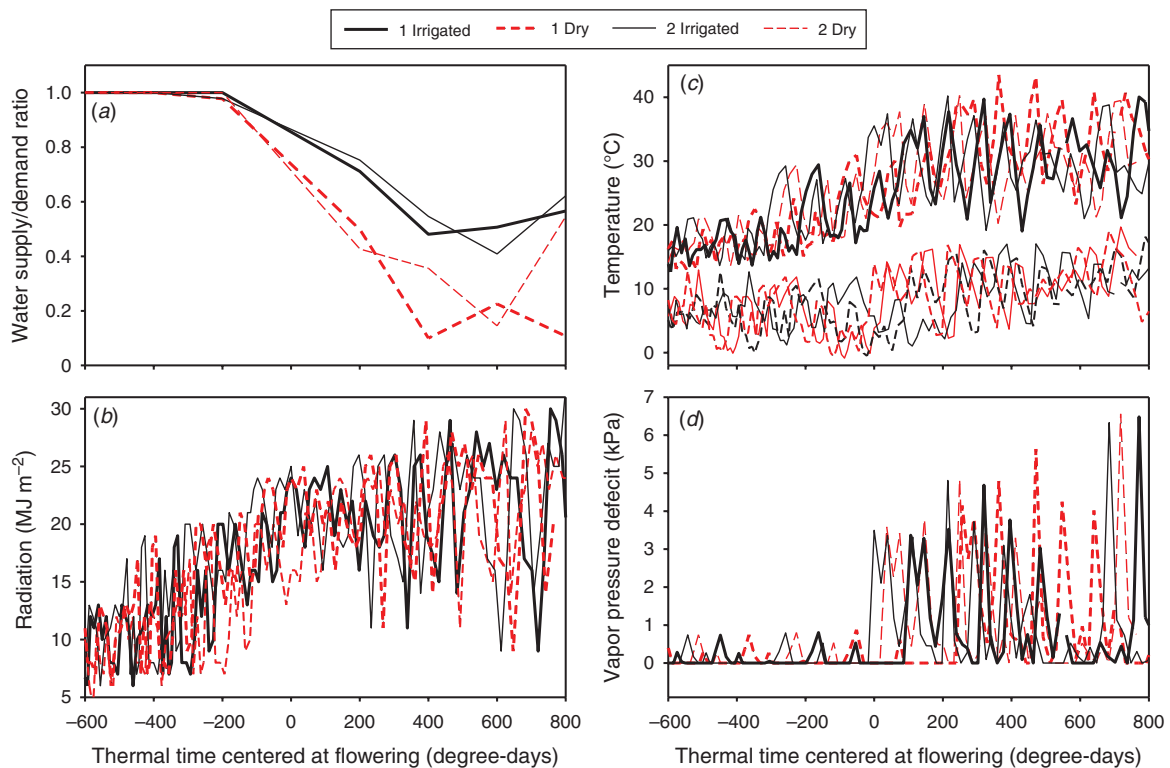
Fig. 1. Seasonal patterns of: (*a*) water supply/demand patterns for the four environments, with 1 indicating no stress and 0 indicating maximum stress; (*b*) radiation; (*c*) minimum and maximum temperature; and (*d*) vapour pressure deficit. The numbers in the key for environments denote the first (1) and second (2) sowing date.

was used around early podding to prevent damage from *Helicoverpa* spp.

Measurements

Phenology

Phenology was scored weekly to establish time to 50% of plants reaching flowering, pod emergence (developing pods 2–4 mm in length), end of flowering and maturity (yellowing pods) (Berger *et al.* 2004). We used a thermal time scale to express phenology, calculated from daily mean temperature and base temperature of 0°C (Berger *et al.* 2006).

Biomass, crop growth rate, yield and yield components

Biomass samples were collected six times over the growing season beginning 617 degree-days after sowing until maturity. Samples were collected from two 0.5-m lineal cuts from central rows of plots, leaving at least 50 cm between samples. We then fitted polynomials to characterise growth of biomass over time, and used the models to estimate biomass at any given time in the season.

Crop growth rate was measured by using the normalised difference vegetation index (NDVI) with the method of Lake and Sadras (2016). Crop growth rate was calculated in the period 200 degree-days before to 200 degree-days after flowering when the crop is highly responsive to stress (Lake and Sadras 2014); this period is closely related to yield and fits within the confines of NDVI ability to detect biomass change (Lake and Sadras 2016). NDVI was measured approximately every 7 days after crops had reached 50% of soil covered by canopy, required to avoid distortions from a high soil : vegetation ratio (Baret and Guyot 1991). Polynomials were fitted to these data to capture the progression of NDVI over time and calibration equations were then used to convert NDVI to biomass and crop growth rate (for equations see Lake and Sadras 2016).

Yield and components were measured in two 1-m lineal samples taken from inner rows near the centre of plots. We determined seed weight, seed number, pod number, seed size, number of seeds per pod, shoot biomass and the derived traits harvest index (seed yield/shoot biomass) and pod wall ratio (pod wall weight/whole pod weight) (Lagunes-Espinoza *et al.* 1999; Clements *et al.* 2005; Lake and Sadras 2014).

Radiation interception and use efficiency

To measure PAR_{int}, we used an Accupar LP-80 Ceptometer (Decagon Devices, Pullman, WA, USA). Using the method of Giunta *et al.* (2009), three measurements of PAR were taken randomly within the central part of the plot on clear cloudless days between 11 : 00 and 14 : 00. PAR was measured above the canopy (PARa) and at the soil surface (PARb), holding the probe horizontal at right angles to the rows. Measurements were taken every 10–20 days across the season. We calculated PAR_{int} as the product between daily solar PAR obtained from the Roseworthy weather station (50% of solar radiation) and the fraction of PAR intercepted by the crop (Jahansooz *et al.* 2007).

Polynomials were fit to quantify the progression of fractional PAR_{int} over time. RUE was then calculated as the ratio of biomass production and PAR_{int} over three periods: the growing season, emergence to flowering, and flowering to maturity.

Environmental characterisation and data analysis

Daily rainfall, temperature, radiation, and vapour pressure were collected from Roseworthy's weather station (www.longpaddock. qld.gov.au/silo/).

The chickpea module of Agricultural Production Systems Simulator (APSIM) software and actual weather data were used to simulate the daily water-stress index (Keating *et al.* 2003; Holzworth *et al.* 2014) of our crops. The range of water-stress index is 1 (no stress) to 0 (maximum stress). Water-stress index is calculated as the ratio between water supply (soil and root characteristics) and demand (temperature, radiation and humidity).

We tested the effects of environment, line and the interaction using analysis of variance. Linear and nonlinear models were fitted to explore the associations between crop traits and between crop traits and environmental variables. Model II regression was used because the *x* and the *y* variables were subject to error (Ludbrook 2012).

Using XLSTAT (Addinsoft, New York) for Microsoft Excel, we conducted a principal component analysis (PCA) to explore the associations among crop traits (yield, yield components, phenology, PAR_{int} and RUE) and between crop traits and environmental variables. Data were analysed by using the mean of the three replicates for each combination of line and environment.

Results

Environmental conditions

Figure 1 presents the water and photothermal environments. Growing-season rainfall (including irrigation) for the four environments was 360 mm for early-sown irrigated, 103 mm for early-sown dry, 308 mm for late-sown irrigated, and 169 mm for late-sown dry. There was no water stress early in the season; trajectories of water supply/demand between dry and irrigated environments diverged 200 day-degrees before flowering. Dry environments were 20% more stressed from ~300 day-degrees before flowering to 600 day-degrees after flowering and were 27% more stressed at the most critical stage for yield determination ~200 day-degrees after flowering (Lake and Sadras 2014). Late-sown crops received on average 1.8 MJ m^{-2} more radiation per day, ambient temperature 0.5°C warmer during the day and 0.2°C warmer at night, and a vapour pressure deficit 0.08 kPa greater than their early-sown counterparts.

Yield and phenology

Yield was affected by line ($P = 0.0392$) and environment ($P < 0.0001$) with no significant interaction. The variation of yield between environments was 3-fold, with average yields of 3.4 t ha^{-1} for the early-sown irrigated crop, 1.1 t ha^{-1} for the early-sown dry crop, 2.8 t ha^{-1} for the late-sown irrigated crop, and 1.1 t ha^{-1} for the late-sown dry crop. Yield variation between lines across environments was 5-fold. PBA Boundary produced the lowest yield of 0.72 t ha^{-1} in the late-sown dry environment, whereas Genesis 836 was equally sensitive to stress, yielding 0.82 t ha^{-1} in the late-sown dry environment. PBA Boundary and CICA 1229 were the highest yielding in favourable conditions, both producing ~3.70 t ha^{-1} in the early-sown irrigated environment.

Environment and line both affected time to flowering ($P < 0.0001$); the earliest flowering line was CICA 1229 (1044 day-degrees) with Genesis 836 flowering latest (1108 day-degrees). The earliest environment flowered in 974 day-degrees (late-sown rainfed) and the latest took 1220 day-degrees (early-sown irrigated). Longer time to flowering had a negative association with yield in the dry crops ($P = 0.0564$, $R^2 = 0.18$ for early-sown; $P = 0.0005$, $R^2 = 0.50$ for late-sown).

Yield, radiation interception and radiation-use efficiency

To determine the main driver of variation in biomass and subsequent yield, we looked at PAR_{int} and RUE in three stages: the whole crop growth cycle, emergence to flowering, and flowering to maturity. We also explored variation between dry and irrigated environments.

The ANOVA revealed significant effects of line, environment, stage, and interactions between line and environment and between environment and stage on both PAR_{int} and RUE (Table 1). The interaction between line and phenological stage also affected RUE.

Across environments, lines and growth stages, variation in RUE was ~5-fold (0.55–2.44 g MJ^{-1}), whereas variation in PAR was ~12-fold (50–606 MJ^{-1}) (Fig. 2). Canopy growth and PAR_{int} were higher in irrigated environments but RUE varied depending on phenological stage. Averaged across lines and environments, RUE dropped from 1.45 g MJ^{-1} before flowering to 0.96 g MJ^{-1} after flowering. Seasonal RUE averaged 1.14 g MJ^{-1} and dropped from 1.3 g MJ^{-1} in irrigated crops to 0.98 g MJ^{-1} in dry crops. Compared with irrigated crops, RUE was 0.22 g MJ^{-1} higher in the dry environments before flowering ($P = 0.0268$), but was 0.44 g MJ^{-1} lower after flowering ($P < 0.0001$) when dry environments became increasingly stressed. Intercepted PAR after flowering was also reduced by water stress, with mean PAR intercepted for irrigated crops being 183 MJ^{-1} more than in their dry counterparts (Fig. 2).

Across all crops, yield was positively related to PAR_{int} for all three stages; environment was the main driver of this relationship (Fig. 2). The relationships between yield and both PAR_{int} and RUE were stronger in irrigated crops, and stronger for the seasonal or after-flowering stages. Yield was related to seasonal PAR_{int} and PAR_{int} only after flowering in the irrigated crops; in the dry environments, there was no relationship between yield and PAR_{int}. Yield was positively associated with seasonal RUE and RUE after flowering when all crops were combined. When crops were separated by water regime, yield was associated with RUE for all stages in irrigated crops; however, in the dry environments yield was associated only with seasonal RUE.

Figure 3 presents a PCA of the main variables and Supplementary Materials table 1 (available at the journal's website) lists correlations. Yield was strongly associated with seed number ($P < 0.0001$, $R^2 = 0.81$), biomass ($P < 0.0001$, $R^2 = 0.94$) and crop growth rate ($P < 0.0001$, $R^2 = 0.49$); weakly associated with HI ($P = 0.0021$, $R^2 = 0.27$); weakly and negatively associated with number of seeds per pod ($P = 0.0006$, $R^2 = 0.14$); and unrelated with seed size or pod number. The association of yield with PAR_{int} was strongest after flowering ($P < 0.0001$, $R^2 = 0.83$) and for the season ($P < 0.0001$, $R^2 = 0.80$), with weaker association before flowering ($P < 0.0001$, $R^2 = 0.36$). The association of yield with RUE was not significant before flowering and highly significant ($P < 0.0001$) for the season ($R^2 = 0.73$) and after flowering RUE ($R^2 = 0.75$). Seasonal water-stress index had a significant ($P < 0.0001$) negative association with yield ($R^2 = 0.71$), seasonal RUE ($R^2 = 0.46$), RUE after flowering ($R^2 = 0.47$), seasonal PAR ($R^2 = 0.85$), and PAR before ($R^2 = 0.56$) and after ($R^2 = 0.83$) flowering; the relationship with RUE before flowering was not significant. The sum of rainfall and irrigation had strong ($P < 0.0001$) positive association with yield ($R^2 = 0.76$), seasonal RUE ($R^2 = 0.50$), RUE after flowering ($R^2 = 0.51$), seasonal PAR ($R^2 = 0.86$), and PAR before ($R^2 = 0.54$) and after ($R^2 = 0.84$) flowering; RUE before flowering did not have a significant relationship. Maximum temperature had a significant ($P < 0.0001$) negative association with crop growth rate ($R^2 = 0.69$), flowering ($R^2 = 0.52$) and maturity ($R^2 = 0.69$). Minimum temperature also had a significant ($P < 0.0001$) negative association with crop growth rate ($R^2 = 0.52$), flowering ($R^2 = 0.44$) and maturity ($R^2 = 0.52$).

Discussion

Environmental variation

Our water regimes produced both well-watered and water-stressed crops consistent with the range in Australian water-stress environments for chickpea (Lake *et al.* 2016a). Likewise, the range in our experimental yield represents the variability associated with environments across the South Australian chickpea production region, with published National Variety Trials in 2015 reporting a maximum yield of 2.5 t ha^{-1}, a minimum of 0.55 t ha^{-1} and average 1.6 t ha^{-1} (www.nvtonline.com.au/).

Variation in radiation interception and radiation-use efficiency

Our intercepted PAR and RUE fit within the range reported from other work in chickpea. Soltani *et al.* (2006) reported an average RUE of 1.0 g MJ^{-1}; Tesfaye *et al.* (2006) reported a range in intercepted PAR of ~300–650 MJ m^{-2} and RUE from 1.45 to 2.07 g MJ^{-1}; and Leach and Beech (1988) reported a range of intercepted PAR of ~480–700 MJ m^{-2} and RUE of 1.4 g MJ^{-1}. The reduced PAR_{int} and RUE that we observed in the dry environments has been widely reported previously in many

Table 1. *P*-values from analysis of variance testing the effect of seven lines (L), four environments (E), three crop stages (S) and their interactions on radiation-use efficiency (RUE) and intercepted photosynthetically active radiation (PAR)

ANOVA	L	E	S	L × E	L × S	E × S	L × E × S
RUE	0.0081	<0.0001	<0.0001	0.0625	0.0002	<0.0001	0.0959
PAR	0.0004	<0.0001	<0.0001	0.0096	0.1322	<0.0001	0.9932
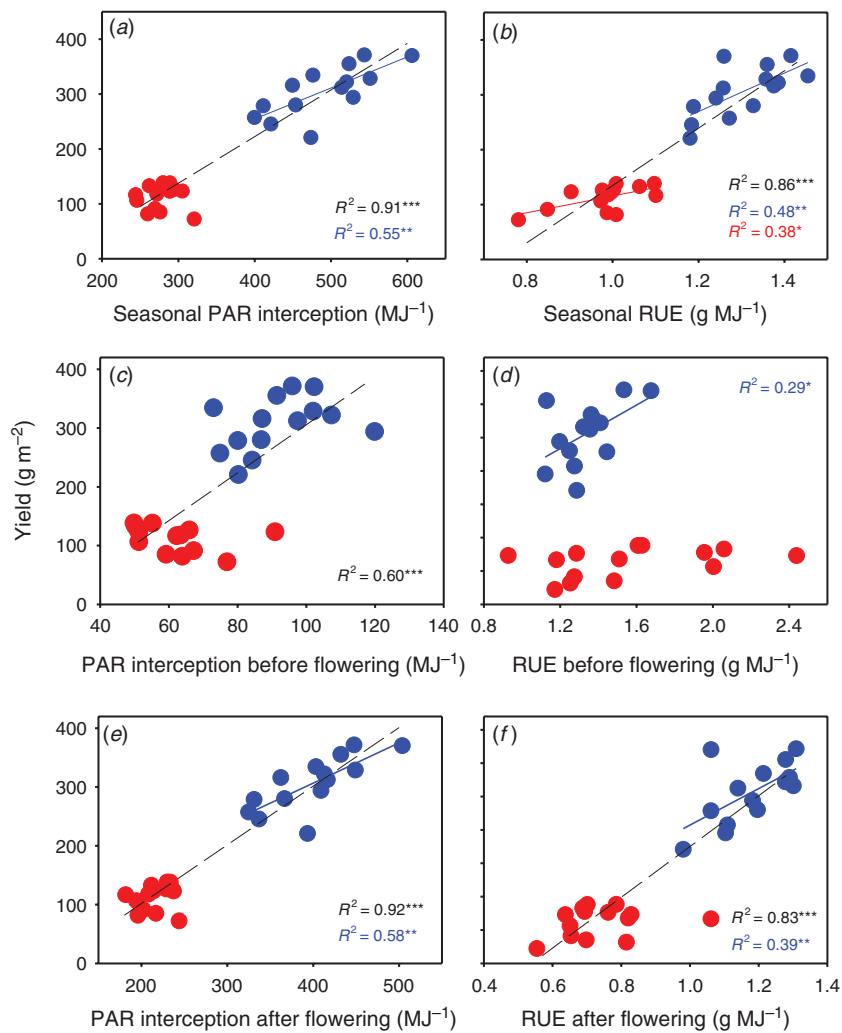
Fig. 2. Relationship between yield and: (*a*) total PAR$_{int}$, (*b*) seasonal RUE, (*c*) PAR$_{int}$ before flowering, (*d*) RUE before flowering, (*e*) PAR$_{int}$ after flowering, and (*f*) RUE after flowering. Linear regression was fitted across environments and for dry and irrigated environments separately; only significant relationships are presented. Lines are Model II (reduced major axis) regression accounting for error in both variables (Ludbrook 2012). Red represents dry environments and blue represents irrigated ones. Black lines are for regression across environments. Significance is denoted as *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$. Note the difference in the *x*-scale among panels, reflecting the difference in range of PAR$_{int}$ and RUE during the different intervals.

crops (Green *et al*. 1985; Singh and Sri Rama 1989; Earl and Davis 2003; Tesfaye *et al*. 2006; Hao *et al*. 2016).

The variability demonstrated in PAR$_{int}$ and RUE that occurs between lines, environments and growth stages can be explained by the environmental conditions, the physiology of the crop and their interactions. Compared with vegetative tissue, seed production requires more energy, which partially explains our observed reduction in RUE after flowering; senescence and leaf drop also contribute to post-flowering reductions in RUE (De Vries *et al*. 1974; Lecoeur and Ney 2003; Albrizio and Steduto 2005; Soltani *et al*. 2006). Stress can reduce interception of PAR by two mechanisms: reduced canopy size, and reduced interception per unit leaf area index (e.g. associated with wilting or leaf folding; Matthews *et al*. 1988). Our results showed

an increase in RUE when PAR$_{int}$ was reduced in the dry environments, but this increase was predominantly in the pre-flowering period where water was not yet limiting. This increased RUE associated with reduced PAR$_{int}$ has also been shown in soybean, field pea and sunflower (Ridao *et al*. 1996; Bange *et al*. 1997; Purcell *et al*. 2002; Adeboye *et al*. 2016). Our observed increase in RUE when PAR$_{int}$ was reduced may help to explain why our seasonal PAR$_{int}$ showed less association with yield in dry crops than seasonal RUE.

Research looking at PAR$_{int}$ and RUE in chickpea has shown that increased radiation interception is likely to provide the largest improvement in biomass and yield in unstressed crops, whereas research under water deficit concluded that increases in both traits would result in yield benefits (Singh and Rama 1989;
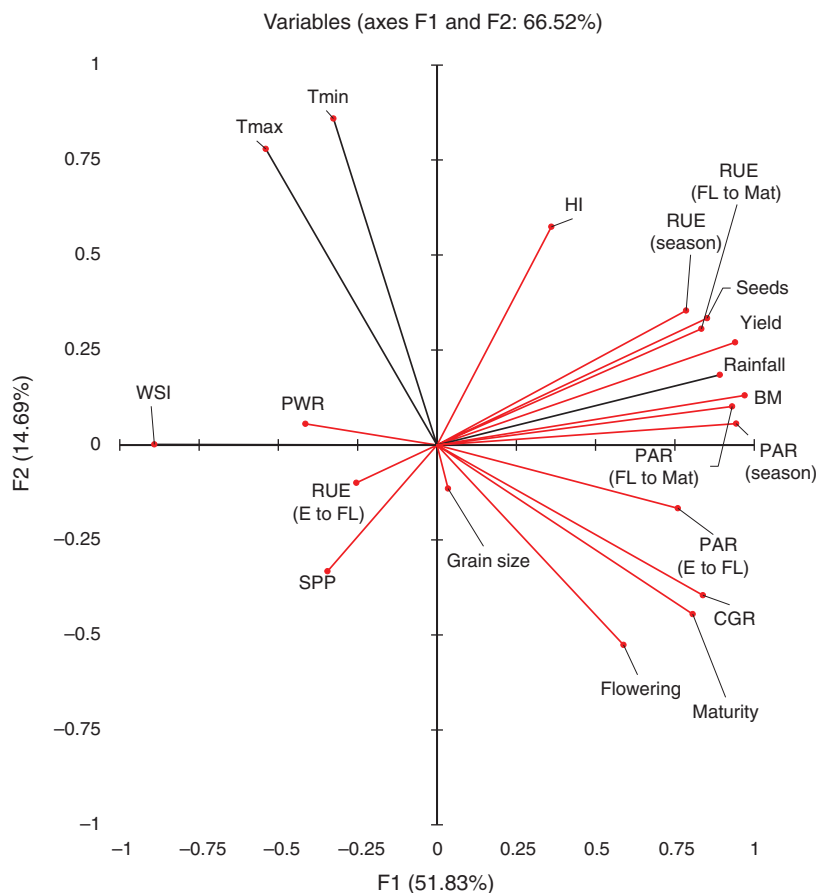
Fig. 3. Principal component analysis of crop yield (yield g m⁻²), measured traits and environmental variables. E, Emergence; FL, flowering; Mat, maturity; PWR, pod wall ratio (Sadras *et al.* 2013); SPP, number of seeds per pod; WSI, water stress index; HI, harvest index; BM, biomass; CGR, crop growth rate. Black vectors are environmental and red are biological.

Tesfaye *et al.* 2006; Li *et al.* 2008). Our results show that interactions between yield, RUE and PAR in different environments are complex and have highlighted the critical importance of understanding genotype × environment interactions and the need for quantitative environmental characterisation (Chenu 2015; Lake *et al.* 2016*a*).

Previous research in grain legumes has identified little variation in RUE within or between species, although many of these studies relied on small numbers of lines (Lecoeur and Ney 2003; Li *et al.* 2008; Giunta *et al.* 2009). Our results were also based on few lines, but these are from a larger set screened for related traits including crop growth rate (Lake and Sadras 2016; Sadras *et al.* 2016). We thus showed significant variation between lines for RUE, a result also demonstrated in maize, where significant variation was found between hybrids but only when RUE was measured at specific growth stages (Hao *et al.* 2016).

In conclusion, we have characterised the relationship between yield, biomass, PAR$_{int}$ and RUE among contrasting chickpea lines under contrasting water regimes. Grain yield and biomass were strongly associated with PAR$_{int}$ and RUE, with a dominant environmental effect. Increased RUE and PAR$_{int}$ were both related to yield in unstressed environments, but only seasonal

RUE was associated with yield in dry conditions. Across lines and environments, we found significant variation for PAR$_{int}$ and RUE, with interactions between line, environment and stage. These results have implications for growth analysis, modelling and selection strategies for adaptation breeding.

Acknowledgements

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Chapter 7

General discussion, conclusions and future research

General discussion, conclusions and future research

During the course of this research the Australian chickpea crop overtook lupin as the biggest pulse crop in Australia, sown over more than 600,000 hectares. This highlights the growing importance of this crop to Australian farming and the inherent value of increasing yield and reliability. With recent prices of over AU$800 dollars per tonne, revenue would be increased by ~ AU$50 million dollars for every 0.1 t ha^{-1} increase to yield. To this end and in accordance with our objectives presented in Chapter 1, this research describes the critical period for yield determination, quantifies the major Australian water and temperature stress environment types, and uses this knowledge in conjunction with detailed phenotyping experiments to identify potential strategies and trait combinations for enhancing yield and reliability. This research is relevant both nationally and internationally and has applications in other crops species (Sadras and Dreccer, 2015, Chenu et al., 2013, Chapman et al., 2000a).

The accurate description of the critical period for yield determination in chickpea (Chapter 2) is beneficial for several reasons: (i) this knowledge can be used by agronomists and growers to minimise stress exposure at critical points in the lifecycle of the crop by choosing appropriate variety and sowing date combinations; (ii) breeders can use this knowledge when selecting for stress screening environments in order to more accurately match stress exposure to the critical times; (iii) the critical period can be used to increase the predictive power of modelling with more accurate predictions of phenotypes associated with GxE; (iv) the critical period can be used to more accurately model the predicted effects of climate change on yield. This research subsequently used the critical period for experimental planning and interpretation of results in Chapters 3 – 6 and should be considered in all relevant yield based physiological research in chickpea.

Quantitative environmental characterisation for water stress (Chapter 3) has been developing rapidly since the early work of Muchow et al. (1996) and Chapman et

al. (2000a). This is the first study that describes the variation in not only the major water stress environment types, but also the thermal environment types of the Australian chickpea growing regions. This knowledge of the dominant water and temperature patterns can be combined with the critical period identified in Chapter 2 to help achieve points (i) and (ii) (above). This knowledge will also be valuable in enabling researchers and breeders to better match environments selected in an MET to reflect environments of the TPE, thus reducing the need for as many environments, reducing costs and reducing the likelihood of misrepresenting the TPE. Another potentially valuable application is to search for novel or adapted germplasm based on environmental quantification of native environments.

The negative relationship between competitive ability and yield identified in Chapter 4 conforms with research in cereals and is the first research of this kind in the morphologically and physiologically distinct grain legumes. The implications of this research suggest that communal rather than competitive traits are more likely to be associated with yield gain. This is a concept that challenges early generation selection from observations on performance of individuals or from single rows. Different genomic regions that this research identified as under selection for yield in relaxed and normal competition reinforce the dangers of selection for yield traits in non-communal environments; Fst genome scan is a relatively new and robust method able to detect these genomic regions with relatively small numbers of genotypes (Sadras et al., 2016, Fumagalli et al., 2013). These genomic regions and the regions that are identified as undergoing selection for response to competition deserve further research. Potential for developing genomic selection tools for early generation selection exists within breeding programs, provided this returns higher rates of improvement or reduces breeding cost (Sadras and Richards, 2014). Variation in plant architecture and morphology could also be explored for association with improved communal performance (Abbo et al., 2013); such research is currently taking place looking at reduced tillering in wheat for improved adaptation and yield (Mitchell et al., 2012, Mitchell et al., 2013).

Crop growth rate integrates environmental and genotypic sources of variation and hence is a valuable measure of both yield potential and performance under stress; accurate predictions of crop growth rate are critical in modelling (Sadras et al., 2013, Wiegand and Richardson, 1990). Crop growth rate is often measured and associated with yield using various methods. Previous research in chickpea has estimated crop growth rate from final biomass and total growing time (Krishnamurthy et al., 2013, Krishnamurthy et al., 1999), which gives little insight into trends within physiologically meaningful windows. Our results using NDVI growth curves show that crop growth rate was most closely associated with yield within the critical period for yield determination (Chapter 2) and that crop growth rate within this period is more important for yield under water stress (Chapter 5); this has important implications for accurate modelling and growth analysis. The usefulness of crop growth rate within the critical period as a secondary trait associated with improved yield and reliability will be determined by the genetic variation available; there were no trade-offs for crop growth rate between stress and non-stress environments. Results from Chapters 2 and 3 should be considered when selecting environments to screen for crop growth rate. It must also be noted that a reduced response to competition and high crop growth rate can both be associated with improved yield as they are mutually exclusive traits; crop growth rate is assessed in the communal environment and is the sum of all individuals, whilst response to competition is the sum difference between individuals.

As established in Chapter 5, there is a tight coupling between crop growth rate and yield within physiologically meaningful windows with implications for modelling and improved yield and reliability under stress. Chapter 6 tests the association of yield with two of the main determinants of crop growth rate - PAR_{int} and RUE. Results demonstrate that yield is associated with both PAR_{int} and RUE but the relationship varies depending on the ontogeny of the crop and environment; this conforms with previous research in common bean, cowpea,

chickpea, faba bean and pea (Tesfaye et al., 2006, Kang et al., 2008, Ridao et al., 1996). Using either PAR$_{int}$ or RUE as secondary traits for improved yield is likely to be successful when making selection under non-stress conditions (excluding PAR$_{int}$ before flowering); accurate screening requires cloudless days and measurement to be taken in a window between 12 and 3pm potentially limiting throughput rate. Evidence of RUE varying with ontogeny also has implications for accurate modelling and growth analysis.

The results from Chapters 5 and 6 emphasise that knowledge about trait by environment (Chapter 3) by phenological stage (Chapter 2) interaction is critical for successful genetic advancement and increased adaptation. These results can also be used to refine modelling approaches to more accurately predict growth and development. Further research into the potential for improved yield and reliability associated with communal traits, increased crop growth rate, radiation interception and radiation use efficiency along with their genetic basis is warranted.

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