Mechanisms contributing to wheat and maize yield under no-till, stubble retention and nitrogen fertilization in contrasting environments

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Acronyms and abbreviations

ACIAR	Australian Centre for International Agricultural Research
ACT	African Conservation Tillage Network
AE	Nitrogen agronomic efficiency
ANOVA	Analysis of variance
ASI	Anthesis silking interval
C	Carbon
CA	Conservation agriculture
CGR	Crop growth rate
CIMMYT	International Maize and Wheat Improvement Center
CIRAD	Centre de Coopération Internationale en Recherche Agronomique pour le Développement (French Agricultural Research Centre for International Development)
CT	Conventional tillage
DK	DeKalb
DM	Dry mass
EC50	Loss of 50% of $SPAD_{max}$
EC90	Onset of senescence
FAO	Food and Agriculture Organisation of the United Nations
g	Grams
ha	Hectare
ICARDA	International Center for Agricultural Research in the Dry Areas
ICRAF	International Centre for Research in Agroforestry (World Agroforestry Centre)
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IE	Nitrogen internal efficiency
kg	Kilograms
L	Litre
LSD	Fisher’s Least significant difference
N	Nitrogen
NEPAD	New Partnership for Africa's Development
Nc	Critical N concentration
NHI	Nitrogen harvest index
NNI	Nitrogen nutrition index
NRE	Nitrogen remobilization efficiency
NT	No-till
NUE	Nitrogen use efficiency
Nupt	Nitrogen uptake efficiency
NutE	Nitrogen utilization efficiency
^{o}C	Degree celsius
^{o}C d	Growing degree day
P	Phosphorus
p	Probability value for testing hypothesis in statistics
PE	Nitrogen physiological efficiency
R	Correlation coefficient
R^2	Regression coefficient
RE	Nitrogen recovery efficiency
RUE	Radiation use efficiency

S0	Zero stubble retention
S1	Low stubble
S2	Moderate stubble
S3	High stubble
SADC	Southern African Development Community
SIMLESA	Sustainable Intensification of Maize-Legume cropping systems for food security in Eastern and Southern Africa program
SPAD	Chlorophyll unit
$SPAD_{max}$	Maximum SPAD
$SPAD_{min}$	Minimum SPAD
SSA	sub-Saharan Africa
t	Tonnes
USA	United States of America
V12	12-leaf stage
V6	Six-leaf stage
W	Biomass yield
WUE	Water use efficiency
Y	Grain yield
Δ	Increase in N uptake and utilization efficiency, grain yield and biomass

Abstract

Tillage, stubble retention and nitrogen fertilization are management practices that influence the productivity and sustainability of rainfed cropping systems. However, the application of these practices is limited by our understanding of the mechanisms that contribute to crop growth and yield, including water and nitrogen use efficiency. Canopy development and patterns of leaf senescence alter the partitioning of water and nitrogen (N) use, both before and after flowering, which impacts grain yield.

The two central questions for this research were: (1) what are mechanisms of canopy development that contribute to yield in no-till and stubble retention systems?; and (2) under what circumstances do they increase yield, water and N use efficiency? The aims for this thesis were to evaluate crop response to no-till, stubble retention and N fertilization, in the contrasting systems of wheat (*Triticum aestivum* L.) and maize (*Zea mays* L.), to better understand mechanisms that regulate crop growth, patterns of senescence and yield, in addition to water and nitrogen use efficiency (NUE). A physiological approach that linked the traits regulating crop growth and yield was used to interpret crop responses to treatments.

It is hypothesised that there are similarities in the mechanisms operating in no-till and stubble retention systems that could be improved to increase yield. Field experiments were conducted in the dryland wheat growing environments of southern Australia and in maize systems in a sub-humid tropical environment in Kenya. In Australia, experiments were conducted at Roseworthy and Karoonda using two tillage treatments (conventional tillage, CT and no-till, NT), four rates of stubble (zero, low, moderate and high) and three N timings, splitting the application of 100 kg N ha^{-1} between sowing, tillering (GS22) and awn emergence (GS49) in the ratios of 100-0-0, 25-50-25, 0-50-50. At Roseworthy, historic Australian wheat varieties were evaluated under NT with the retention of moderate amounts of stubble and under CT without stubble. In Kenya, field experiments were conducted at Embu research station to evaluate the responses of maize to CT and NT, three amounts of stubble (0, 3 and 5 t ha^{-1}) and N rates of 0, 80 and 120 kg N ha^{-1}, as well as timing the of supply of 80 kg N ha^{-1} at sowing, six leaf stage (V6) and 12-leaf stage (V12) in the fractions of 0-0-0, 80-0-0, 27-53-0, 27-27-27 and 0-40-40.

Wheat grain yield ranged from 1.5-3.2 t ha^{-1}, and the effects of tillage were marginal. Grain yield increased from bare ground up to the application of moderate amounts of stubble but reduced at high amounts of stubble. Benefits of water capture and storage did not improve with the application of high amounts of stubble. Crop growth rate (CGR) between stem elongation and flowering was inversely correlated with tiller numbers, and explained most of the treatment differences. Sowing application of N produced large vegetative biomass which led to a decrease in CGR and radiation use efficiency between stem elongation and flowering, resulting in a decrease in grain yield compared with delayed N supply.

Five decades of selection has not provided greater adaptation to NT and stubble retention in Australian wheat, despite grain yield increases of 21 kg ha^{-1} year^{-1} between 1958 and 2011. Substantial changes in canopy architecture were detected from older taller varieties with closed canopies to modern short-stature varieties with more open canopies. Modern varieties had greener leaves but showed faster rates of leaf senescence compared with the older counterparts.

Maize grain yield ranged from 2.3-5.3 t ha^{-1}, with small effects from tillage and stubble supply. Rate and timing of N supply produced large effects and modified crop response to tillage and stubble. When stubble was removed, grain yield reduced by 10% while water storage at sowing decreased by 8% under NT compared with CT. Crop growth rate between six-leaf stage (V6) and flowering, and nitrogen nutrition index (NNI) partially explained treatment differences.

Retention of stubble reduced CGR and NNI compared with bare ground. The value of stubble in water storage at sowing, and crop growth and yield was greater in a season that received < 300 mm rainfall compared with where rainfall was > 600 mm. Delaying N supply increased NNI, CGR and traits associated with NUE and grain yield compared with sowing applications of N.

Patterns of senescence in maize, at both whole-plant and canopy-layer scales were marginally impacted by tillage and stubble retention. Leaf senescence was primarily driven by N supply and sink size. Time to loss of 50% of maximum leaf greenness was earlier in fertilized crops but delayed in the unfertilized controls. Rate of senescence was faster in fertilized crops compared with unfertilized controls at both whole-plant and canopy-layer scales. Grain yield, kernel number and nitrogen remobilization efficiency were associated with a faster rate of senescence in the top and mid layer leaves but with slower rates of senescence in the bottom layer.

There were similarities in treatment effects and the mechanisms that regulated crop growth and yield between the two systems: (1) Grain yield was a function grain number, which in turn was proportional to CGR during the critical period of determination. Strategic supply of N at sowing and later stages increased CGR during the critical period for grain set, improved NNI and increased RUE, hence higher grain yield; (2) Grain yield was maximized at 2-3 t ha^{-1} of stubble as demonstrated by the analysis of yield gaps, potentially due to water capture and storage and the regulation of soil temperature which impacted emergence and early growth; (3) N supply and sink size modified the patterns of senescence in both crops, whereby faster rates of senescence were associated with higher grain yield; and (4) N supply modified crop response to tillage and stubble. Treatment interactions were few, and varied with N supply and season.

Effects of tillage system were marginal and independent of season. A mechanistic approach is discussed, which links treatment effects and the mechanisms regulating grain yield.

In conclusion, the mechanisms of canopy development and yield limitation operating in NT and stubble retention were similar in both cropping systems. Higher fertilizer N rates and better timing of N supply are required for yield improvement in NT and stubble retention systems. While NT alone reduced yield, moderate amounts of stubble can improve water storage and grain yield, but this is subject to seasonal rainfall. Critical thresholds of 2-3 t ha^{-1} of stubble indicate amounts over this limit could be allocated to alternative uses. Results show the importance of interpreting crop responses to NT and stubble retention on the basis of physiological principles.

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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2nd March 2018

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Chapter 1 General introduction

1.1 Introduction

In recent years, there has been a world-wide shift from land tillage and the removal or burning of stubble to conservation agriculture (CA), in a bid to arrest land degradation and increase crop production (Friedrich et al., 2012). The Food and Agriculture Organization (FAO) of the United Nations defines CA in a set of three integrated practices, which include: (1) minimum soil disturbance or no-till (NT); (2) permanent soil cover with stubble mulch or cover crops; and; (3) the rotation or intercropping of crops (FAO, 2015).

Full adoption of the three principles of CA is limited. For agronomic and socio-economic reasons, farmers have frequently adopted only one or two of the principles of CA as observed in Australia (Kirkegaard et al., 2014), sub-Saharan Africa (SSA) (Giller et al., 2009; Andersson and D'Souza, 2014) and Brazil (Bolliger et al., 2006). Partial adoption makes sense in the farmers' flexibility to adopt specific practices (Kirkegaard et al., 2014; Giller et al., 2015). Pittelkow et al. (2015a) observed that the implementation of stubble retention and crop rotations is a challenge in resource-poor smallholder systems, and may predispose farmers to yield losses. In Zimbabwe, legumes were grown in the fertile fields closer to the homesteads, rather than on poor outfields (Zingore et al., 2007).

There is controversy around the benefits of CA and the underpinning science (Kirkegaard et al., 2014; Stevenson et al., 2014; Giller et al., 2015; Powlson et al., 2016). Giller et al. (2009) questioned the suitability of some of the CA principles in SSA, and the approach used in its promotion. While there could be considerable labour and time saving with NT, the benefits of water capture and storage by stubble in drylands is variable (Scott et al., 2013). In many situations, however, NT reduces yield (Alvarez and Steinbach, 2009; Rusinamhodzi et al., 2011; Pittelkow et al., 2015a) but its negative effects are minimised when combined with the retention of stubble (Pittelkow et al., 2015a). On the other hand, nitrogen plays an important role in these systems (Sadras et al., 2012c; Sommer et al., 2014; Vanlauwe et al., 2014). Sadras et al. (2012c) discuss how N is critical in the capture of the benefits of water conservation and reciprocally how water supply is important to capture the benefits of N supply.

The most relevant question on the suitability of NT and stubble retention is probably not whether these systems 'work or not?' but rather, 'under what conditions do they work?'. This will lead to better matching of NT and stubble retention to local circumstances (Giller et al., 2015) and improve pragmatism in their application (Kirkegaard et al., 2014). For this to be realised, better understanding of the mechanisms operating in these systems is a pre-requisite (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Implementation of tillage and stubble retention practices in maize-based systems of SSA follows successes in other regions. Australia, where the majority of systems are wheat-based, is one of the leading supporters through ACIAR funded projects such as the sustainable intensification of maize-legume cropping systems for food security in eastern and southern Africa program (SIMLESA).

Despite differences in socio-economic circumstances between maize systems in Africa and wheat systems in Australia, some biophysical challenges and economic realities are shared, which include variable weather patterns, infertile soils, low inputs, low yields, small profit margins, variable income and integrated crop-livestock systems (Kirkegaard et al., 2014). Lessons could thus be drawn by comparing and contrasting these diverse systems. In addition to empirical evidence, mechanistic approaches are required to link management practices to yield, which could identify potential processes that can advance agronomy and crop physiology (Giller et al., 2015).

1.2 Aims

This thesis investigates crop responses to conventional tillage and no-till, different amounts of stubble as well as N rates and timing of N supply in two contrasting environments, the dryland wheat-based systems in the Mediterranean-type climate of southern Australia and maize-based systems in the sub-humid tropical climate of Kenya, in SSA. The overall aim of this research was to understand the mechanisms that regulate crop growth, patterns of senescence and yield, as well as water and nitrogen use efficiency in NT and stubble retention systems. Figure 1.1 schematises the specific questions developed as experiments in each environment, showing linkages to the overall research question, and the structure of this thesis.

1.3 Thesis structure

This thesis is structured into seven chapters. **Chapter 1** provides a general introduction, states the purpose of this research and outlines the structure of the thesis. **Chapter 2** provides a critical review of literature on no-till, stubble retention and N fertilization. It emphasises the drivers and constraints for crop growth, patterns of senescence, yield, as well as water and nitrogen use efficiency in these systems. **Chapter 3**, evaluates the effect of tillage, stubble retention and timing of nitrogen supply on dryland wheat in southern Australia. **Chapter 4** evaluates historic Australian wheat varieties for adaptation to no-till and stubble retention in southern Australia. **Chapter 5** evaluates tillage, stubble retention, rates and timing of N supply in maize systems in a sub-humid environment in Kenya. **Chapter 6** looks at the time-course patterns of leaf senescence in maize under contrasting tillage systems, stubble amount and N rate. Treatment effects and mechanisms that contributed to crop growth and yield, in addition to water and N use efficiency are discussed in **Chapter 7**. In this chapter, a mechanistic approach that links tillage, stubble and nitrogen management to yield and drivers for yield is suggested. Conclusions and potential areas for further research are provided.

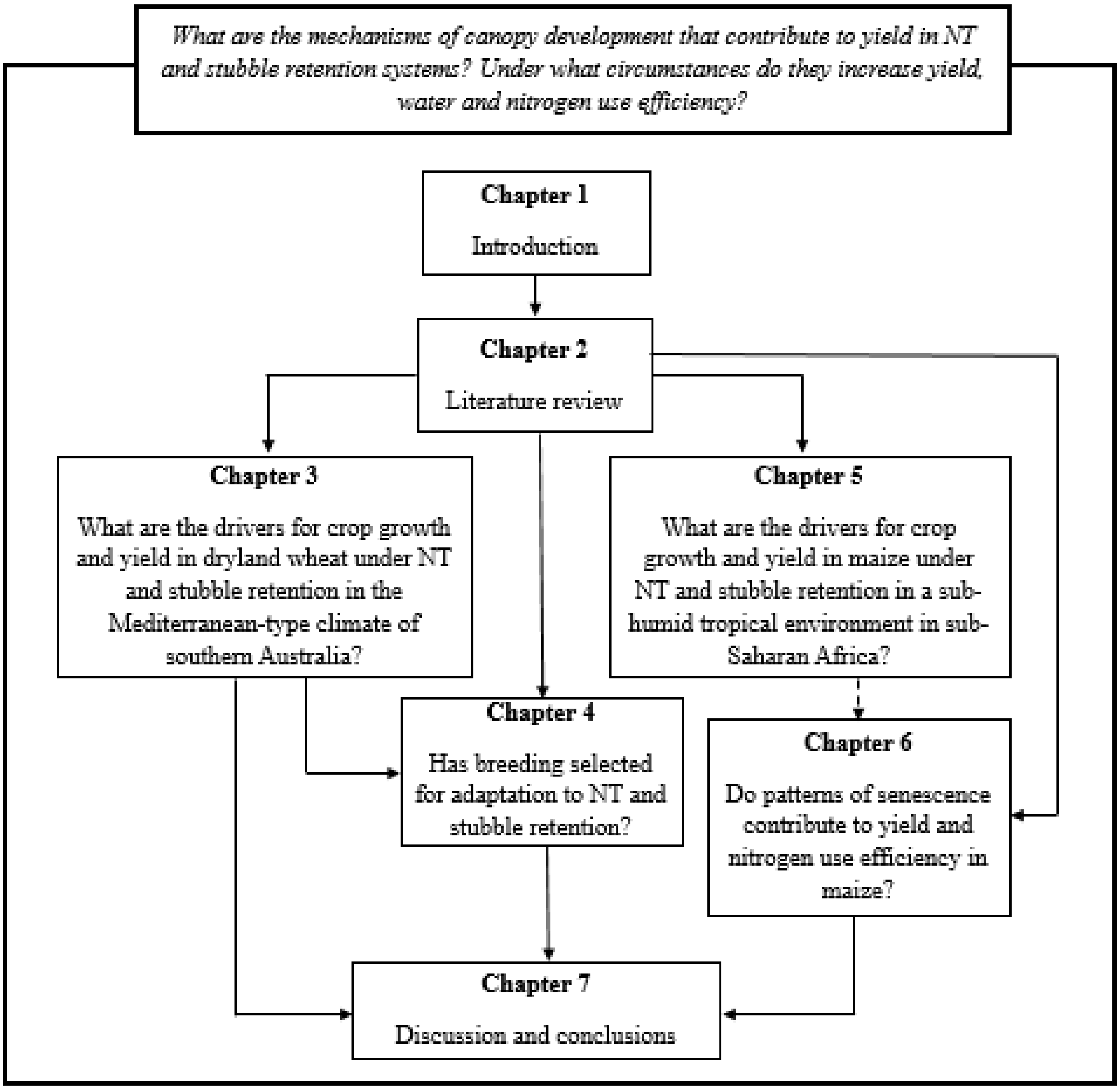

Figure 1.1. Thesis structure, highlighting the relationships among chapters, the overall research questions and specific research questions for the experimental chapters.

Chapter 2 Review of literature

2.1 Introduction

This chapter provides a background on the state of no-till (NT) and stubble retention practices in wheat systems in the Mediterranean-type climate of southern Australia and maize systems in the sub-humid tropical environments of sub-Saharan Africa (SSA). The yield-limiting factors of NT and stubble retention are analysed and potential avenues to improve yield, water and N use efficiency are explored. The physiological mechanisms that regulate crop growth, patterns of senescence and grain yield, as well as water and N use efficiency in these systems are scrutinized. Critical knowledge gaps are summarised. Research questions and objectives are formulated.

2.2 The state of no-till and stubble retention in southern Australia

Worldwide, the area under NT and stubble retention is estimated to be 125 M ha with 62% of this area dedicated in almost equal proportions to United States, Argentina and Brazil (Friedrich et al., 2012). In Australia, 17 M ha are managed under NT, which is about 14% of the global CA total. Introduction of NT and stubble retention in Australia dates back to 1970s to control wind and water erosion (Llewellyn et al., 2012). In addition to soil conservation, growers use this technology to reduce labour and fuel costs, improve timeliness in sowing operations and economic returns (Scott et al., 2013).

The diffusion of NT and stubble retention in Australia is close to reaching a plateau in many grain growing regions but adoption rates have varied. The motivating factors for adoption of these practices vary depending on the farmer’s goals (Llewellyn et al., 2012). Regions that have high adoption rates are Western Australia and Queensland, while lower rates are reported in South Australia, Victoria and New South Wales (Llewellyn and D'Emden, 2010). In the low rainfall regions of southern Australia, the need to conserve moisture for crop production has provided the incentive for growers to retain stubble (Llewellyn et al., 2012).

A high flexibility with regard to tillage and stubble retention is practiced in this region. Farmers continue some form of tillage to remove problems associated with continuous NT such as soil compaction, weeds and stratification of nutrients in soil (Kirkegaard et al., 2014). In addition, growers retain stubble opportunistically; often reducing stubble loads through controlled burning (Scott et al., 2013) and grazing sheep (Hunt et al., 2016). Lack of enough soil cover is a problem in dry seasons, and a challenge when excess amounts of stubble are produced during high rainfall (Scott et al., 2013).

2.3 The state of no-till and stubble retention in sub-Saharan Africa

The current area under NT and stubble retention in SSA is estimated to be 707,000 ha, which accounts for 0.6% of global CA (Friedrich et al., 2012). Leading adopters in this region are South Africa, Zimbabwe and Zambia (Wall et al., 2014). Maize (*Zea mays*) is the main crop in these systems, often grown in pure stands and in combination or rotation with legumes such as common beans (*Phaseolus vulgaris*), pigeon pea (*Cajanus cajan*), mung beans (*Vigna radiata*), dolichos beans (*Lablab purpureus*) as well as legume trees and fodders. However, the heterogeneous nature of smallholder farming systems in this region has made the integration of rotational or intercropping legumes problematic (Farrow et al., 2016).

The earliest experiences of NT and stubble retention in this region are reported around 1970s in Kenya, South Africa and Zimbabwe, and later in other countries such as Zambia and Tanzania (Berry et al., 2001; Wall et al., 2014). Recently, CA has been promoted by regional organizations such as ACT, NEPAD, SADC and international research organisations, for example CIMMYT, ICRISAT, CIRAD, ICARDA and ICRAF. Government and nongovernmental organizations such as FAO are also involved (Wall et al., 2014). The development of productive, resilient and sustainable cropping systems in this region has relied on experiences from other countries. Australia in particular, has led research initiatives through ACIAR funded projects such as SIMLESA.

Controversies in scientific evidence supporting the benefits of NT and stubble retention have led to low adoption rates in SSA (Giller et al., 2009; Andersson and D'Souza, 2014; Giller et al., 2015). In addition, the appropriateness of these practices within the socio-economic circumstances of smallholder farmers has been questioned (Giller et al., 2009). Some pertinent concerns about the claims made for NT and stubble retention in this region include: (1) the minimum amount of stubble that is required to provide the benefits of mulching in circumstances where stubble allocation for soil cover competes with livestock feeding; (2) fertilizer N rates that are required to increase yield and counter possible immobilization by high C:N ratio cereal stubble; and (3) the potential avenues to increase N use efficiency in these systems (Giller et al., 2009; Giller et al., 2011).

2.4 Benefits of no-till and stubble retention

The benefits of NT and stubble retention can be grouped as agronomic, economic and environmental (FAO, 2015). Agronomic benefits are as a result of increased soil organic matter, increased rain water infiltration and storage plus the improvement of soil structure. Soil organic matter promotes the aggregation of soil particles which improves water and nutrient retention, soil porosity and rooting environment (Bronick and Lal, 2005). This leads to higher water and fertilizer uptake and use efficiency. Rusinamhodzi et al. (2011) associated increases in maize yields with the improvement of soil texture over time. Moisture conservation in fallows can also permit early sowing (Passioura and Angus, 2010)

Economic benefits arising from NT and stubble retention include reduced costs of labour and fuel, as well as cheap operational and maintenance costs for machinery. There is increased timeliness of sowing operations with NT, which maximises the use of seasonal rainfall, hence higher system efficiency (FAO, 2015).

Putative environmental benefits of NT and stubble retention include carbon sequestration, increased microbial biodiversity, improvement of water and air quality as well as reduced eutrophication and silting of water bodies (FAO, 2015). However, the potential for carbon sequestration has been challenged (Govaerts et al., 2009b). Claims for reduced greenhouse gas emissions are also disputable (Maraseni and Cockfield, 2011). There were little differences in the emission of nitrous oxide (N_2O) from NT compared with tilled soils in dryland wheat systems in Spain (Tellez-Rio et al., 2017).

The benefits of NT and stubble retention appear both in the short-term and long-term. Short-term benefits are associated with improved soil water balance (Rockström et al., 2009). Benefits that take a long time to accrue, often appearing in more than 10 years, include soil organic matter build-up, the improvement of soil structure, texture and biodiversity (Giller et al., 2009; Govaerts et al., 2009a; Rusinamhodzi et al., 2011).

2.5 Productivity limits of no-till

Meta-analyses performed by Rusinamhodzi et al. (2011) and Pittelkow et al. (2015a) found that NT reduces crop yield. However, the reports found that under certain conditions, NT can produce equivalent or even greater yield than CT. Yield reduction in NT is exacerbated when stubble is removed, particularly in drylands (Rusinamhodzi et al., 2011; Pittelkow et al., 2015a). Continuous NT contributes to some yield-reducing factors such as soil compaction, stratification of nutrients in soil in addition to increased weeds, pests and disease problems (Kirkegaard et al., 2014).

2.5.1 Soil compaction, nutrient stratification and weeds

Reducing the number of tillage operations reduces fuel, labour and machinery costs and improves timeliness of sowing operations which makes better use of seasonal rainfall (Hobbs et al., 2008; Scott et al., 2013). However, continuous NT contributes to soil compaction which increases runoff and slows internal drainage in clayey soils (Baudron et al., 2012). There is increased risk of nutrient stratification in NT soils, particularly for slowly mobile nutrients such as phosphorus (P) (Deubel et al., 2011; Bell et al., 2012). This leads to sub-soil depletion and inefficiency of nutrient uptake, as well as the eutrophication of water bodies through runoff. Non-inversion of soils can increase the build-up of weed seed bank (Farooq et al., 2011), while the dependence on herbicides has led to herbicide resistance, for example in ryegrass (Boutsalis et al., 2014; Kirkegaard et al., 2014).

2.5.2 Strategic tillage

To manage the problems of continuous NT, occasional tillage using narrow tynes rather than discs is practised by Australian farmers (Llewellyn et al., 2012; Kirkegaard et al., 2014; Dang et al., 2018) as well as in the USA (Purakayastha et al., 2008; Wortmann et al., 2010). However, some studies have argued that one-time tillage in continuous NT soils may have irreversible damage to the soil (Grandy et al., 2006). Other reports show that one-time tillage improves soil conditions and crop growth, for example in northern Australia (Dang et al., 2015a; Dang et al., 2015b; Dang et al., 2018) and some regions in the USA (Purakayastha et al., 2008; Wortmann et al., 2010).

Reviews (Dang et al., 2015a) and experiments (Quincke et al., 2007; Wortmann et al., 2010; Dang et al., 2018) showed that strategic tillage improved water and P availability and reduced weeds and soil-borne diseases. In the short-term, there were grain yield increases, soil carbon and N decreased but there were no effects in the long-term (Dang et al., 2015a).

2.6 Productivity limits of stubble retention

2.6.1 Water infiltration and storage: the 'pulse paradigm'

Rain water infiltration and storage increases water use efficiency in drylands (Verburg et al., 2012). Stubble can reduce runoff, evaporation and promote infiltration. However, the benefits of stubble in water capture and storage are variable, and depend on rainfall intensity, frequency of events, evaporative demand and soil type (Gregory et al., 2000; Monzon et al., 2006; Hunt and Kirkegaard, 2011; Verburg et al., 2012). By considering pulse size, frequency, duration and depth, Verburg et al. (2012) suggested that for stubble to be effective in water conservation, rainfall events must be large and frequent enough to push some water beyond the evaporation zone of the soil profile.

Simulation experiments by Gregory et al. (2000) showed that the benefit of stubble retention in reducing soil evaporation was greatest under clayey soil, frequent rainfall events and low evaporative demand but least for sandy soil, sporadic rainfall and high evaporative demand. In a combination of field and modeling experiments, Monzon et al. (2006) observed that the addition of stubble was not useful in conditions where evaporative demand exceeded rainfall but reduced evaporation with respect to bare soil when rainfall increased. However, the benefit of stubble declined up to the point at which rainfall was high enough to meet both storage and evaporative demands.

Although the scope for stubble to improve water storage depends on many factors, the critical amounts of stubble at which water capture and storage is maximised are not known. Retention of stubble had minor effects on water conservation in fallow-wheat of southern Australia

(Sadras et al., 2012c; Hunt et al., 2013). Ward et al. (2009) found little differences in cumulative evaporation between bare ground and mulched soil, particularly during prolonged dry periods. In addition, the architecture of stubble, whether surface spread or standing had negligible effects on water conservation (Sadras et al., 2012c; Hunt et al., 2013).

2.6.2 Soil temperature regulation

Stubble moderates soil temperature fluctuations by influencing the balance between incoming and outgoing radiation (Verhulst et al., 2010). Soil temperature influences germination, root activity and early crop growth. In dryland tropical climates, mulch can moderate soil temperatures, which sometimes go too high for optimum crop growth. In winter cropping, stubble reduced diurnal soil temperature variation (Zhou et al., 2016). Low soil temperature reduced emergence and slowed initial growth in winter wheat (Yunusa et al., 1994; Zhou et al., 2016) and spring-maize (Cai and Wang, 2002). Nonetheless, the effect of stubble on germination and crop growth is not comprehensively understood.

2.6.3 Competition for stubble

Competition for stubble between soil cover and livestock feed limits the full implementation of stubble retention. This problem is not only chronic in low yielding systems of SSA (Jaleta et al., 2012; Baudron et al., 2015; Rusinamhodzi et al., 2016) but a real challenge in Australia (Kirkegaard et al., 2014). In addition to livestock feeding, stubble in many households in SSA is used as fuelwood as well as construction of fences and storage structures (Jaleta et al., 2012). Strategies to increase the amount of soil cover should be developed based on agroecology, cropping systems and the existing crop-livestock interactions (Jaleta et al., 2012). In addition, alternative sources of soil cover such as perennial legumes and plastic mulches are required.

2.6.4 Critical soil cover thresholds

An important question is: what are the critical soil cover thresholds that provide the benefit of mulching without counteracting other soil processes (Giller et al., 2011; Kirkegaard et al., 2014)? Understanding these thresholds in terms of the effects of stubble on soil protection, water storage, crop growth and grain yield can provide for flexibility in the removal stubble for other purposes such as livestock feed (Giller et al., 2009; Giller et al., 2011; Kirkegaard et al., 2014).

Evidence of the effects of stubble on crop growth and yield, and other functions is limited (Giller et al., 2011). Baudron et al. (2014) suggested that stubble does not always increase maize grain yield, and that when mulching is beneficial, yields do not increase linearly with the amount of soil cover applied. As a result, the application of more than 1 t ha^{-1} stubble did not improve maize yield in sub-humid environments of Kenya and Ethiopia (Baudron et al., 2014). In drylands, relatively higher amounts of stubble increased maize yield but the application of more than 4 t ha^{-1} was not beneficial (Mupangwa et al., 2007; Mupangwa et al., 2012; Baudron et al., 2014).

In Australia, yield response to stubble has been shown to vary with rainfall amount. In wetter seasons (>300 mm) stubble reduced yield compared with bare ground but on many occasions stubble did have effects on grain yield when rainfall was < 250 mm (Heenan et al., 1994; Kirkegaard et al., 1994), also summarised in Giller et al. (2015). Scott et al. (2013) and Hunt et al. (2016) recommend at least 70% soil cover which translates to about 2-3 t ha^{-1} of stubble. Grazing sheep on stubble increased soil strength and bulk density and reduced rainfall infiltration, but not to levels that were detrimental to crop growth and yield (Hunt et al., 2016).

2.7 Productivity limits of nitrogen fertilization

Nitrogen is the most important nutrient limiting crop growth and is a vital constituent of plant cell walls, cytoplasmic proteins, nucleic acids and chlorophyll (Atwell, 1999). NT and stubble retention impact N cycling and use efficiency (Grahmann et al., 2013). Low N use efficiency in these systems partly originates from N immobilization by high C:N ratio cereal stubble (Giller et al., 2009). Immobilization describes the conversion of inorganic N from the soil by micro-organisms to organic compounds which are inaccessible by the plant. This process occurs when stubble with more than 30 C:N ratio is applied (Hodges, 2010).

Adjustment of fertilizer management is required to alleviate the problems of low N use efficiency in NT and stubble retention systems (Grahmann et al., 2013; Lundy et al., 2015). In addition, higher N rates can increase biomass production, hence reduced trade-offs in the allocation of stubble (Vanlauwe et al., 2014). The importance of N is further recognised by Vanlauwe et al. (2014) and Giller et al. (2015) who called for the inclusion N fertilization as the fourth principle in the definition of CA. However, Sommer et al. (2014) disagree with Vanlauwe et al (2014) but agree that N use is crucial for increasing crop yields. Across a set of crops, Pittelkow et al. (2015a) observed a 12% yield reduction in NT when fertilizer N was not added but the gap reduced to 4% when fertilizer was applied. However, this effect varied with climate, and the severity of lack of N supply was smaller in drylands compared with humid environments.

The management of fertilizer N can be divided into four crucial components, which include the rate of supply, the type of fertilizer, the timing and method of application and placement (Roberts, 2008). This section will discuss strategies relating to each of these components for the improvement of N uptake in NT and stubble retention systems.

2.7.1 Nitrogen application rate

The rate of N supply is the most important component of fertilizer management to increase yield, and particularly essential in countering yield declines in NT and stubble retention systems. Lundy et al. (2015) showed that farmers who apply low N rates in NT and stubble retention systems could raise yields if N rates are increased. A meta-analysis performed by Rusinamhodzi et al. (2011) showed that the application of more than 100 kg N ha^{-1} increased maize yield while lower N rates reduced yield in NT and stubble retention systems. This suggests that these systems are N input intensive, and for SSA, where fertilizer rates have stagnated since 1960s, higher rates are required (Dimes et al. 2015).

There is insufficient evidence on how much fertilizer N and timing of supply is required in NT and stubble retention systems. This could depend on the quality and quantity of stubble used (Giller et al. 2009) as well as rainfall patterns (Sadras et al. 2012). In addition, the integration of rotational legumes is likely to impact fertilizer requirements. However, increased N rates should minimise potential losses to the environment. In a maize-soybean rotation system in the USA, Al-Kaisi and Kwaw-Mensah (2007) did not find maize yield increases with applications above 85 kg N ha^{-1}. In a sub-humid environment in western Kenya, the application of more than 60 kg N ha^{-1} did not increase maize yield (Kihara et al., 2012).

2.7.2 Type of fertilizer

Key sources of fertilizer are both inorganic fertilizers and organic manures such as compost and animal manure, green manure, crop stubble, and N fixation by legumes. Urea (46% N) and ammonium sulphate (21% N) are the most common inorganic N fertilizers (Fageria and Baligar, 2005). Anhydrous ammonia (NH_3) is a cheap source of N which is widely used in USA but not used in Africa due to the lack of equipment for its application (Riar and Coventry, 2013). Urea is widely used in Australia and Africa as its application is easy, often broadcast prior to sufficient rainfall to promote its movement into the soil. Other forms such as slow release fertilizers, N stabilizers and denitrification inhibitors are available, but they are expensive and have traditionally been used on high-value crops (Roberts, 2008).

2.7.3 Timing of N application

The recovery of N is more efficient when the timing of application is synchronized with crop demand for the nutrient (Roberts, 2008). Poor synchrony occurs when large sowing applications are available before the crop has sufficient root capacity for N uptake, in addition to low shoot uptake demand. Sowing applications can produce large vegetative canopies with large transpiration surfaces that could lead to excess water use early in season. This condition can predispose the reproductive phase to water stress in winter-rainfall environments (van Herwaarden et al., 1998).

Nitrogen timing strategies have been used to manipulate canopy development for balanced pre- and post-flowering water and N use, hence higher grain yield and quality (Hooper et al., 2015; Zhou et al., 2017). In wheat, delaying N supply initially produced a thin and more open canopy that led to increased radiation use efficiency, better water use patterns and higher grain yield compared with sowing applications (Zhou et al., 2017).

2.7.4 Mechanization, disease and pest burden

The combination of NT with stubble retention requires investment in expensive machinery such as seed drills, as well as superior management skills. Sowing into stubble is a challenge but advances in farm machinery have allowed for inter-row sowing so that successive crops are less affected by stubble-borne diseases hosted by the previous crops (Rainbow and Derpsch, 2011). Mechanization has efficiently been applied in Australian large scale systems but the diverse smallholder systems of Africa are largely not mechanized (Thierfelder et al., 2012).

Retention of stubble leads to disease carry-over (Scott et al. 2013), provides habitat to pests and insects (Hoffmann et al., 2008), slugs and snails (Baker, 2012) while some materials have phyto-toxic chemicals (Weston, 1996), that could impair the growth of other crop species.

2.7.5 Fertilizer application and placement method

Fertilizer application method is critical for N uptake, and should be placed as close as possible to the plant uptake region. Difficulties in applying N under high amounts of stubble can lead to reduced N recovery (Hobbs et al., 1998), except if the goal is to build soil organic matter. Fertilizer should be applied so as to minimise contact with stubble, which could otherwise promote immobilization or volatilization losses (Grahmann et al., 2013). Sub-surface placement minimises fertilizer contact with stubble (Verachtert et al., 2009).

Sub-surface N banding improved fertilizer recovery, grain yield and grain N content in NT and stubble retention wheat systems compared with broadcast systems (Rao and Dao, 1996). Suitable and inexpensive equipment for sub-surface delivery of fertilizer in NT and stubble retention systems are not available, particularly in the smallholder systems in developing countries (Riar and Coventry, 2013). Alternatives such as injection techniques for liquid N (Angás et al., 2006) and foliar sprays (Pushman and Bingham, 1976) can be explored.

2.8 Water use efficiency

Crops can be managed or bred to improve water uptake, transpiration efficiency for biomass production, and harvest index (Condon et al., 2004; Passioura and Angus, 2010). Water use efficiency (WUE) can be defined at three scales: (1) at the whole-plant scale as the ratio of total dry matter to seasonal evapotranspiration; (2) economic scale as the ratio of grain yield per unit area to seasonal evapotranspiration; and (3) leaf scale as the ratio of instantaneous Carbon (IV) Oxide (CO_2) assimilation rate to transpiration rate (Ali and Talukder, 2008).

Evapotranspiration is the difference between cumulative seasonal rainfall and soil water content at physiological maturity, assuming runoff and deep drainage are negligible (Schultz and French, 1984). In this thesis, WUE will refer to the ratio of grain yield to seasonal evapotranspiration.

The following section explores a range of agronomic practices that can improve water uptake and use efficiency in NT and stubble retention systems. Potential practices include the improvement of water supply, reduction of evaporative losses, improvement of transpiration efficiency, as well as matching crop growth and development with water availability (Condon et al., 2004; Passioura and Angus, 2010).

2.8.1 Soil water balance

Water that infiltrates beyond the evaporation zone of the soil becomes stored moisture (Rockström et al., 2009). Stubble reduces the impact of rain drops and runoff velocity, which promotes infiltration. In diverse environments with sandy to clay soils in the sub-humid tropics of Malawi, NT and stubble retention increased infiltration by 24-40% compared with CT, thus increased maize grain yield (Thierfelder et al., 2013).

Soil structure influences the ability of the soil to capture, transmit and store water. Soil structure describes the aggregation of soil particles by soil organic matter. Tillage destroys soil structure by accelerating the depletion of organic matter (Mrabet, 2002; Paul et al., 2013). No-till and stubble retention increases soil aggregate stability (Bronick and Lal, 2005) and improves structure (Page et al., 2013), which promotes water infiltration and storage (Gowing and Palmer, 2008; Palm et al., 2013; Paul et al., 2013).

Lower temperature and reduced speed of wind on mulched soil moderates evaporation (Hatfield et al., 2001) but under conditions that are not too dry or too wet (Monzon et al., 2006).

Soil compaction due to continuous NT leads to decreased soil porosity and air permeability (Mielke et al., 1986; Li et al., 2007). This predisposes the soil to waterlogging and higher risks of anaerobic processes such as denitrification in wet periods (Linn and Doran, 1984). High amounts of stubble could intercept rain water, thereby exposing it to evaporative losses but little information is available (Passioura and Angus, 2010).

2.8.2 Transpiration efficiency and harvest index

At the leaf scale, Condon et al. (2002) defined "intrinsic WUE" (W_T) as the ratio of the instantaneous rates of $C0_2$ assimilation (A) and transpiration (T) at the stomata. The rates of A and T are a product of stomatal conductance, which is regulated by the concentration gradient between the inside and outside of the leaf for CO_2 and water vapour, respectively (Condon et al., 2002). Intrinsic WUE can thus be improved by lowering the ratio between intracellular to atmospheric CO_2 (Condon et al., 2002). This can be manipulated by selecting for lower stomatal conductance and higher photosynthetic capacity (Farquhar et al., 1989). In environments with terminal water stress, such as winter-rainfall environments of southern Australia and the drylands of SSA, adjusting sowing time can improve earliness to maximise growth when evaporative demand is low. This raises the A/T ratio and increases grain yield (Condon et al., 2004).

In the consideration of WUE as the ratio of grain yield to evapotranspiration, grain yield (Y) is a function of evapotranspiration (ET), the proportion transpired by the crop (T/ET), transpiration efficiency of biomass production (W) and the efficiency with which the biomass is converted into grain, the harvest index (HI) (Condon et al., 2004). Simply, $Y = ET * T/ET * W * HI$. The introduction of dwarfing genes in wheat led to increases in wheat HI (Siddique et al., 1989a; Siddique et al., 1989b; Sadras and Lawson, 2011), but further increases are contradictory (Fischer, 2011; Sadras and Lawson, 2011). Similarly, short-stature hybrids have increased maize HI and grain yield (Johnson et al., 1986). Further, improvements in HI have led to higher grain yield in both adequate, as well as water- and N-limited environments (Sinclair, 1998).

In wheat and maize, a good harvest index for dryland systems is about 0.40, as high temperatures and water stress reduces this trait (Passioura and Angus, 2010). Passioura and Angus (2010) described three challenges for increasing HI and grain yield: (1) the promotion of floret survival during heat, frost or water stress; (2) balanced proportion of transpiration between vegetative and reproductive stages; and (3) the remobilization efficiency of stored assimilates to the grain.

2.8.3 Crop management practices that improve water use efficiency

Timing of flowering is one of the most important physiological traits for adapting crops to water-limited environments (Passioura and Angus, 2010). Optimal flowering seeks to balance water use between vegetative, grain set and grain filling requirements (Angus and van Herwaarden, 2001). In Mediterranean-type climates, early flowering risks floral damage by frost while late flowering often coincides with water and heat stress (Passioura and Angus, 2010). Short anthesis silking interval, the time difference between the appearance of the male (anther) and female (silk) flowers, improves adaptation to stress and promotes grain set in maize (Bolaños and Edmeades, 1993; Bänziger et al., 1999). In addition to breeding, agronomic variables such as sowing time and N nutrition can manipulate crop developmental rates which impacts flowering time (Angus and van Herwaarden, 2001).

The modulation of crop growth both before and after flowering impacts WUE, HI and the final grain yield. In water constrained environments, high vegetative growth may lead to excessive pre-flowering water use which may deplete reserves for the reproductive phase (van

Herwaarden et al., 1998). A thinner vegetative canopy can be obtained by delaying N supply (Hooper et al., 2015; Zhou et al., 2017), which leads to soil moisture conservation for water-demanding grain formation and filling processes. In this respect, if not well managed, additional water made available to the crop by NT and stubble retention may lead to excessive pre-flowering growth, which could predispose the crop to acute water shortage later in the season, especially in drylands (van Herwaarden et al., 1998).

The management of crop growth can employ both strategic and tactical approaches (Passioura and Angus, 2010). Strategic practices are those that are effected before or at the start of season, and work best in areas with reliable water supply (Passioura and Angus, 2010). Examples of strategic practices include early sowing, correction of acute nutrient deficiency, liming and cropping geometry. Tactical practices are those that vary between and within seasons, in response to crop growth and development, growing conditions and changes in grain prices and input costs (Passioura and Angus, 2010). Strategic N application to manipulate canopy development and water use patterns is common feature of dryland cropping in Mediterranean climates (van Herwaarden et al., 1998; Hooper et al., 2015; Zhou et al., 2017).

2.8.4 Water-limited yield potential

Water-limited yield potential is the maximum yield achievable under rainfed conditions when soil water capture and storage is maximised and nutrient constraints are removed (Tittonell and Giller, 2013). Shortage of moisture is not the only factor limiting WUE as scarcity of N is as critical (French and Schultz, 1984; Sadras and Roget, 2004; Sadras et al., 2012c). This emphasises the need to match the supply of N and water availability, as has been widely mentioned in this review of literature. However, matching the two resources remains a challenge, particularly with variable rainfall (Sadras et al., 2016), and even worse when N availability is altered by tillage and stubble retention practices. The combination of uncertain rainfall and under-fertilization commonly leads to large gaps between actual yield and water-limited yield potential yield (French and Schultz, 1984; Sadras and Roget, 2004), even when high yielding genotypes are used (Tittonell and Giller, 2013).

2.9 Nitrogen use efficiency

Nitrogen use efficiency (NUE) can be divided into two broad components: (1) N uptake efficiency (NuptE), which is the increase in N uptake by the crop as N supply in the soil is increased; and (2) N utilization efficiency (NutE), the capacity to produce more biomass per unit of N uptake. In cereals, harvest index (HI), the ratio of grain yield (Y) to total biomass (W) affects NUE (Gastal et al. 2015).

$$\mathrm{NUE} = \frac{\Delta \mathrm{Nupt}}{\Delta \mathrm{Nut}} * \frac{\Delta \mathrm{W}}{\Delta \mathrm{Nupt}} * \frac{\Delta \mathrm{Y}}{\Delta \mathrm{W}} \qquad (2.1)$$

Thus, NUE is a function of N recovery from the soil, the internal efficiency with which N is used for biomass production and harvest index (Gastal et al., 2015). In Eq. 2.1, Δ is the increase in N uptake efficiency, N utilization efficiency, grain yield and biomass.

$$\mathrm{NUE} = \mathrm{NuptE} * \mathrm{NutE} * \mathrm{HI} \qquad (2.2)$$

2.9.1 Components of nitrogen use efficiency

Components of NUE include recovery efficiency, physiological efficiency, internal utilization efficiency and agronomic efficiency. Others are N harvest index and N remobilization efficiency.

2.9.1.1 Nitrogen recovery efficiency (RE)

$$\mathrm{RE\ (kg\ kg^{-1}\ N)} = \frac{\text{N uptake with fertilizer} - \text{N uptake without fertilizer}}{\text{amount of fertilizer N applied}} \qquad (2.3)$$

Recovery efficiency is affected by the type, rate, timing and placement method of fertilizer as well as genotype, climate, plant density as well as abiotic and biotic stresses (Dobermann, 2007). In cereal systems, RE ranges from 0.30-0.50 but in well-managed systems with low N it may range from 0.50-0.80 kg kg^{-1} N (Dobermann, 2007).

2.9.1.2 Nitrogen physiological efficiency (PE)

$$\mathrm{PE\ (kg\ kg^{-1}\ N)} = \frac{\text{grain yield with fertilizer} - \text{grain yield without fertilizer}}{\text{N uptake with fertilizer} - \text{N uptake without fertilizer}} \qquad (2.4)$$

Physiological efficiency depends on environmental stresses and genotype (McDonald, 1989; Dobermann, 2007), and ranges between 40-60 kg kg^{-1} N. Values >50 kg kg^{-1} N are achievable in well-managed systems and at low N use. Low PE suggests the possibility of nutrient deficiencies, drought stress, heat stress, mineral toxicities or pests and diseases (Dobermann 2007).

2.9.2 Nitrogen internal efficiency (IE)

$$\mathrm{IE\ (kg\ kg^{-1}\ N)} = \frac{\text{grain yield}}{\text{N uptake}} \qquad 2.5$$

Nitrogen internal efficiency is the ability of a plant to transform both soil N and fertilizer N into grain, and depends on genotype, environment and management (Dobermann, 2007). Generally, IE ranges from 30-90 kg kg^{-1} N, in values. However, at high yield and balanced nutrition, the range is higher, between 55-65 kg kg^{-1} N (Dobermann, 2007). Nutrient deficiency, water and heat stress, mineral toxicities and pests and diseases reduces IE (Dobermann, 2007).

2.9.2.1 Nitrogen agronomic efficiency (AE)

$$\text{AE (kg kg}^{-1}\text{ N)} = \frac{\text{yield with fertilizer} - \text{ yield without fertilizer}}{\text{amount of fertilizer N applied}} \qquad 2.6$$

Agronomic efficiency is an indicator of grain yield increase in response to applied N, and reflects the efficiency with which applied nitrogen is used to produce extra grain (Dobermann, 2007). In cereal systems, AE ranges from 10-30 kg kg^{-1} N, and usually >25 in well-managed systems with low N (Dobermann, 2007). AE depends on management practices that affect both RE and PE (Dobermann, 2007).

2.9.3 Increasing nitrogen uptake and use efficiency

The first step to increase NUE in cropping systems is the ability to increase N uptake (Gastal et al., 2015; Rossini et al., 2018). Roots intercept and take up mineral N in the form nitrates (NO_3-N) and ammonium (NH_4-N). The absorption of N by plants is related to water absorption, thus soil water content plays a critical role in N uptake (Craswell and Godwin, 1984). Dissolved solutes are absorbed and taken up the transpiration stream by mass flow or convection, and as the soil dries out, N uptake declines (Craswell and Godwin, 1984).

The fate of N in the soil and its availability for uptake can be affected by an array of biological and physical transformations that include; mineralization, immobilization, nitrification, denitrification, volatilization, leaching and erosion by water (Álvarez et al., 2008). Strict adherence to the foundations of best management practices of fertilizer N, including the right product, at the right rate and timing of supply and the right application method, contributes to higher uptake and reduced losses (Roberts, 2008).

Some key physiological components of NUE are N harvest index (NHI) and N remobilization efficiency (NRE). Selection for yield in maize increased grain HI and NHI, which suggested there exists strong dependency between N and dry matter allocation to grain (Ciampitti and Vyn, 2012). Selection for yield in wheat also increased NHI, despite a decrease in grain protein concentration (Sadras and Lawson, 2013). During senescence, the remobilization of N from the senescing leaves to the grain contributes to NUE (Wu et al., 2012; Thomas and Ougham, 2015). Accumulated N compounds (proteins and enzymes) in shoots are remobilized by protein hydrolysis and amino acids are exported to the grain (Ciampitti et al., 2013; Barraclough et al., 2014)

2.9.4 Delaying the application of nitrogen

The strategic application of N offers opportunities to alter canopy development for a balanced water and N use to improve grain yield and NUE (Hooper et al., 2015; Zhou et al., 2017). Hooper et al. (2015) and Zhou et al. (2017) observed that delaying N supply initially produced a smaller and more open canopy compared with sowing applications. There was higher shoot mortality in wheat crops under sowing application compared with delayed N supply, which exemplified ‘haying-off, conditions (van Herwaarden et al., 1998; Zhou et al., 2017). Crops are said to have ‘hayed off’ when they senescence prematurely due to high N fertilization rates and moisture stress (van Herwaarden et al., 1998). Rainfall variability in drylands brings a dilemma to N fertilization, partly due to risks of crops ‘haying-off’ when fertilizer is supplied at sowing and the possibility of poor uptake when late applications coincides with low water availability.

2.10 Water-nitrogen co-limitation

Water and N exhibit strong synergistic interactions and yield is maximised when both resources are equally limiting (Sadras, 2005; Cossani et al., 2010; Riar et al., 2016). In the dryland environments of southern Australia, Sadras et al. (2012c) showed that when wheat yield response was related to the interaction between water and N, both capture and efficiency in the use of both resources was critical. Other studies have similarly shown how N is critical to capture the benefits of water conservation and reciprocally how adequate water supply is required to capture the benefits of N supply (Norton and Wachsmann, 2006; Sinclair and Rufty, 2012; Riar et al., 2016). In canola *(Brassica napus* L.) and mustard (*Brassica juncea* L.) in southern Australia, grain yield increased as the degree of water-N co-limitation increased but with considerable variations due to season and genotype (Riar et al., 2016).

2.11 Genotype × management interactions

Plant breeding and advancement in agronomy have contributed to increased productivity of cropping systems (Fischer, 2009). As the cropped area under NT and stubble retention continues to expand, adapted cultivars are required (Trethowan et al., 2005). Particularly important are traits that promote vigorous growth with the physical and biological constraints of unploughed soils (Watt et al., 2005; Rebetzke et al., 2014). No-till and stubble retention introduce new challenges to plant breeders such as soil compaction which can impede crop emergence and growth, stubble-borne diseases, weeds, pests, N immobilization by stubble and altered soil temperature (Trethowan et al., 2005; Joshi et al., 2007; Herrera et al., 2013).

Currently there are no varieties that are specifically bred for adaptation to NT and stubble retention, partly due to infrequent and contradictory occurrence of genotype × management interactions (Trethowan et al., 2012; Herrera et al., 2013). However, there have been efforts to select traits that can promote crop growth and grain yield in these systems (Herrera et al., 2013; Rebetzke et al., 2014). Some adaptation could have occurred inadvertently in the modern varieties which have had greater exposure to NT and stubble retention during their selection compared with older varieties. Wheat breeders are selecting for long and thick coleoptiles to permit emergence from depth, seedling vigour and tolerance to extreme temperatures, root architecture and increased water and NUE, resistance to stubble-borne diseases and enhanced rate of stubble decomposition (Joshi et al., 2007; Trethowan et al., 2009).

Few studies have reported genotype × tillage interactions in wheat (Hall and Cholick, 1989; Cox, 1991) or maize (Brakke et al., 1983). A majority of studies did not find interactions in wheat (Kirkegaard, 1995; Carr et al., 2003; Kumudini et al., 2008; Trethowan et al., 2012) and maize (Wall and Stobbe, 1983; Anderson, 1986; Newhouse and Crosbie, 1986). Meta-analysis by Herrera et al. (2013) which compared a range of maize and wheat genotypes under contrasting tillage systems showed 5% higher yield under CT compared with NT for both crops. Further, they observed that in studies where selection had been conducted under NT, the effect of tillage was modified by genotype. In wheat, Hwu and Allan (1992) and Higginbotham et al. (2011) found that varieties that had been developed under CT or NT performed better under tillage systems in which they were bred. This specificity to tillage system suggests that some key physiological traits are enhanced under a particular tillage system.

Genotype × management interactions are contingent to environment (Chenu et al., 2011; Tardieu, 2011). Thus, the value of certain traits will vary across environments. Joshi et al. (2007) suggests that traits that promote faster emergence, ability to emerge when deep sown and seedling vigour could allow for early sowing in NT and stubble retention systems. However, prolific root architecture can only utilise stored moisture in environments that favour sub-soil moisture storage (Kirkegaard et al., 2007).

The manipulation of the patterns of leaf senescence can impact WUE. Extended leaf greenness has contributed current yield increases in cereals (Jordan et al., 2012; Gregersen et al., 2013). Prolongation of leaf greenness improved sorghum (*Sorghum bicolor)* adaptation to terminal drought by affording the crop the ability to extract and transpire more water, as well as extended photosynthetic duration (Vadez et al., 2011). However, patterns of leaf senescence are bound to vary with both environment and management.

2.12 Physiological mechanisms that contribute to wheat and maize yield in NT and stubble retention systems

Physiological mechanisms that regulate yield formation in NT and stubble retention systems have remained largely unexplored (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Previous studies used end-of-season yield and yield components, which overlooked within-season variations and associated physiological consequences on crop growth and yield (Brennan et al., 2014; Singh et al., 2015). The following section discusses the mechanisms which determine yield in wheat and maize.

2.12.1 Grain number and grain weight

Grain number depends on crop growth during the critical period of yield determination, and the partitioning of dry matter to the grain (Andrade et al., 2005). Theory and empirical evidence show positive relationships between both grain number and grain yield, and crop growth rate (Andrade et al., 2005). However, this relationship varies among species depending on the plasticity of the reproductive organs and tolerance to stress during grain formation (Vega et al., 2001). Tillering in wheat and branching in soybean both provide high plasticity in vegetative growth, thus grain number and crop growth rate are linearly related (Vega et al., 2001). For crops with limited plasticity of the reproductive growth due to lack of tillering or branching, such as maize and sunflower the relationship between grain number and crop growth rate tends to be curvilinear (Vega et al., 2001).

Synchronism in flowering and pollination, plus competition for assimilates among sinks limits grain set efficiency, both in wheat (Ferrante et al., 2012) and maize (Uribelarrea et al., 2002;

Andrade et al., 2005; Worku et al., 2016). Water and N availability affect floret development. In wheat, N fertilization increased the survival of fertile florets and grain set (Ferrante et al., 2012). In maize, short anthesis silking intervals (ASI) promote fertilization and the formation of kernels while long ASI leads to few kernels (Bolaños and Edmeades, 1993). In a range of stress intensities, high grain yield was associated with early anthesis and short ASI in maize (Bänziger et al., 1999).

2.12.2 Biomass accumulation

Biomass accumulation follows a sigmoid curve. During the seedling phase, growth is slow but increases steadily to the six-leaf stage (V6) in maize or tillering (GS22) in wheat, then rapid growth and N uptake follows. The period of rapid biomass accumulation coincides with the critical phase for yield determination. In wheat, the critical window for grain set falls between stem elongation (GS31) and 10 days after flowering (GS65) (Slafer et al., 2014). Kernel number is determined from a few days after V6 to few days after silking in maize (Andrade et al., 2005). In other crop species such as soybean, the critical period for yield determination extends from flowering to grain filling (Andrade et al., 2005). Management practices that maximise growth during this period increase grain number and yield.

2.12.3 Radiation interception and radiation use efficiency

The initial steps of photosynthesis involve the interception and absorption of solar radiation by photosynthetic organs (Atwell, 1999). During photosynthesis, light photons are harnessed to produce biomass from the fixation of CO_2. The interception of photosynthetically active radiation (PAR), which ranges from 400-700 nm of the electromagnetic spectrum depends on leaf area, orientation and surface features of the leaf (Atwell, 1999). Plant architecture, particularly with regard to the arrangement of leaves influences the interception of PAR within the canopy depths, with considerable light attenuation at the bottom leaves (Maddonni et al., 2001). More open canopies are likely to have better distribution of light at all leaf layers compared with closed canopies, hence higher RUE (Sadras et al., 2012b). Leaf area is positively correlated with leaf area expansion, a function of both leaf number and size, and leaf senescence (Andrade et al., 2005).

Radiation use efficiency (RUE) is the biomass produced per unit of intercepted PAR. This trait varies with photosynthetic metabolism and leaf longevity of each species (Foulkes et al., 2009). During grain set, RUE is important for the determination of grain number and potential grain size in both wheat (Sadras, 2007; Sadras and Slafer, 2012) and maize (Sinclair and Muchow, 1999). Environmental factors such as temperature, water and N stress as well as the proportion of diffuse radiation influence this trait (Muchow and Sinclair, 1994; Earl and Davis, 2003; Andrade et al., 2005). The improvement of RUE remains a challenge in NT and stubble systems, particularly when N uptake is constrained by the application of stubble. Better matching of N supply at critical growth stages can modify crop developmental rates and consequently RUE.

2.12.4 Nitrogen nutrition

The N nutritional status of a crop can be quantified through nitrogen nutrition index (NNI), a trait that is useful in the interpretation of crop response to management practices (Gastal et al., 2015). NNI is the ratio of actual N concentration in crop biomass to the critical N concentration required to achieve maximum mass (Gastal et al., 2015). When N uptake is higher than critical N concentration then the crop experiences ‘luxury’ N consumption while N deficiency occurs if N uptake is lower than the critical N concentration (Gastal et al., 2015). The concept of NNI has not been comprehensively used in the interpretation of crop responses to NT and stubble retention. Monitoring the crop N status using NNI can inform the strategic supply of N to match crop requirements for N in these systems.

2.12.5 Patterns of leaf senescence

Leaf senescence is the loss of leaf green area due to age or in response to environmental conditions. This physiological process regulates photosynthesis, water uptake, N remobilization from old leaves to young leaves and grain, and grain yield (Wu et al., 2012; Gregersen et al., 2013). In monocarpic plants such as wheat and maize, leaf senescence overlaps with the critical period for grain set and might reduce yield if induced prematurely (Gregersen et al., 2013; Thomas and Ougham, 2015). Grain yield is a function of green leaf area and duration (Gregersen et al., 2013), where the prolongation of the photosynthetic duration has been associated with increased water and N uptake and higher grain yield (Wu et al., 2012).

High yield potential in wheat and maize has been achieved through breeding for extended photosynthetic duration (Gregersen et al., 2013). Based on the patterns of senescence, varieties and hybrids can be classified as senescent and ‘stay-green’ phenotypes, where the former senesce earlier irrespective of growing conditions while the later have prolonged leaf greenness (Gregersen et al., 2013). Sadras and Richards (2014) summarised five combinations of traits and environments that contribute to stay green. The most fundamental are: (1) traits that conserve water and reduce stress during grain filling, including a small canopy and early maturity; (2) traits that enhance water uptake, such as a deep rooting system in the right combination of soil and rainfall; and (3) metabolic traits that promote the allocation of carbon and N to the roots during grain filling.

Patterns of leaf senescence can be explored for the improvement of grain yield and quality, and NUE in NT and stubble retention systems. Leaf senescence ideotypes for the maximization of grain yield have been described (Wu et al., 2012): delayed onset of senescence or stay-green to prolong photosynthetic duration; and faster rate of senescence to improve the efficiency of nutrient remobilization to the grain. In wheat, delayed onset of senescence coupled with a fast rate of senescence increased grain yield and individual grain filling rate and weight (Xie et al., 2016).

2.13 Summary and critical knowledge gaps

A paradigm shift from questioning whether NT and stubble retention systems "*work or not*", to asking "*under what circumstances these systems work*", is required. There are limitations in understanding the mechanisms that operate in these systems, including:

- The effects of tillage, stubble and fertilizer N, and their interactions on crop growth and yield, as well as water and N use efficiency
- The critical soil cover thresholds at which water infiltration and storage as well as crop growth and yield is maximised
- N management that captures the benefits of water conservation in NT and stubble retention, and ameliorates the yield-reducing effects in these systems
- The extent to which breeding is selecting for adaptation to NT and stubble retention
- The implication of the patterns of leaf senescence on grain yield, yield components and N use efficiency

2.14 Research questions, justification and objectives

The key research questions for this thesis were: *what are the mechanisms of canopy development that contribute to yield in NT and stubble retention systems? Under what circumstances do they increase yield, water and N use efficiency?* The overall aim of this study was to better understand the mechanisms that regulate crop growth, patterns of senescence and yield, in addition to water and nitrogen use efficiency in NT and stubble retention systems.

The objectives of this research have been organised into chapters. The chapters will:

- Evaluate the effect of tillage, stubble amount and timing of nitrogen supply on dryland wheat in a Mediterranean-type environment in southern Australia (Chapter 3)
- Assess the extent to which wheat breeding in the Mediterranean-type climate of southern Australia is selecting for adaptation to no-till and stubble retention systems (Chapter 4)
- Investigate the effect of tillage, stubble amount as well as rate and timing of nitrogen supply on maize in a sub-humid tropical environment in Kenya (Chapter 5)
- Characterise the time-course of leaf senescence of maize under conventional tillage and no-till, different rates of stubble and nitrogen supply. Establish relationships between senescence and grain yield, in addition to traits associated with nitrogen use efficiency (Chapter 6)
- Summarise the main effects of tillage, stubble retention and N fertilization and their interactions. Identify similarities and differences in the mechanisms of crop growth, patterns of senescence and yield, and water and nitrogen use efficiency between the wheat and maize systems. Advance a mechanistic approach that describes the linkage between management and yield (Chapter 7).

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Chapter 3 Canopy development and grain yield of dryland wheat is modulated by strategic nitrogen supply and stubble management

Abstract

Yield in dryland wheat could be improved through a better understanding of crop responses to no-till (NT), stubble retention and N timing. Field experiments were established at Roseworthy and Karoonda in South Australia to evaluate wheat crop responses to contrasting tillage systems, different amounts of stubble, and timing of nitrogen (N) application. Biomass, driven by tiller number, was higher under NT crops compared with conventional tillage. Application of high amounts of stubble (5 t ha^{-1}) reduced biomass at harvest compared with moderate amounts of stubble (2.5 t ha^{-1}) or bare ground. Sowing applications of N produced large vegetative biomass compared with split supply. However, N timing allowed more rapid accumulation of biomass between stem elongation and flowering, the critical window for yield determination. Crop growth rate (CGR) in this period positively correlated with grain number ($R^2 = 0.44$), and negatively with tiller number ($R^2 = 0.66$), suggesting that the large vegetative biomass reduced growth rates during the critical window, hence reduced yields. Grain yield declined with stubble in excess of moderate amounts, irrespective of stubble orientation (horizontal or vertical); similarly there was no advantage in soil conservation benefits afforded by additional stubble. The results demonstrate that yield in dryland wheat can be improved at 'critical thresholds' of stubble and through fine-tuning of crop development rates, particularly from stem elongation to a few days after flowering. In NT and stubble retention systems, N timing reduced early biomass production and increased crop growth rates between stem elongation and flowering to provide a better match between water use patterns and crop N demand.

Key words: Tillage; Stubble amount; N timing; Biomass; Crop growth rate; Dryland wheat

3.1 Introduction

Sustainable dryland cropping typically promotes no-till (NT), stubble retention and effective nitrogen (N) fertilization. However, the mechanisms operating among tillage systems, stubble amounts and N fertilization are only partially understood. Limitations arise from a poor understanding of how these management practices impact crop developmental rates to improve yield potential. This limitation is compounded by challenges in matching water use patterns to N availability and crop demand for N. Uncertainties on the optimal amount of stubble to retain, the impact that its orientation (horizontal or vertical) has, as well as post-harvest handling challenges limit the scope for stubble management to improve water and N availability.

Tillage and stubble application affect soil water and N economies, the fundamental constraints in dryland cropping systems. Together with stubble retention, NT conserves soil through reduced runoff, erosion and evaporation, and increased infiltration (Kirkegaard, 1995; Alvarez and Steinbach, 2009). Yield gains associated with increases in water availability depend on many factors, such as crop biomass, which influences water and N use patterns (Sadras and Lemaire, 2014). Events between stem elongation and flowering are more relevant for yield in wheat, when potential grain number is determined and rapid N uptake begins (Miralles and Slafer, 2007; Slafer et al., 2015). Little is documented on how crop developmental rates impact yield in NT-stubble retention systems, especially during the yield determination window.

Wheat and maize crops grown under a NT-stubble retention system showed a growth lag during the early vegetative phase compared with crops under conventionally tilled soils (Verhulst et al., 2011). However, these slow growth rates were compensated in later stages, and the crops achieved significant yield increases. The authors attributed the slow start and the subsequent compensation at late stages to poor synchronization of N availability with crop demand for N, compared with an initial flush of N in tilled soils. However, from a physiological point of view, the shift in biomass indicates changes in crop growth rate during the reproductive phase. Nitrogen deficiency will impact differently at different growth stages during crop growth (Ravier et al., 2017). Therefore, low N initially, when plant available water is high, are poorly matched but may lead to high yield if some water is conserved for later stages. Water limitations during the yield determination window reduce N recovery, potentially reducing leaf area, photosynthetic activity and grain number (Slafer et al., 2015). Studies evaluating management practices only use end-of-season yield components (Brennan et al., 2014; Singh et al., 2015), which provide little information about the physiological consequences of management practices on growth and yield formation.

Rainfall uncertainties make N fertilization a risky venture in drylands, which leads to large gaps between actual and water-limited potential yield (Sadras et al., 2016). Nonetheless, improved moisture regimes under NT-stubble systems provide opportunities for better N management, particularly with late applications (Riar and Coventry, 2013). Single N applications at sowing may assist in overcoming the difficulties of N fertilization in drylands (Sadras et al., 2016), but there is a potential trade-off in the build-up of large vegetative biomass that can deplete soil moisture before the crop enters the reproductive phase which squanders valuable soil moisture (van Herwaarden et al., 1998; Zhou et al., 2017). In addition, wheat crops require small amounts of N in the early stages, and single N applications at sowing are not an effective means to assist the conversion of biomass to yield (Hooper et al., 2015; Zhou et al., 2017), thus early sown N is predisposed to leaching losses (Alley et al., 1996). Partitioning N supply is one mechanism used to manage biomass to better match rainfall patterns and balance water use, both before and after flowering (Zhou et al., 2017). Late applications of N provide better N recovery and increased yield potential, in addition to improving grain quality (Coventry et al., 2011). Thus, the success of fine-tuning crop developmental rates under NT-stubble systems can be attributed partially to the management of N supply.

A pragmatic approach to stubble management in NT systems is used in Australia, which involves the removal of excess stubble to minimise physical impairment to seeding operations and crop establishment (Scott et al., 2013; Rochecouste and Crabtree, 2014; Flower et al., 2017). However, of concern is retention of the right amount of stubble to maximise soil conservation benefits and yield (Kirkegaard et al., 2014). Outcomes of recent research are conflicting, with some reports of yield increases as stubble amounts are increased (Yunusa et al., 1994; Scott et al., 2013) while others show a negative relationship (Flower et al., 2017). Yield gains are attributed to conservation of water and nutrients, while losses are ascribed to reduced plant numbers due to physical obstruction by stubble and diseases and pests (Scott et al., 2013); yet the minimum amount of stubble required to off-set losses and maximise benefits is not known. Yield responses to stubble depend on the type and amount of stubble. High amounts of cereal stubble have larger negative effects compared with legume or brassica materials (Flower et al., 2017), presumably due to lower C:N ratios in the latter types. However, cereal stubbles are dominant, and understanding the critical quantities of stubble will provide a theoretical basis and technical support to inform the critical amounts to retain and the post-harvest handling techniques (Kirkegaard et al., 2014). These amounts may be independent of the cropping environment and system.

In view of the identified limitations, which prevent growers from maximising yield, this study examined crop growth and yield, as affected by tillage, stubble and N timing in contrasting environments. We hypothesised that: (i) the effects of management practices on yield are mediated by changes in crop growth rate between stem elongation and flowering; (ii) yield response to tillage and stubble is modified by N supply; (iii) the critical amount of stubble to maximise dryland wheat yield is independent of cropping environment. In NT systems, an optimal amount of stubble in combination with better N timing strategies would reduce wheat yield gaps in winter-rainfall Australian environments.

3.2 Materials and methods

3.2.1 Sites

Field experiments combining tillage systems, different amounts of stubble application and N timing were conducted in 2013 through 2015 in two contrasting dryland wheat growing Mediterranean-type environments in South Australia. The sites had a history of commercial production, with rotation of cereals, canola and crop legumes under continuous NT and use of direct drill sowing equipment; stubble was typically reduced by grazing livestock. Experiments were conducted in 2013 through 2015 at Roseworthy farm of the University of Adelaide (34.52 °S, 138.68 °E, 63 m altitude) and in 2013 and 2014 at Karoonda (35.04 °S, 140·05 °E, 75 m altitude).

Roseworthy has 463 mm average annual rainfall, with 315 mm in the growing season between April and October. The site has mean maximum temperature of 22.5 °C and mean minimum temperature of 10.0 °C during this cropping period. Soil is red-brown earth and classified as sodic, supracalcic, red chromosol with a firm sandy loam surface in the A horizon (Isbell, 2002). Soil tests before sowing at 0-20 cm depth returned a pH of 6.6 in $CaCl_2$, EC of 244 µS cm^{-1}, total N of 0.07% by weight (Kjedahl method) and organic carbon of 1.41% by weight (Walkley-Black chromic acid wet oxidation method). At 20–40 cm depth, the soil had a pH of 6.7, 252 µS cm^{-1} EC, 0.05% total N by weight and 1.21% organic carbon (C) by weight.

Karoonda is located in the Murray Mallee with lower rainfall than Roseworthy. Annual rainfall at this site is 310 mm, and approximately 70% falls between April and October cropping season. Mean maximum temperature at this site is 24.0 ^{o}C whereas the mean minimum temperature is 9.0 ^{o}C. Karoonda soils are sandy with a shallow profile of approximately 60 cm on rock. At 0-20 cm depth, tests returned a pH of 6.6, 163 µS cm^{-1} EC, 0.02% by weight total N and 0.63% by weight organic carbon (C). At 20-40 cm depth the soil has a pH of 7.2, an EC of 629 µS cm^{-1}, 0.01% total N by weight and 1.07% C by weight.

3.2.2 Treatments and experiment design

At Roseworthy, two tillage systems (conventional tillage, CT, and no-till, NT), four rates of stubble (zero, low, moderate and high) and three timings of fertilizer N application were evaluated. The N timing represented normal (single sowing application), low yield (early application) and high yield (late application) based on the results of Hooper et al. (2015). The N treatments comprised, (i) single sowing application of 100 kg N ha^{-1} (N1), (ii) 100 kg N ha^{-1} split as 25% at sowing, 50% at tillering and 25% at awn emergence (N2), and (iii) 100 kg N ha^{-1} divided as 50% at tillering and 50% at awn emergence (N3). The experimental design was a split-split plot arrangement in a randomized complete block design with three replications. Tillage system was assigned to the main plots, residue amount formed the sub-plots, while the N timing made the sub-sub-plots. Sub-plots measured 12 m long and 1.2 m wide, with six rows in each plot, spaced at 0.25 m.

In Karoonda, two tillage systems (CT and NT) and four rates of stubble (zero, low, moderate and high stubble) were evaluated with a uniform supply of 100 kg N ha^{-1} at sowing. The experiment design was a split plot arrangement in a randomized complete block design with four replications. Tillage system was assigned to the main plots and stubble amounts were assigned to the sub-plots. Sub-plots were 10 m long and 1.2 m wide, with six rows spaced at 0.25 m.

3.2.3 Experiment management

In both experiments, crops of wheat (*Triticum aestivum* L.), Justica CL Plus, a variety that is well-adapted to Australian conditions were grown. Crops were sown on 29th May in 2013, 10th June in 2014 and 24th June in 2015 at Roseworthy while at Karoonda, crops were sown on 28th of May in both 2013 and 2014. In 2013, crops were sown into surface applied stubble mulch, and into standing stubble in 2014 and 2015. The surface spread mulch was applied manually at zero stubble (0 t ha^{-1}), low stubble (0.5 t ha^{-1}), medium stubble (2.5 t ha^{-1}) and high stubble (5 t ha^{-1}). Standing stubble was applied by cutting the previous crop stubble to different heights. After harvesting the heads, a plot harvester was used to cut stubble to different heights: at ground level for zero stubble, 15 cm from the ground level for low stubble, 25 cm for moderate stubble and 35 cm for high stubble. Conventional tillage plots were prepared using multiple tillage passes with a spring-tyne plough to 5 cm depth, the usual cultivation depth for loamy and sandy soils in Australia. In this treatment, stubble was thoroughly incorporated while the NT plots remained undisturbed. In both tillage systems, a six-row narrow tyne direct-drill seeder with press wheels was used for seed and basal fertilizer placement.

Wheat crops were seeded at the rate of 95 kg seed ha^{-1} and a basal fertilizer of single superphosphate was supplied with seed at the rate of 12 kg P ha^{-1}. The fertilizer N treatments were supplied from urea (46% N) and the in-crop fractions were hand broadcast at the set growth stage, prior to at least 5 mm of rainfall. Weeds were controlled with herbicide sprays of 1.5 L ha^{-1} of glyphosate and 85 mL ha^{-1} of Goal® (240 g L^{-1} oxyfluorfen, 108 g L^{-1} N-methyl pyrrdidone and 606 g L^{-1} liquid hydrocarbons) before sowing and 1.5 L ha^{-1} of glyphosate and 2.5 L ha^{-1} Boxer Gold® (800 g L^{-1} prosulfocarb and 120 g L^{-1} S-metolachlor) after sowing.

Diseases were controlled with fungicides and micro-nutrient deficiencies were checked with trace element foliar sprays.

3.2.4 Measurements

In 2013, after sowing, data loggers (UA-002-64, One Temp Pty. Ltd., MA, USA) for measuring temperature were placed on the soil surface of plots with 0, 2.5 and 5 t ha^{-1} stubble treatments at Roseworthy, while temperature was recorded under 0 and 2.5 t ha^{-1} stubble at Karoonda. The data loggers were not shaded. At 28 days after sowing (DAS), soil cores in each plot were sampled by inserting a 5 cm diameter tube to measure bulk density from 0 to 140 cm depth of the profile. Measurements of rainfall, temperature, evaporation, relative humidity and radiation were obtained from the Australian Bureau of Meteorology stations at both sites.

Soil water content (SWC) was measured with a neutron moisture meter (NMM) (Model 503, Campbell Pacific Nuclear Corp., Martinez, CA, USA), at Roseworthy only. In 2013, all N timing treatments were sampled while in 2014 and 2015 only N1 treatments were sampled. Aluminium access tubes (5 cm diameter × 150 cm length) were inserted into the middle of each plot for NMM probe to pass through. The NMM readings were calibrated using corresponding soil volumetric water content that was obtained gravimetrically at the designated depths. Measurements were taken at 20 cm intervals from 20-140 cm depth. Water content at 0-10 cm depth was estimated gravimetrically. Since each NMM reading indicated the average for a volume of soil within a 10-cm radius of the probe, the actual SWC at 10-140 cm was calculated. Water use at 0-140 cm depth was estimated as change in water content between sowing and maturity plus rainfall in the same period (French and Schultz, 1984). Water use efficiency (WUE) was computed by dividing grain yield by water use.

Phenology was monitored regularly using Zadoks scale (Zadoks et al., 1974) to establish the time of critical stages, which guided the application of the fertilizer N treatments. In three randomly selected 1 m row lengths per plot, plants were counted at 15 and 27 DAS to establish plant emergence and survival, respectively. Shoot biomass was measured from 0.25 m^2 samples at around GS16 (six leaves unfolded), GS22 (tillering), GS31 (stem elongation), GS65 (flowering) and GS94 (maturity); oven dried at 60 ^{O}C for 72 hours and weighed. Crop growth rate between GS31 and GS65 was determined and expressed in grams per unit area per day (g m^{-2} day^{-1}).

At Roseworthy, canopy interception of photosynthetically active radiation (PAR) was measured at mid-day under clear sky using a ceptometer (AccuPAR LP-80; Pullman, WA, USA) on four occasions. The ceptometer sensor was inserted below the canopy, close to the ground level at 90° to the rows. Three measurements were taken below and another above the canopy at randomly selected locations in a plot. Percentage PAR interception was expressed as the difference between mean above- and below-canopy readings. Radiation use efficiency (RUE) was calculated as the ratio of crop growth and cumulative PAR between stem elongation and flowering, and expressed in millijoules per unit area per day (MJ m^{-2}).

At maturity, tiller and head numbers were counted per 1 m row length at three random locations of each plot, and converted to tillers m^{-2}. Four random 25 cm sections of central rows were hand-harvested to measure shoot biomass and harvest index. Excluding the outer rows, the whole plot was harvested for grain using a plot harvester and expressed in t ha^{-1}. A subsample of the harvested grain was used for the determination of 1000 kernel weight and grain N content. In 2013, grain N content (%) was determined using the semi-micro Kjeldahl method (Kjeltec 8200 Auto Distillation Unit, Foss, Hillerød, Denmark) (Dai et al., 2013) after grinding the samples though a 0.5 mm sieve. In 2014 and 2015, grain protein content was determined by near infra-red spectroscopy using FOSS Infratec® 1241 grain analyser. Equivalent % N content was obtained by dividing the % protein content by 5.7 (Herridge, 2013).

3.2.5 Data analysis

Analysis of variance (ANOVA) using GenStat 18th Edition (VSN International Ltd., Hertfordshire, UK) was used to assess the effects of the experimental sources of variation. Combinations of tillage, stubble amount and timing of N application were analysed for Roseworthy across the seasons (environments). Combinations for tillage and stubble amount under a single N application at sowing were analysed across five environments, including the three seasons at Roseworthy and two seasons at Karoonda. Differences among treatment means were compared and separated using Fisher's Least Significant difference (LSD) test at $P \leq 0.05$ (Gomez and Gomez, 1984). In the presence of significant interactions, the response of main effects was investigated by partitioning the factorial combinations by the use of graphical displays to identify crossover and non-crossover interactions or both (Vargas et al., 2015). Least square regression was used to explore relationships between parameters.

Due to sizeable environment-to-environment variation for actual yields, the amounts of standing stubble retained and grain yield were estimated on a relative basis, as a percentage of the plot yield to the environmental mean. Management-driven gaps between water-limited potential yield and actual yield were estimated by comparing actual yield and water use with a boundary line representing the water-limited potential yield in south-eastern Australian environments. A boundary function showing the upper limit of wheat yield against water use was parameterised; accounting for evaporation (Sadras and Roget, 2004) and WUE of contemporary wheat varieties (Sadras and Lawson, 2013).

3.3 Results

3.3.1 Environmental conditions

Growing conditions are summarised in Table 3.1. They typify winter cropping conditions in the Mediterranean-type dryland Australian wheat belts, which are characterised by a narrow rainfall-evapotranspiration ratio at the start of the season but rainfall tapers off as the crop ages. During the winter, cropping temperatures, vapour pressure deficit and solar radiation are low in the early crop stages and rise as the crop matures. In Roseworthy, growing season rainfall was 208 mm in 2013, 162 mm in 2014 and 177 mm in 2015 while Karoonda received 183 mm in 2013 and 107 mm in 2014. Accounting for the last 20 years in Roseworthy, seasonal rainfall from April to October fell within the rank of decile 6 for 2013 and 2014 while 2015 was a decile 2 season. In Karoonda, 2013 was a decile 3 season while 2014 was a decile 2. A decile ten season falls within the top 10% of the wettest seasons while a decile 1 falls within the bottom 10%, which represents a dry season (Hayman and Alexander, 2010)

3.3.2 Soil conditions and plant establishment

In the structured loamy soils of Roseworthy, CT increased surface bulk density (BD) (0-2 cm depth) but reduced BD at shallow depths (2-10 cm) compared with NT but without differences in the medium to deep soil profile (10-140 cm depth). In the unstructured sandy soils of Karoonda, tillage did not impact BD of the whole measured soil profile. Plant establishment did not correlate with BD in both environments. However, NT improved emergence in the structured soils of Roseworthy, with no significant effects in the unstructured soils of Karoonda, but the effects of stubble and its interaction with tillage were few and inconsistent across the environments.

The application of stubble mulch at the rate of 2.5-5 t ha^{-1} led to 10-12 °C lower soil surface temperature in the daytime, but a 3-5 °C rise at night, compared with bare ground (Figure 3.1

a, b). Despite the moderation of soil surface temperature by the application of stubble, there were no noticeable relationships between temperature and the establishment of wheat crops. Tillage × stubble interactions affected plant establishment ($P = 0.002$), with increases in plant numbers under NT combined with 2.5 t ha^{-1} but plant numbers reduced with the application of 5 t ha^{-1} stubble (Figure 3.1 c). At a high stubble amount of 5 t ha^{-1}, NT improved plant establishment compared with CT ($P = 0.004$) while stubble amounts of 2.5 and 5 t ha^{-1} reduced plant numbers compared with bare ground under CT.

3.3.3 Grain yield and its components

Where factorial combinations were tested across three environments (years) at Roseworthy, the main effects of environment, tillage, stubble and N timing influenced grain yield and yield components as well as some interactive effects (Table 3.2). While grain yield varied with the cropping environment ($P < 0.001$), the interaction between environment and tillage system did not affect yield ($P = 0.121$). However, environment significantly influenced yield responses to stubble ($P = 0.004$) and N timing ($P < 0.001$). The timing of N application modified the effects of tillage ($P < 0.001$) and stubble ($P = 0.002$) on yield. In Roseworthy and Karoonda, ANOVA for the factorial combination of tillage system and stubble amount under a single N application at sowing showed effects of environment effects ($P < 0.001$), tillage ($P = 0.005$), stubble ($P = 0.005$) and tillage × stubble interaction ($P = 0.016$) on grain (Table 3.3).

Across environments in Roseworthy, grain yield ranged from 3.2 to 1.5 t ha^{-1}, with a 12% yield increase under NT compared with CT. Small but significant yield increases of 15% were measured under stubble application compared with bare ground while a 7% increase was obtained with split N supply relative to single N supply at sowing. Under single N application at sowing, NT improved yield by 7% relative to CT, while the application of stubble improved yield by 12% compared with bare ground. The interaction between environment and tillage system showed no patterns of interaction. No-till combined with the application of low and high stubble (0.5 and 5 t ha^{-1} stubble) produced higher grain yield than CT but there were no yield differences between the two tillage systems under medium amounts (2.5 t ha^{-1}) of stubble (Figure 3.2 a).

Grain yield correlated positively with grain number (Figure 3.3 b). Across the three seasons in Roseworthy, grain number differed among the environments ($P < 0.001$), between tillage systems ($P = 0.04$) and among the stubble amounts ($P = 0.001$) (Table 3.2). The timing of N application did not affect grain number ($P = 0.078$) but its interactions with tillage ($P = 0.042$) and stubble amount ($P = 0.030$) were significant. Across Roseworthy and Karoonda with the combination of tillage and stubble under a single N application at sowing, tillage ($P = 0.058$), stubble amount ($P = 0.054$) and their interaction ($P = 0.078$) did not affect grain number (Table 3.3). However, large environmental effects ($P < 0.001$) were recorded. Despite significant environment × stubble interaction ($P = 0.021$), neither linear nor quadratic responses to stubble increases were apparent.

Patterns depicting yield increases from bare ground to the application of moderate amounts of stubble, then a decline upon the application of high amounts of stubble, were evident. During the first experimental season when (non-standing) stubble mulch was applied to both sites, yields declined at stubble amounts in excess of 2.5 t ha^{-1} (Figure 3.2 a). A similar trend was measured with the retention of standing stubble (Figure 3.2 b). Yield responses to the rate of stubble application did not differ between tillage. In two of the five environments, significant quadratic responses of the rate of stubble application indicated that increases in grain number with the application of up to moderate (2.5 t ha^{-1}) stubble was followed by a decline under high amounts (5 t ha^{-1}) of stubble. Despite the effects of stubble amount × tillage interaction on grain number, linear or quadratic responses were not apparent. Kernel weight did not differ among the stubble amounts within the two tillage treatments and there were no significant responses to stubble increases measured.

Timing of N application mediated the responses of tillage and stubble amount, although there was a large environmental influence. ANOVA returned large environment × N timing effects on grain yield and its components ($P < 0.001$) except for harvest index (Table 3.2). Split application of the fertilizer N, both N2 and N3, increased grain yield and kernel weight compared with single N application at sowing, while grain number increased with the split applications in one of three environments. Timing of N supply did not influence the effects of CT on grain yield, grain number and kernel weight. However, N2 fertilization strategy increased grain yield and grain number compared with N1 and N3 under NT. Yield response to the application of high amounts of stubble were mediated by N2 timing of fertilizer application compared with N1 and N3 fertilization strategies (Figure 3.2 c, d).

Grain protein varied with cropping environment ($P<0.001$) with higher protein content in 2015 at Roseworthy (Table 3.2). Tillage and stubble amount did not affect grain protein. Fertilizer management strategy of N3 produced kernels with the least protein while N2 had increased protein content but not different from N1.

3.3.4 Crop development

Wheat dry matter accumulation was affected by tillage system, stubble amount and the timing of N supply, with few and somewhat erratic treatment interactions. Across the five environments and throughout the crop cycle, crops under NT produced more biomass than their counterparts under CT (Figure 3.3 c). Application of high amounts of stubble, of 5 t ha^{-1} stubble mulch or the full height of standing stubble, reduced plant establishment (Figure 3.1 c) and biomass yield at establishment, compared with bare ground and low amounts of stubble (Figure

3.3 d). However, the differences disappeared as the crop entered the flowering phase, but they reappeared as the crop aged, with marked low biomass yield under high stubble. Crops supplied with sowing application (N1) had a quick early start compared with split applications (N2 and N3). However, as the crop entered the flowering phase, canopies under N2 and N3 management were larger than those of N1 and the trend continued through to maturity (Figure 3.3 e).

Wheat crop growth rate (CGR) between stem elongation and flowering differed with cropping environment (Table 3.2 and 3.3). The main factor effects of tillage, stubble amount and the timing of N supply did not impact CGR during this critical period of yield determination (Table 3.2 and 3.3). Hardly any treatment interactions were measured except that of environment × tillage × N timing ($P = 0.003$) (Table3. 2), where N3 consistently reduced CGR under both tillage systems in two out of three environments.

Radiation use efficiency (RUE) between stem elongation and flowering varied with cropping environment ($P = 0.010$): wheat crops of 2014 used 0.5 MJ m^{-2} more radiation compared with crops grown in 2015 (Table 3.2). Crops grown under CT had higher RUE compared with counterparts under NT ($P = 0.042$). Environment × tillage interaction ($P = 0.028$) impacted RUE, with a slight increase under NT in 2015 (Table 3.2).

Increases in CGR improved grain number, confirming the consequences of crop development on yield (Figure 3.3 f). A linear relationship was established between CGR and RUE (Figure 3.3 g) and between grain number and RUE (R2 = 0.40; $P < 0.0001$). Nonetheless, neither the rate of stubble application nor the timing of the application of fertilizer N showed a relationship with changes in CGR, RUE or grain number. Crop growth rate negatively correlated with tiller number (Figure 3.3 h).

Despite the negative relationship between CGR and tiller numbers, neither tiller nor head numbers were affected by tillage, stubble amount nor their interactions, but differences in tiller and head numbers were affected by environments (Table 3.1 and 3.2). Wheat crops had increased tiller numbers in the wetter seasons compared with drier seasons. Split applications of fertilizer N, in N2 and N3, reduced tiller numbers by 30 stems m^{-2} compared with sowing application (N1), but without differences in head numbers.

3.3.5 Water storage, use and water-limited yield gaps

Across environments at Roseworthy, there were significant effects of environment and stubble on water storage, water use and WUE, while tillage had effects on water storage and water use but not WUE. The timing of N supply affected water use and WUE. Treatment interactions were measured across environments for tillage, stubble and N timing (Table 3.2).

In the 0-140 cm soil profile, NT conserved 7 mm of extra water compared with CT, while 30 mm were conserved with the application of stubble compared with bare ground. However, there were no significant differences in water storage under moderate (2.5 t ha^{-1}) and high (5 t ha^{-1}) amounts of stubble (Figure 3.4 a). Water use and WUE increased from bare ground to moderate stubble, but high amounts of stubble reduced WUE by 0.5 kg ha^{-1} mm^{-1} compared with the application of moderate amount (Figure 3.4 b, c). Interestingly, NT improved water use under the application high amounts of stubble.

Despite its effect on water use and WUE, the timing of N supply did not moderate tillage and stubble effects on water use. Crops supplied with sowing application (N1) extracted an extra 20 mm of water compared with crops supplied with split N applications. However, the increased water use did not lead to higher WUE compared with 1 kg ha^{-1} mm^{-1} increase with split N supply.

Relationships between soil water storage at sowing with plant establishment, tiller numbers, biomass and yield were not apparent. However, increases in water storage at sowing increased WUE (Figure 3.4 d) and grain yield (Figure 3.4 e). Water use and yield relationships were not evident but enhanced water use increased wheat harvest index (Figure 3.4 f).

Yield gap analysis established large yield gaps between water-limited potential yield and actual yield (Figure 3.5 a). Both tillage systems had yield gaps of -3.8 t ha^{-1} (Figure 3.5 b) while the application of moderate stubble reduced the yield gap by 400 kg ha^{-1} compared with bare ground or the retention of high amounts of stubble (Figure 3.5 c). Relatively small yield gaps were measured under the split application of fertilizer N, where N2 reduced the yield gap by 600 kg ha^{-1} compared with sowing application of N (Figure 3.5 d).

3.4 Discussion

In this study, the consequences of crop development on grain yield were confirmed by the simultaneous increases in CGR and grain number. However, CGR was negatively correlated with tiller numbers, a trade-off that suggests that large vegetative biomass was detrimental to yield. N-driven mediation of crop responses to tillage and stubble application were measured, whereby split N applications altered crop developmental rates and improved yield compared with single N application at sowing. A tendency for yield to decline with the application of high amounts of stubble, whether mulch or standing stubble, was measured, at which water conservation benefits did not increase in comparison with a ‘critical threshold’ of moderate stubble loads. Grain yield and its components in the present study were commensurate with expectations from south-eastern Australian dryland environments, where yield is principally driven by seasonal rainfall (Sadras et al., 2016; Anderson et al., 2017). Although the effects of tillage, stubble and N timing, and their interactions, were somewhat small, large environmental effects were measured. Crop growth rate between stem elongation and flowering was the prime driver of RUE and grain number.

3.4.1 Crop development rates and yield

In wheat, the critical developmental phase for yield determination falls between stem elongation and flowering, when grain number is determined (Slafer et al., 1996; Slafer et al., 2015). The present study established positive relationships between CGR and RUE; increases in these factors resulted in improved grain number. Increases in grain number with increasing CGR supports the notion that CGR between stem elongation and flowering determines yield (Miralles and Slafer, 2007; Slafer et al., 2015). Tiller number, the prime driver of CGR in the present study, was markedly reduced under split N supply compared with single application at sowing.

Rainfall and management practices, especially the timing of N supply, influenced crop development through the regulation of tiller production. Growing conditions were favourable up to stem elongation in all years. Thereafter, flowering and grain filling coincided with water deficit, rising temperatures and vapour pressure deficit (Table 3.1), which reduced leaf area and photosynthetic capacity. These post-flowering yield-reducing factors are exacerbated in crops with large vegetative biomass (van Herwaarden et al., 1998; Kitonyo et al., 2017). In the present study, large vegetative biomass with many tiller numbers significantly reduced CGR during the critical period for yield determination, perhaps due to early growth and water use leading to premature senescence under water stress (van Herwaarden et al., 1998; Zhou et al., 2017). In contrast, crops with fewer tillers achieved higher growth rates, particularly under the N2 regime where crops received N fractions at sowing, tillering and awn emergence. The positive correlation between CGR and RUE could be attributed to increased leaf expansion during stem elongation (Alley et al., 1996). In addition, rapid growth rates during the yield determination window increase N uptake, hence improved yield and quality (Alley et al., 1996; Coventry et al., 2011).

In response to environmental cues, tiller number is the most adaptive yield component in wheat (Sadras and Slafer, 2012) and better management practices improve spike fertility and grain number (Elhani et al., 2007; Mitchell et al., 2013). Our results support the working hypothesis that the effect of management practices on yield are mediated by changes in CGR between stem elongation and flowering. Canopy size at the vegetative stage impacted CGR at this critical window for yield determination. This has practical implications in canopy management and the choice of varieties. Thus, management practices or varieties with restricted tillering, rather than those that promote tiller numbers would complement NT-stubble and better N supply strategies to improve yield in dryland systems (Elhani et al., 2007). Low tiller numbers reduce early season water use, thus allocating more water to the reproductive window, which promotes the development of larger, fertile spikes for increased grain number (Mitchell et al., 2012; Mitchell et al., 2013).

3.4.2 Nitrogen mediates tillage and stubble responses

Yield under NT, unlike under CT, was mediated by the N fertilization strategy, whereby crops supplied with split N application (N2) produced higher grain number and grain yield compared with counterparts under N1 and N3 supply strategies. Under moderate and high stubble loads, N2 facilitated yield increases compared with N1 and N3 application strategies. The yield responses under NT are partly attributed to increased biomass under this tillage system compared with CT, throughout the crop cycle (Figure 3.3 a). On the other hand, modification of canopy size by the split supply of N moderated water use, potentially availing more water to the reproductive and maturation phases, hence increasing yield. This is demonstrated by the large initial biomass with a single N application at sowing, compared with smaller canopies under split applications. The large vegetative biomass used more water but achieved the least yield, which suggests possible premature senescence (van Herwaarden et al., 1998; Kitonyo et al. 2017). Split supply of N by targeting the yield-determining window modified canopy development and water use patterns and hence improved yield (Hooper et al., 2015; Zhou et al., 2017).

In addition to canopy alteration and water use mechanisms demonstrated in the present study, split supply of N modifies both the soil and plant N economy. Decomposition of stubble impacts the flux of N (mineralisation-immobilisation turnover), where immobilisation reduces the immediate availability of mineral N to crops. To meet both the requirements of the growing crop and hasten microbial decomposition of stubble, fertilizer N is required (Newton, 2001; Moran et al., 2005; Perakis et al., 2012). However, to match the availability of mineral N and crop demand for N, the timing of the application of fertilizer is an important management strategy (Riar and Coventry, 2013). Results of the present study support the working hypothesis that yield response to tillage and stubble depends on fertilizer N. Further, splitting applications at sowing, tillering and awn emergence (N2) produced higher yield, even under high amounts of stubble, compared with one application at sowing (N1) and in applications that omitted N at sowing (N3). In this regard, the N2 split application strategy modified the soil-plant system to maintain a critical N uptake to allow the minimum N uptake necessary to achieve maximum crop biomass (Lemaire et al., 2007; Sadras and Lemaire, 2014), irrespective of stubble amount. This led to a more efficient conversion of biomass to yield.

The present study supports prior work on the significance of strategic N supply for dryland wheat (Hooper et al., 2015; Zhou et al., 2017), and importantly emphasises better N management strategies to fine-tune crop development in NT-stubble systems, to improve water and N economies. Essentially, yield is a function of rainfall in drylands (Sadras et al., 2016) but better N supply will shift water use to critical phenostages, to maximise growth and improve yield (Monjardino et al., 2013; Hooper et al., 2015). As discussed in section 3.4.1, N timing strategies that reduced biomass production during the initial growth stages and quickly compensated for biomass yield during the later stages by increasing crop growth rate between stem elongation and flowering increased grain yield. In addition, this fertilization strategy conserves water and improves N recovery by better matching N availability and crop demand for N in NT-stubble retention systems (Newton, 2001; Sommer et al., 2014).

3.4.3 Stubble amount and its effect on yield

Irrespective of the cropping environment and the orientation of stubble, an apparent optimal amount of stubble was measured, where less or more stubble resulted in yield decline. With the application of stubble mulch, grain yield increased from bare ground up to the application of 2.5 t ha^{-1} stubble, and declined when 5 t ha^{-1} stubble was applied. A similar trend was measured for standing stubble, whereby higher yield was obtained when half-height of the previous crop stubble was retained but yield declined when the full-height of the stubble was retained. These results suggest that the yield of dryland wheat is maximised at an optimal amount of stubble. In these environments, cereal stubbles are the predominant soil cover material, with proportionally less stubbles from rotational crop legumes and brassicas. In low rainfall south-western Australia, reduction of stubble loads to approximately 3 t ha^{-1} also increased wheat yield (Flower et al., 2017) while the orientation of stubble does not affect soil conservation benefits (Sadras et al., 2012c).

Mechanisms related to the response of wheat yield to stubble amount in the present study are not known (Figure 3.2 a, b). Treatment interactions, which could have partially explained the mechanisms, were few and inconsistent. However, the similarities in yield response to either mulch or standing stubble signify a ‘critical threshold’, where adequate groundcover is achieved, soil conserved and yield maximised, despite mechanisms not being understood. Clearly, the gain in 30 mm of stored water under stubble compared with bare ground contributed to higher yield than that of bare ground. This is reinforced by the improvement in WUE with increased SWC at sowing when stubble was applied (Figure 3.4 a). Lack of differences in water storage between moderate and high (2.5 and 5 t ha^{-1}) stubble loads annuls the likelihood that water storage was the only driver for the yield response. Indeed, for similar environments, water conservation benefits with the application of stubble were achieved when rainfall ranged between 65-250 mm, but the benefits declined when rainfall exceeded 250 mm, irrespective of stubble cover (Monzon et al., 2006).

The yield decline with the application of high stubble loads in the present study is due to other factors, including reduced plant establishment vigour. Reduced plant establishment was measured under high stubble loads (Figure 3.2 c), and the effects were independent of both environmental and edaphic differences (Table 3.2). However, even with a lower plant density, crops under 5 t ha^{-1} did not compensate for the differences in plant number, perhaps via increased tiller numbers, an outcome that suggests other factors constrained growth in this treatment. Although increased stubble may have contributed to a larger disease burden (Scott et al., 2013), the crops were protected with chemical sprays, and colonization with stubble-borne fungal diseases was not evident. Possible causes of reduced vigour could be physical obstruction of crops by stubble (Yunusa et al., 1994), stubble-borne phyto-toxic chemicals (Weston, 1996) or N immobilisation-related factors. Top dressing N applications were made prior to a substantial rainfall event, but this study does not rule out the possibility that large amounts of stubble intercepted broadcasted urea granules, leading to losses through immobilisation and volatilisation (Grahmann et al., 2014).

Advantages and disadvantages of stubble retention are multiple, however, the relationship between stubble amount and yield described in the present study has practical implications for the management of stubble. Under the study conditions, header cutting height of up to 25 cm of the previous crop stubble could be adequate for soil conservation and yield improvement. In addition to the ease of application, cutting stubble to this height, as opposed to spreading mulch, achieves uniformity of application, for improved plant establishment. In these environments, contemporary wheat varieties yield approximately 2.5 t ha^{-1} (Anderson et al., 2017; Sadras et al., 2016), and assuming harvest indices of 0.4-0.5, stubble production would less likely exceed 5 t ha^{-1}. Consequently, chances to exceed the “critical threshold” of moderate amounts stubble could be minimal. However, excess stubble could be harvested for livestock feeding or even for biofuel. In addition to this, in many traditional systems, stubbles are grazed, and therefore trampled, to provide for animal production during low feed availability (Allan et al., 2016). We did not quantify stubble breakdown rates, but it is estimated that more than half of the previous material is decomposed before the application of new stubble (Scott et al., 2013). Additionally, the carry-over stubble has minimal nutrient legacy effects in these environments due to dry summer conditions (Nguyen et al., 2016). To maximise the efficiency of sowing operations and to limit the potential for root disease carry-over, inter-sowing into standing stubble is preferred.

3.4.4 Cropping environment dominates management practices in drylands

In the backdrop of small treatment effects and large environmental influences, results of the present study affirm that environmental conditions, particularly rainfall, drive dryland farming systems (Adcock et al. unpublished). A wheat crop in south-eastern Australian environments is expected to use about 475 mm water to maximise yield (French and Schultz, 1984). In these environments, our treatments achieved less than 75% of the benchmarked water use and WUEs were far below the benchmarked efficiency of 24 kg ha^{-1} mm^{-1} for modern wheat varieties in these environments (Sadras and Lawson, 2013). In the present study, the water conservation benefits of NT and stubble appear to be of less value in closing yield gaps, suggesting that yield was dependent on in-crop rainfall and was less reliant on stored moisture. Despite moderating yield responses to NT and stubble, split application of fertilizer did not produce marked yield increases, but rather provided the potential for managing risk, by modulating crop biomass to improve water and N economies.

3.5 Conclusion

Results of this study suggest that split supply of N coupled with moderate amounts of stubble retention could moderate crop growth rates in dryland NT-wheat systems, leading to higher yield. Higher CGR between stem elongation and flowering increased radiation use efficiency and grain number. CGR during this critical window for yield determination was regulated by the size of vegetative biomass, whereby crops with lean initial biomass achieved higher CGR. Split N supply mediated crop responses to tillage and stubble by altering biomass production before flowering, compared with a single N supply at sowing. The yield of dryland wheat and water conservation benefits were maximised at a ‘critical threshold’ of moderate stubble (2.5 t ha^{-1}), irrespective of its orientation.

Table 3.1. Growing conditions for wheat crops in 2013, 2014 and 2015 at Roseworthy and Karoonda, South Australia. Environment is the experimental site and season, and conditions are shown for the entire cropping season and in three phenostages, including the period between sowing to stem elongation, stem elongation to flowering and flowering to maturity. ETo is the reference evapotranspiration, Tmax is the average maximum temperature, Tmin is the average minimum temperature, VPD is the vapour pressure deficit estimated at the time of daily maximum temperature.

Environment and phenostages	Grain yield (t ha-1)	Rainfall (mm)	ETo (mm)	Rain:ETo ratio	Tmax (oC)	Tmin (oC)	VPD (kPa)	Radiation (MJ m-2day-1)
Sowing to maturity								
Roseworthy								
2013	3.27	208	667	0.31	20.3	7.7	0.80	15.1
2014	2.17	162	717	0.23	21.1	6.8	0.93	15.9
2015	1.52	177	678	0.26	20.9	7.4	0.93	16.0
Karoonda								
2013	2.29	183	489	0.37	19.8	6.9	0.62	13.7
2014	2.06	127	523	0.20	19.6	5.9	0.63	14.2
Sowing to stem elongation								
Roseworthy								
2013	3.27	156	159	0.98	16.0	6.8	0.38	9.1
2014	2.17	120	173	0.69	15.9	5.2	0.42	9.9
2015	1.52	125	158	0.79	15.4	5.9	0.41	9.0
Karoonda								
2013	2.29	136	146	0.93	16.5	5.6	0.37	9.5
2014	2.06	75	163	0.48	16.0	4.8	0.38	9.7
Stem elongation to flowering								
Roseworthy								
2013	3.27	35	110	0.32	21.6	9.4	0.72	15.8
2014	2.17	15	158	0.10	22.8	6.6	0.96	18.6
2015	1.52	28	91	0.31	18.1	4.9	0.55	14.2
Karoonda								
2013	2.29	31	112	0.28	22.5	8.4	0.71	15.2
2014	2.06	23	105	0.15	21.1	5.1	0.65	17.0
Flowering to maturity								
Roseworthy								
2013	3.27	17	397	0.04	25.7	8.2	1.42	23.2
2014	2.17	27	386	0.07	28.5	9.4	1.73	23.7
2015	1.52	24	429	0.06	27.7	10.2	1.60	23.1
Karoonda								
2013	2.29	15	231	0.07	24.8	8.4	1.06	21.4
2014	2.06	29	256	0.05	26.7	8.8	1.17	22.2

Table 3.2. Analysis of variance for dryland wheat grown under conventional tillage and no-till, different amounts of stubble application and different timing of fertilizer N application in field experiments conducted in 2013 through 2015 at Roseworthy, South Australia. Environments are the three experiment seasons in Roseworthy, including 2013, 2014 and 2015. Data were analysed across environments and treatments. Significance levels in parentheses are for 2013 when water use was measured for N treatments. *significant at 0.05%; **significant at 0.01%; ***significant at 0.001% probability level; ns: not significant at 0.05% probability level; na: not applicable, where data was collected for only one environment.

Source of variation	Grain yield (t ha^{-1})	Grain number (m^{-2})	1000 Kernel weight (g)	Crop growth rate (g DM ha^{-1} day^{-1})	Radiation use efficiency (MJ m^{-2})	Biomass (t ha^{-1})	Harvest index (unit less)	Protein	Plant establishment (m^{-2})	Tillers (m^{-2})	Heads (m^{-2})	Water storage (mm)	Water use (mm)	Water use efficiency (kg ha^{-1} mm^{-1})
Environment (Env)	***	***	***	*	**	***	***	***	ns	*	***	***	***	**
Tillage (Til)	***	*	***	ns	*	ns	ns	ns	**	ns	ns	*	*	ns
Stubble (Stub)	***	***	***	ns	ns	*	*	ns	ns	ns	ns	***	***	***
N-timing (N-tim)	***	ns	ns	ns	ns	*	*	**	ns	**	ns	na	(***)	(***)
Environment × Tillage	ns	**	***	ns	*	ns	ns	*	ns	ns	***	***	*	***
Environment × Stubble	**	ns	***	ns	ns	*	ns	ns	ns	ns	ns	***	**	***
Environment × N-timing	***	***	***	ns	ns	ns	ns	***	ns	*	ns	na	na	na
Tillage × Stubble	ns	ns	**	ns	ns	ns	ns	ns	ns	ns	ns	ns	***	ns
Tillage × N-timing	***	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	na	(ns)	(ns)
Stub × N-timing	**	*	ns	ns	ns	*	ns	ns	ns	ns	ns	na	(ns)	(ns)
Env × Til × Stub	ns	*	***	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	ns
Env × Til × N-tim	***	**	ns	**	ns	ns	ns	ns	ns	ns	ns	na	na	na
Env × Stub × N-tim	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	na	na	na
Til × Stub × N-tim	ns	ns	ns	ns	ns	*	ns	***	*	ns	ns	na	(*)	(ns)
Env × Til × Stub × N-tim	ns	ns	ns	ns	ns	*	ns	*	ns	ns	ns	na	na	na

Crop growth rate and radiation use efficiency were computed between stem elongation and flowering. Water storage is soil water content at sowing. Water use and use efficiency was computed for the whole season

Table 3.3 Analysis of variance for dryland wheat grown under conventional tillage and no-till and different amounts of stubble application under a one-off basal N supply in field experiments conducted in 2013 through 2015 at Roseworthy and Karoonda, South Australia. Environments are the experiment seasons, including three seasons in Roseworthy (2013, 2014 and 2015) and two seasons in Karoonda (2014 and 2015). Data were analysed across the five environments and treatments.*significant at 0.05%; **significant at 0.01%; ***significant at 0.001% probability level; ns: not significant at 0.05% probability level.

Source of variation	Grain yield (t ha^{-1})	Grain number (m^{-2})	1000 Kernel weight (g)	Crop growth rate (g DM ha^{-1} day^{-1})	Biomass (t ha^{-1})	Harvest index (unit less)	Protein	Plant establishment (m^{-2})	Tillers (m^{-2})	Heads (m^{-2})
Environment	***	***	***	***	***	***	***	***	*	***
Tillage	**	ns	**	ns	ns	ns	ns	**	ns	ns
Stubble	**	ns	***	ns	ns	ns	ns	***	ns	ns
Environment × Tillage	**	**	**	ns	ns	*	ns	***	ns	ns
Environment × Stubble	ns	ns	***	ns	ns	ns	ns	*	ns	ns
Tillage × Stubble	*	ns	ns	ns	ns	*	*	**	ns	ns
Environment × Tillage × Stubble	ns	ns	**	ns	ns	ns	*	ns	ns	ns

Crop growth rate and radiation use efficiency were computed between stem elongation and flowering. Water storage is soil water content at sowing. Water use and use efficiency was computed for the whole season

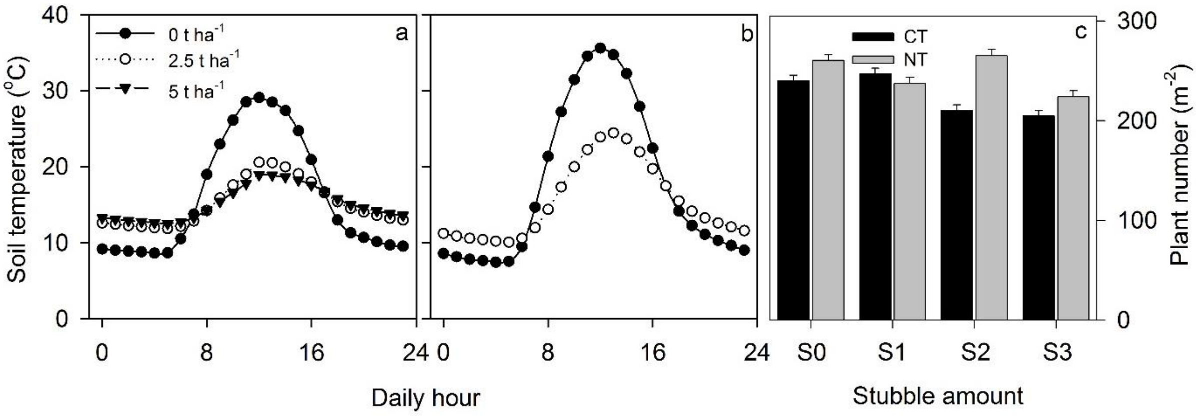

Figure 3.1 Diurnal soil surface temperature under different amounts of stubble in 2013 at Roseworthy (a) and Karoonda (b). The interaction between tillage (conventional tillage and no-tillage, CT and NT) and stubble amount (S0: zero stubble; S1: low stubble; S2: medium stubble; S3: high stubble) on plant establishment (c). Plant establishment data was analysed across the five environments, including three for Roseworthy (2013, 2014 and 2015) and two for Karoonda (2013 and 2015). Error bars are 1 standard error of mean.

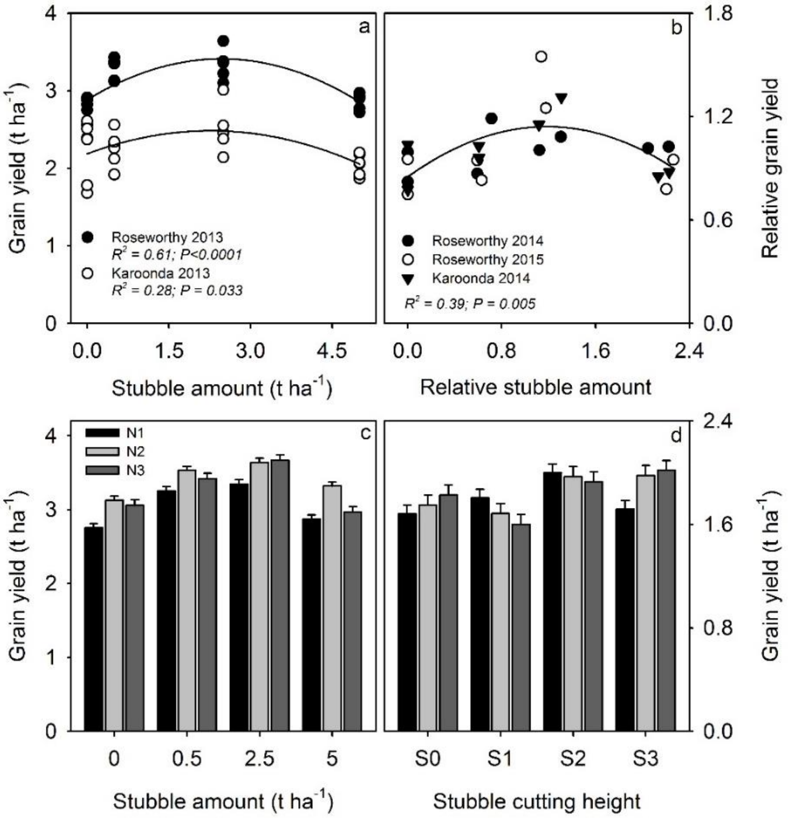

Figure 3.2 Grain yield response to stubble and stubble dependence on fertilizer N for dryland wheat grown under contrasting tillage systems, different amounts of stubble application and different timing of fertilizer N application in field experiments conducted in 2013 through 2015 at Roseworthy and Karoonda, South Australia. Yield response to stubble mulch at Roseworthy and Karoonda in 2013 (a). Yield response to different cutting heights for standing stubble at Roseworthy in 2014 and 2015, and at Karoonda in 2014 (b). In ‘a’ and ‘b’, data are pooled across tillage, stubble and N timing, while the lines are polynomial regression. The relative amount of standing stubble retained and grain yield were estimated on a relative basis, as a percentage of the plot yield to the environmental mean. Lines are least square linear regressions. Grain yield under stubble mulch with different N timing at Roseworthy in 2013 (c). Grain yield under standing stubble with different N timing at Roseworthy across 2014 and 2015 (d). In ‘c’ and ‘d’, data are pooled across N timing. N1: 100 kg N ha^{-1} sowing application; N2: 100 kg N ha^{-1} split as 25% at sowing, 50% at tillering and 25% at awn emergence; N3: 100 kg N ha^{-1} split as 50% at tillering and 50% at awn emergence. Bars are 1 standard error of mean.

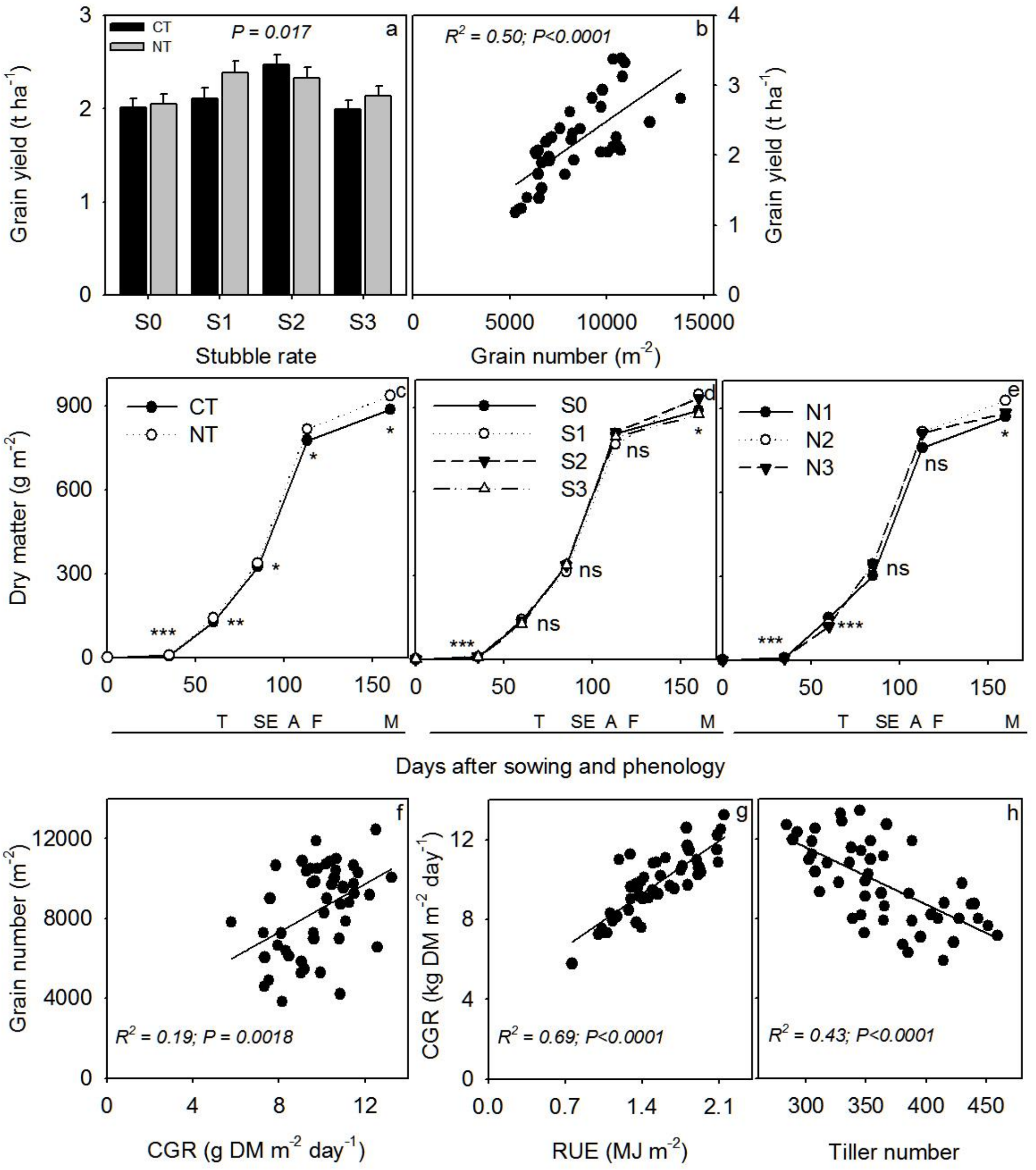

Figure 3.3 Grain yield and yield drivers for dryland wheat grown under conventional (CT) and no-till (NT), stubble amount (S0 for zero stubble, S1 for low stubble, S2 for medium stubble and S3 for high stubble) and different timing of fertilizer N application (N1: 100 kg N ha^{-1} sowing application; N2: 100 kg N ha^{-1} split as 25% at sowing, 50% at tillering and 25% at awn emergence; N3: 100 kg N ha^{-1} split as50% at tillering and 50% at awn emergence) in field experiments conducted in 2013, 2014 and 2015 at Roseworthy and in 2013 and 2014 at Karoonda, South Australia. Grain yield across the five environments, including three seasons at Roseworthy and two seasons for Karoonda (a). Error bars are 1 standard error of mean. Relationship between grain number and grain yield (b). Data was pooled across tillage, stubble amount and N timing across the five environments. Crop development curves under different treatments (c-e). Letters and arrows indicate phenostages, T: tillering; SE: stem elongation; A: awn emergence and F: flowering. Relationship between crop growth rate (CGR) between stem elongation and flowering and grain number (f), radiation use efficiency (RUE) (g), tiller number (e). In ‘f-h’, data is pooled across treatments in the five environments while lines are least square linear regressions.

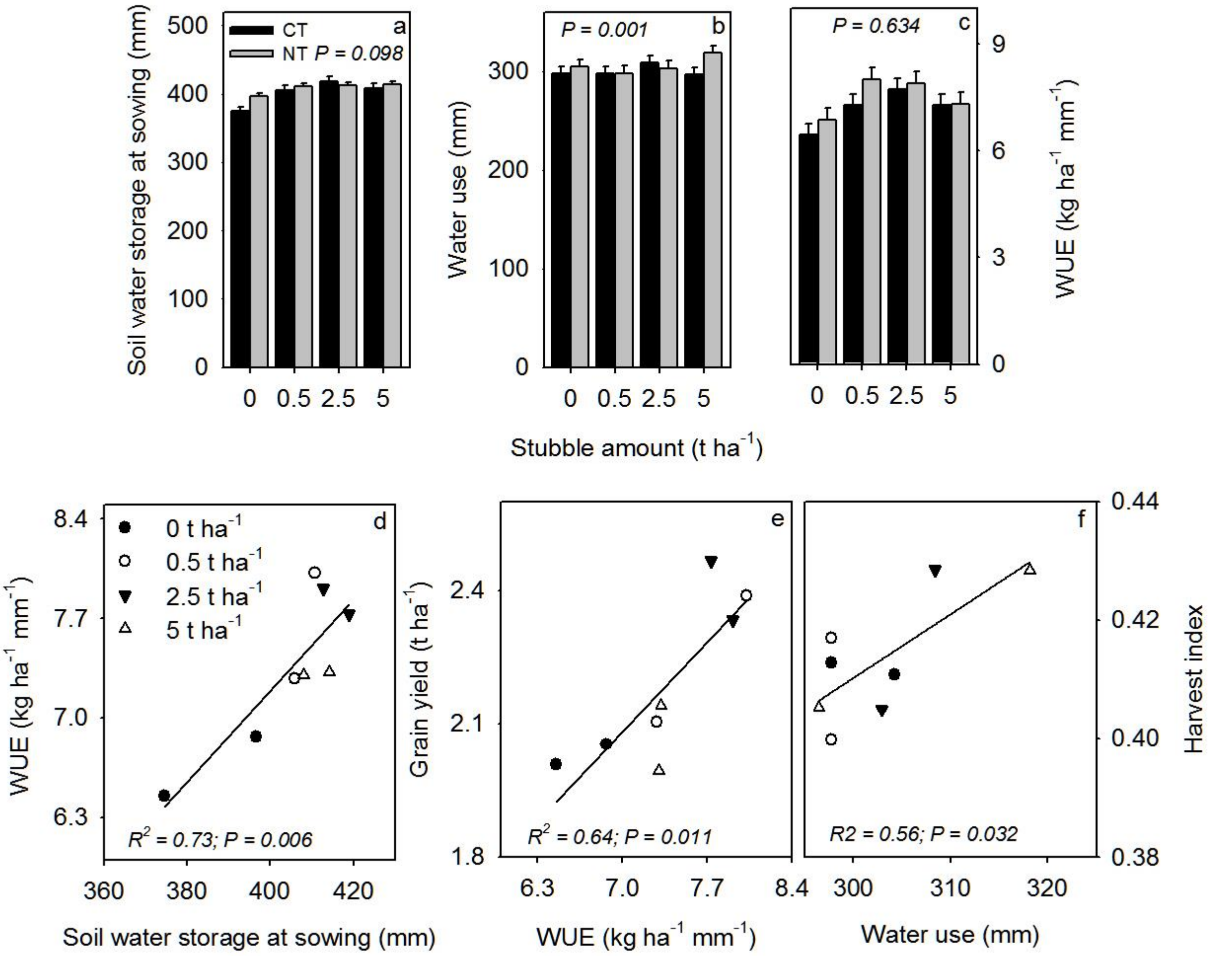

Figure 3.4 Soil water storage and water use by dryland wheat grown under conventional tillage (CT) and no-till (NT) and different amounts of stubble in field experiments conducted in 2013, 2014 and through 2015 at Roseworthy, South Australia. S0 for zero stubble, S1 for low stubble, S2 for medium stubble and S3 for high stubble (a-c). Stubble effects on soil water content at sowing, water use and water use efficiency (WUE). Data was pooled across the three environments for the factorial combination of tillage and stubble under one-off basal N supply. Error bars are 1 standard error of the mean. Relationship between WUE and soil water storage at sowing (d). Relationship between grain yield and WUE (e). Relationship between harvest index and water use. Lines are least square linear regressions (f). Data in ‘d-f’ are pooled for stubble amount across environments.

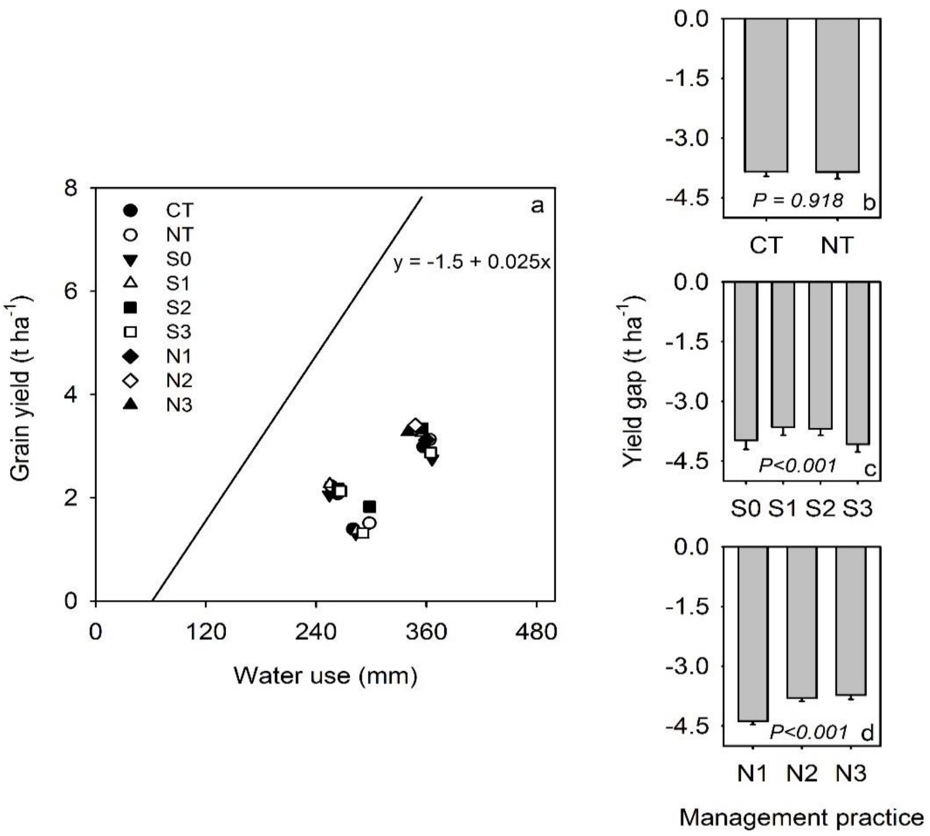

Figure 3.5 Management-driven gap between water-limited potential yield and actual yield of dryland wheat under conventional tillage (CT) and no-till (NT), different amounts of stubble (S0: zero stubble; S1: low stubble; S2: medium stubble; S3: high stubble) and different N timing (N1: 100 kg N ha^{-1} sowing application; N2: 100 kg N ha^{-1} split as 25% at sowing, 50% at tillering and 25% at awn emergence; N3: 100 kg N ha^{-1} split as 50% at tillering and 50% at awn emergence) in 2013 through 2015 at Roseworthy, South Australia. Yield and water use compared with a boundary line representing the water limited potential for yield of modern varieties in south-eastern Australian environments (a). Parameters of the line are x-intercept 60 mm, assuming 60 mm of water is lost to evaporation (Sadras and Roget, 2004) and slope 25 kg ha^{-1} mm^{-1} accounting for the potential of modern varieties in the dryland environments of south-eastern Australia (Sadras and Lawson, 2013). Average yield gap across environments for tillage systems (b) stubble amounts (c). Yield gap for the timing of the application of fertilizer N in experiment conducted in 2013 (d). In ‘a’, the clusters are seasons while in ‘b-d’ the error bars are I standard error of mean.

Statement of Authorship

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Principal Author	Onesmus M. Kitonyo		
Contribution to the Paper	Identification of research gap, field experimentation, data collection, data analysis, interpretation of results, writing of manuscript		
Overall percentage (%)	85%		
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	2/3/2018

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.

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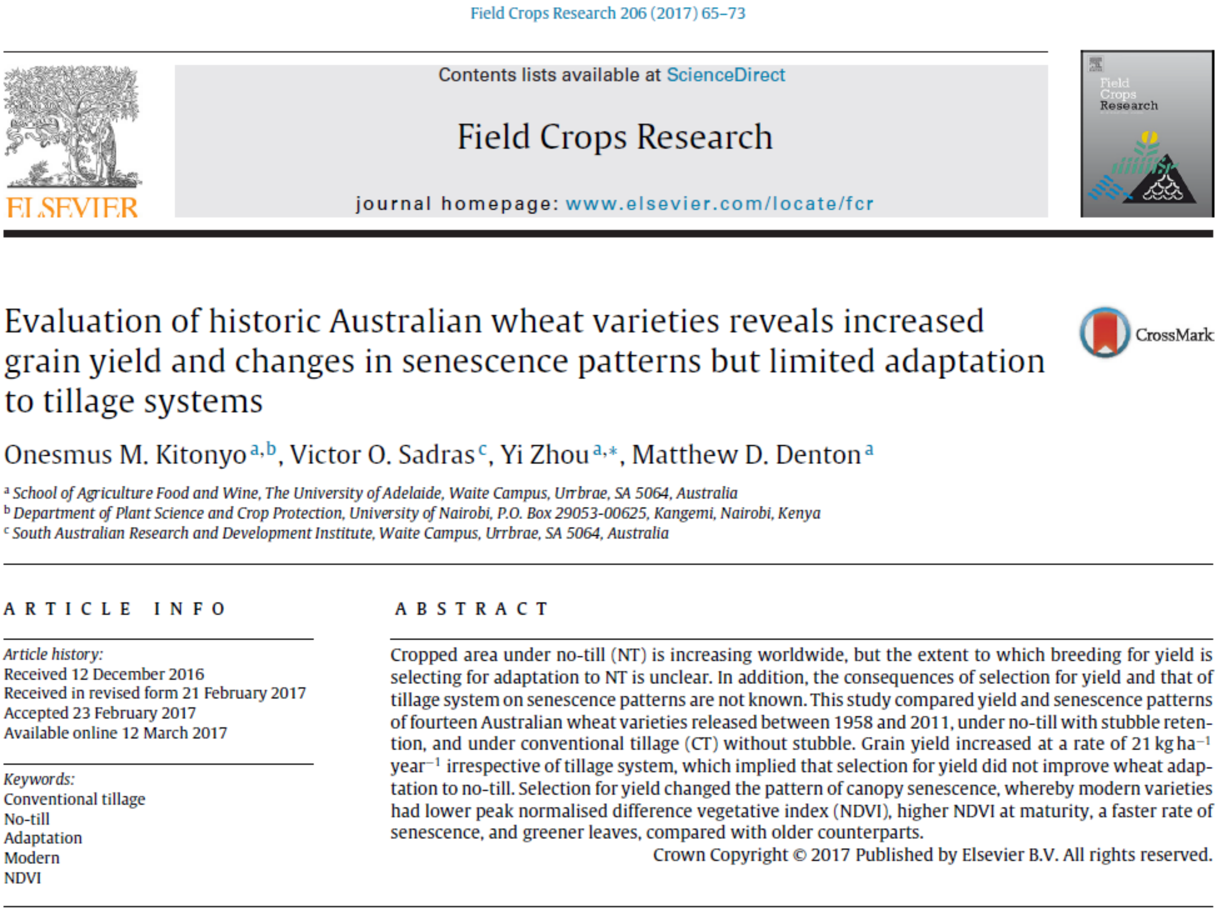
Signature		Date	2/3/2018

Chapter 4 Evaluation of historic Australian wheat varieties reveals increased grain yield and changes in senescence patterns but limited adaptation to tillage systems



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Evaluation of historic Australian wheat varieties reveals increased grain yield and changes in senescence patterns but limited adaptation to tillage systems

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ABSTRACT

Cropped area under no-till (NT) is increasing worldwide, but the extent to which breeding for yield is selecting for adaptation to NT is unclear. In addition, the consequences of selection for yield and that of tillage system on senescence patterns are not known. This study compared yield and senescence patterns of fourteen Australian wheat varieties released between 1958 and 2011, under no-till with stubble retention, and under conventional tillage (CT) without stubble. Grain yield increased at a rate of 21 kg ha^{-1} year^{-1} irrespective of tillage system, which implied that selection for yield did not improve wheat adaptation to no-till. Selection for yield changed the pattern of canopy senescence, whereby modern varieties had lower peak normalised difference vegetative index (NDVI), higher NDVI at maturity, a faster rate of senescence, and greener leaves, compared with older counterparts.

4.1 Introduction

Advances in Australian wheat (*Triticum aestivum* L.) breeding and agronomy have steadily increased grain yield (Fischer, 2009; Richards et al., 2014). Between the 1900s and 2000s, yield increased at the rate of 9 kg ha^{-1} year^{-1} in the driest years and 13 kg ha^{-1} year^{-1} in the most favourable years (Richards et al., 2014). Varieties adapted to winter rainfall environments, and released between 1958 to 2007, showed yield improvement in the range of 18 - 25 kg ha^{-1} year^{-1} (Sadras and Lawson, 2011; Sadras and Lawson, 2013). These rates are commensurate with expectations from low-yielding environments (Sadras et al., 2016a).

The cropped area under no-till (NT) and stubble retention have increased more recently (Kirkegaard et al., 2014). The main drivers of the adoption of NT are soil conservation and reduced costs (Llewellyn et al., 2012; Scott et al., 2013). Despite the conservation benefits, NT can reduce yield compared with conventional tillage (CT) (Pittelkow et al., 2015b). Varieties that are specifically adapted to NT may help to improve yield (Trethowan et al., 2005; Joshi et al., 2007). However, varieties specifically bred for NT are scarce and the extent to which breeding is selecting for adaptation to NT is unclear. Often, the lack of significant variety × tillage system interaction limits the scope to breed for adaptation to NT (Trethowan et al., 2009) but the possibility to breed and adapt wheat to NT exists (Trethowan et al., 2012).

Delayed onset of senescence (stay-green) is a stress adaptation mechanism (Jordan et al., 2012) but it can limit yield if induced prematurely (Gregersen et al., 2013). Some traits that contribute to a stay-green phenotype include, (i) traits that conserve water and reduce stress during grain filling, such as early maturity and reduced canopy size, and (ii) traits that enhance water uptake, such as a deep rooting system (Sadras and Richards, 2014). Successes in stay-green have been observed in sorghum breeding, where this phenotype has been deployed to improve yield and reduce lodging (Jordan et al., 2012). While breeding for yield has altered the nitrogen economy of wheat in diverse environments (Sadras et al., 2016a), its effects on senescence patterns are unknown.

A combination of the traits that contribute to stay-green and adaptation to NT may shift water availability from pre- to post-flowering phase. In that case, delayed senescence would extend the duration of the photosynthetic apparatus to improve grain yield (Wu et al., 2012; Gregersen et al., 2013; Christopher et al., 2016). However, yield improvement from extended maturation may trade-off for reduced grain N concentration (Richards, 2000). To minimise this compromise, a fast rate of senescence is desired to promote the efficiency of nutrient translocation to the grain (Wu et al., 2012; Xie et al., 2016). On the other hand, accelerated senescence shortens the duration of grain filling which can lead to reduced kernel weight if there is not an enhanced remobilisation of resources gained from the longer period of photosynthesis (Brevis et al., 2010). Sink strength, both grain number and size, and N status, influence onset and progression of senescence (Borrell and Hammer, 2000; Borrell et al., 2001; Martre et al., 2006; Bogard et al., 2011). No-till and stubble retention can alter the dynamics of N in the soil and plant (Berry et al., 2002), but the possible consequences on senescence patterns are not known.

The present study examines some historic Australian wheat varieties to: (i) identify time-trends in variety adaptation to conventional tillage and no-till, and (ii) investigate the effects of selection for yield, and of tillage systems, on senescence dynamics. We hypothesised that selection for yield improved the adaptation of Australian wheat to no-till.

4.2 Materials and methods

4.2.1 Site

The experiment was conducted at Roseworthy (34^{o}53'S, 138^{o}724'E), which has a Mediterranean-type climate and is 63 meters above sea level. The site has 463 mm annual rainfall (315 mm during the growing season between April and October) and the growing season has 22.5 ^{o}C mean maximum temperature and 10.0 ^{o}C mean minimum temperature, which represents averages for the recent 60 years (Bureau of Meteorology, 2015). Weather data, including rainfall, evaporation, temperature, solar radiation and relative humidity were obtained from the Roseworthy Agriculture College station, which is located 500 m from the experiment site. Evaporation data were used to calculate reference evapotranspiration (ETo) while the maximum and minimum relative humidity data was used to calculate vapour pressure deficit at the time of daily maximum temperature.

The soil at the site is red-brown earth and classified as sodic, supracalcic, red chromosol with a firm sandy loam surface in the A horizon (Isbell, 2002). Soil tests before sowing at 0-20 cm depth returned a pH of 6.6 in $CaCl_2$, EC of 244 µS cm^{-1}, total N of 0.07% (by weight) measured by the Kjedahl method, and organic carbon of 1.41% (by weight) measured by the Walkley-Black chromic acid wet oxidation method. At 20-40 cm depth, the soil had a pH of 6.7, 252 µS cm^{-1} EC, 0.05% total N by weight and 1.21% organic carbon by weight.

The experimental site had a history of commercial production, with rotation of cereals, canola and crop legumes. Direct drill sowing equipment is typically used and stubble is typically reduced by grazing livestock.

4.2.2 Treatments and experimental design

We established a factorial experiment combining 14 varieties and two tillage systems over three seasons. The historic varieties used were previously studied (Sadras and Lawson, 2011; Sadras et al., 2012; Sadras and Lawson, 2013; Aziz et al., 2016) and comprised, Heron (first released in 1958), Gamenya (1960), Halbard (1969), Condor (1973), Warigal (1978), Spear (1984), Machete (1985), Janz (1989), Frame (1994), Krichauff (1997), Yitpi (1999), Wyalkatchem (2001), Gladius (2007); here we added Justica CL Plus to extend the series to 2011. The experiment was designed as a split-plot design with three replicates. Tillage system was assigned to the main plots, and varieties were allocated to the sub plots. Plots were 7 m long and 1.2 m wide, with six rows per plot and at inter-row spacing of 20 cm. Average plant density was 182 plants m^{-2} and crops were sown into the same plots every season.

4.2.3 Tillage systems and crop management

The two tillage systems were prepared according to Zhou et al. (2016). Briefly, CT plots were cultivated before sowing and all stubble was removed to mimic typical cultural practices prior to the historical introduction of NT. Using a spring-tined cultivator with a 10 cm wide tooth point, five passes were made in the CT plots to 5 cm depth, the usual cultivation depth for loamy soils in Australia. NT plots were sown using a direct-drill seeder fitted with knife-points and press-wheels, with minimal soil disturbance. In 2013, wheat crops were sown into surface applied stubble mulch at the rate of 2.5 t ha^{-1}. In 2014 and 2015, crops were sown into standing stubble, which was retained at full height after harvesting the previous crop. In all plots, basal di-ammonium phosphate fertilizer was applied at 80 kg ha^{-1}. Varieties were sown into the same plots every season at 95 kg seed ha^{-1}. The direct-drill seeder was used for seeding in the thoroughly tilled CT plots. Weeds were controlled with 1.5 L ha^{-1} of Glyphosate® (360 g L^{-1} glyphosate) and 85 ml ha^{-1} of Goal® (240 g L^{-1} oxyfluorfen, 108 g L^{-1} N-methyl pyrrdidone and 606 g L^{-1} liquid hydrocarbons) before sowing and 1.5 L ha^{-1} of glyphosate and 2.5 L ha^{-1} Boxer Gold® (800 g L^{-1} prosulfocarb and 120 g L^{-1} S-metolachlor) after sowing. Crops were protected with fungicides and trace element foliar sprays to correct for micro-nutrient deficiencies.

4.2.4 Measurements

Phenology was recorded regularly during crop growth, using the Zadoks scale (Zadoks et al., 1974). In three randomly selected 1-m row lengths per plot, plants were counted at 14 days after sowing (DAS) and 26 DAS to establish seedling emergence and survival, respectively. Shoot dry matter was sampled every two weeks after sowing and was oven dried at 60°C for 72 hours and weighed. Plant height at maturity was measured using a ruler.

At maturity, the number of heads and tillers were recorded by counting 1 m row length at three random locations of each plot. Four random 25 cm sections of central rows were hand-harvested to measure shoot biomass. Excluding the outer rows, the whole plot was harvested for grain using a plot harvester and expressed as t ha^{-1}. A subsample of the harvested grain was used for the determination of 1000 kernel weight and nitrogen content. In 2014, sheep (*Ovis* *aries* L.) inadvertently grazed the experiment just prior to grain harvest, which prevented yield collection.

In 2013, grain was dried at 60 °C for 48 hours and then ground before being passed through a 0.5 mm size sieve to measure N content by semi-micro Kjeldahl method (Kjeltec 8200 Auto Distillation Unit, Foss, Hillerød, Denmark) (Dai et al., 2013). In 2015, after drying the grain at 60 °C to 11% moisture content, grain protein content (%) was determined by near infra-red spectroscopy, using FOSS Infratec® 1241 grain analyser. The NIR grain analyser was calibrated to wheat grain and two standards were analysed to check for accuracy before analysing the samples. Equivalent % nitrogen content was obtained by dividing the % protein content by 5.7 (Herridge, 2013).

Dynamics of senescence was assessed at leaf and canopy heights. Greenness of the uppermost fully expanded leaf was measured every two weeks from tillering to maturity, five times in 2014 and seven times in 2015. Five randomly selected plants per plot were sampled with a chlorophyll meter (SPAD – 502, Konica Minolta, Japan). In 2015, normalised difference vegetative index (NDVI) was measured at least weekly from two weeks before flowering to physiological maturity. A hand-held GreenSeeker TM® (Trimble© assembled in Mexico) was used to measure NDVI. Moving at a constant speed along the rows, the GreenSeeker TM® was held at 60 cm above the crop canopy, and its effective resolution captured the four inner rows out of six rows in a plot.

4.2.5 Data analyses and estimation of senescence dynamics

Analysis of variance (ANOVA) for split-plot design was used to analyse trait response to tillage system, variety and their interaction, using GenStat 18th edition (VSN International Ltd., Hertfordshire, UK). For inter-season analysis, a split-split plot design was adopted, whereby season was assigned to the main plots, tillage system formed the sub-plots while variety was assigned to the sub-sub plots. Least significant differences (LSD) were calculated to compare means (Gomez and Gomez, 1984). Chronological trends were tested using least-square regression of the trait versus year of release.

For a given variety, trait deviation was calculated as the difference between the trait and its environmental mean (Sadras et al., 2009). As noted earlier, yield was collected for only two seasons, thus four environments were created from the combination of the two tillage systems and two seasons. Spearman's rank correlation coefficients (Rs) were determined in GenStat and their statistical significance assessed at $P \leq 0.05$. Variety rank change was computed as the difference between individual rank under NT and CT.

A logistic regression function was adopted to fit NDVI time-course using SigmaPlot version 12.5 (Systat Software, Inc., San Jose California USA, www.systatsoftware.com). The logistic function estimated five parameters, including minimum NDVI at physiological maturity (minNDVI), maximum NDVI (maxNDVI, near flowering), time to loss of 50% maximum NDVI and canopy senescence rate (SR), in a similar manner to that used by Christopher et al. (2014). A fifth parameter, the onset of senescence (EC90), was estimated by computation. The parameters of senescence were estimated for each plot and subjected to ANOVA.

4.3 Results

4.3.1 Growing conditions and phenology

Growing conditions are summarised in Figure 4.1. Rainfall between sowing and harvest was 208 mm in 2013, 162 mm in 2014 and 188 mm in 2015. When seasonal rainfall between April and October was compared for the last twenty years, 2013 and 2014 were within the rank of decile six while 2014 fell within decile three. Across the three seasons, approximately 70%

rainfall was received between sowing and stem elongation, 20% between stem elongation and flowering and 10% after flowering. Season 2013 was more favourable with average grain yield of 4.1 t ha^{-1} compared with 2015, which produced an average yield of 2.7 t ha^{-1} ($P < 0.001$).

Tillage system did not significantly affect plant establishment ($P = 0.091$). ANOVA showed differences in plant establishment among the varieties ($P < 0.001$), but regression analysis did not detect trends with the year of release ($P = 0.176$). Irrespective of variety × tillage interactions ($P = 0.023$), no trend was apparent ($P = 0.998$) for plant establishment. Seed size and emergence rates did not correlate ($P = 0.151$).

Crop phenology did not differ among varieties for stem elongation ($P = 0.529$), and flowering ($P = 0.130$). Also, neither tillage system nor its interaction with variety affected time to stem elongation ($P = 0.769$) or time to flowering ($P = 0.770$). Shoot biomass did not differ due to tillage system ($P = 0.074$), variety ($P = 0.171$) or their interaction ($P = 0.436$).

4.3.2 Yield and its components

There was significant ($P = 0.015$) variation in grain yield from 2.57 t ha^{-1} under CT in 2015 to 4.67 t ha^{-1} under NT in 2013 (Figure 4.2 a). In 2013, NT outyielded CT by 25% ($P = 0.025$) but no significant yield differences ($P = 0.084$) between tillage systems were found in 2015. In both seasons, modern varieties had higher grain yield compared with the older counterparts ($P < 0.001$). Variety × tillage system interactions were not significant in either 2013 ($P = 0.312$) nor in 2015 ($P = 0.214$). Season × variety × tillage system did not affect grain yield ($P = 0.271$). Rate of yield increase across both years was 21 kg $ha^{-1}year^{-1}$, irrespective of the tillage system (Figure 2 b, c). Despite the lack of tillage × variety interactions, there were rank changes in yield between CT and NT for 2013 ($R_s = 0.86$), 2015 ($R_s = 0.59$) and when data were pooled ($R_s = 0.79$) (Table 4.4A1). On a rank from 1 being the lowest yield to 14 for highest yield, modern varieties were high ranking, between 8 and 14 under either tillage systems in both seasons and across pooled data.

Grain number per m^2 ranged from 10,513 under CT in 2015 to 13,265 under NT in 2013 (Figure 4.3 a). Compared with CT, NT increased grain number by 25% in 2013 and 17% in 2015 (both, $P = 0.030$). Variety × tillage interactions did not affect grain number in either season ($P = 0.235$). Grain number increased with year of release, but independent of tillage system (Figure 4.3 c and e). Although the rate of increase was similar for the two systems, grain number was higher for NT compared with CT. Tiller and head number did not change with year of release or with tillage system.

Kernel weight did not change significantly with tillage system ($P = 0.188$; Figure 3 b), and 2013 had higher mean kernel weight of 34 mg compared with 24 mg in 2015. Kernel weight did not change consistently with the year of release (Figure 4.3 d, f). In 2013, kernels of Heron (1958), Frame (1994), Condor (1997) and Gladius (2007) were larger under NT than CT (variety × tillage interaction: $P = 0.025$).

4.3.3 Canopy senescence

Our collection of varieties showed marked differences in the dynamics of canopy senescence. The dynamics of canopy senescence for the oldest (Heron, 1958) and newest variety (Justica CL Plus, 2011) are presented in Figure 4.4 a to illustrate the meaning of the parameters. The fitted functions are bounded between maximum NDVI (maxNDVI) and minimum NDVI (minNDVI). EC90 signifies the onset of senescence, when 10% of peak NDVI is lost, while EC50 corresponds to the time to 50% of maximum NDVI. Rate of senescence (SR) indicates the rate of NDVI decrease. The oldest variety had a higher maximum NDVI, earlier onset of senescence, a slower rate of senescence and a lower minimum NDVI compared with the newest variety (Figure 4.4 a).

Maximum NDVI was neither significantly affected by tillage system (Figure 4.4 b) nor its interaction with variety ($P = 0.819$), but declined from 1958 to 2011 (Figure 4.4 g). Across the varieties, EC90 and EC50 were delayed by three days under NT compared with CT (Figure 4.4 c, d). However, despite the variety differences which were detected by ANOVA ($P < 0.001$), both parameters did not change with the year of release (Figure 4.4 h, i). Tillage × variety interaction did not alter the onset of either EC90 or EC50.

Rate of senescence did not change with tillage system (Figure 4.4 e). However, ANOVA showed variety differences ($P < 0.001$) and variety × tillage interactions ($P < 0.007$). Rate of senescence ranged from 19.6 to 31.5 $^{o}Cd^{-1}$, and modern varieties senesced faster compared with older counterparts (Figure 4.4 j). Crops had higher minimum NDVI under NT compared with CT (Figure 4.4 f). Modern varieties had higher minimum NDVI than the older counterparts (Figure 4.4 k), but variety × tillage interactions did not affect this trait ($P = 0.374$).

4.3.4 Leaf greenness

The uppermost fully expanded leaves were greener in 2014 compared with 2015, and NT improved leaf greenness compared with CT (Figure 4.5 b, d, f). Tillage system effect on leaf greenness was larger as the crops aged (Figure 4.5 a). Modern varieties had greener leaves at stem elongation, flowering and grain filling than their predecessors (Figure 4.5 c, e, g). Leaf greenness was not affected by variety × tillage system interaction at each of the three sampling stages.

4.3.5 Grain nitrogen concentration

Grain nitrogen (N) concentration was neither affected by tillage system (P = 0.106), variety (P = 0.791) nor their interaction (P = 0.127). Across varieties, grain N content was higher in 2015 (2.48%) compared with 2013 (2.04%) (P = 0.001). A season × tillage interaction was observed (P = 0.037) in 2013, where NT reduced grain N content by 8% compared with CT but no significant tillage effects were measured in 2015. There was no relationship between grain N and year of release (P = 0.481).

4.3.6 Associations between traits

Associations between traits were explored with principal component analysis (PCA) and correlation analyses (Figure 4.6 and Table 4.A2). Grain yield correlated positively with grain number, leaf greenness at stem elongation, the onset of senescence, the rate of senescence and minimum NDVI, but was unrelated with maximum NDVI. Grain N content (%) was unrelated to yield components and the parameters of senescence in both tillage systems.

4.4 Discussion

4.4.1 Yield gain and tillage responses

Our experiments did not support our hypothesis that the rate of genetic gains in Australian wheat yield were related to tillage system. The rate of genetic gain in yield was similar between tillage systems indicating that selection for yield under CT could improve yield under NT (Murphy et al., 2007).

When present, tillage × variety interaction indicates that specific varieties can be bred for improved yield under specific tillage conditions (Murphy et al., 2007; Trethowan et al., 2005). Conversely, lack of variety × tillage interactions in the present study shows a lack of system specificity (Trethowan et al., 2012) and supports previous reports investigating tillage × variety interactions in wheat (Kirkegaard, 1995; Carr et al., 2003; Kumudini et al., 2008; Trethowan et al., 2012). These past studies, however, evaluated varieties that had been bred under conventional tillage (Herrera et al., 2013). In comparison, the older varieties in the present study were most certainly bred under conventional tillage, but the recent varieties are likely to have had some exposure to no-till during their development. Nonetheless, it is not clear when this change in evaluation might have occurred, even though Kirkegaard et al. (2014) suggest that the integration of no-till in Australia cropland began in the 1980s. Furthermore, most previous studies evaluated a narrow chronological range of varieties, unlike the present study which evaluated varieties across five decades of selection.

Selection under specific environmental conditions tends to narrow genetic diversity, which limits performance across other environments. For example, after 10 cycles of recurrent selection of wheat under CT, Maich and Di Rienzo (2014) investigated the response of the population to contrasting tillage systems. The population performed dismally under NT compared with CT. Specificity to tillage system of CT-derived or NT-derived varieties is reported in wheat and maize (Hwu and Allan, 1992; Higginbotham et al., 2011; Herrera et al., 2013). Based on this evidence for tillage system specificity, it appears that the genetic progress depicted in the present study could be in the context of CT, and that NT only offered better conditions for a modest increase in grain yield. Further studies need to be conducted with modern varieties, which may have had stronger exposure to NT, or varieties that have been selected under NT conditions.

The average rate of yield gain of 21 kg ha^{-1} year^{-1} in the present study is within the range of 18 – 25 kg ha^{-1} year^{-1} reported previously for South Australian environments (Sadras and Lawson, 2011; Sadras and Lawson, 2013). Commonly, modern wheat varieties out-yield their predecessors (Sadras et al., 2016a), and the yield gain for our set of varieties relates to increases in biomass, harvest index, radiation use efficiency and nitrogen uptake, despite reduction in the size of root system (Sadras and Lawson, 2011; Sadras et al., 2012; Sadras and Lawson, 2013; Aziz et al., 2016). Our collection showed similarities in phenology, which was consistent with the criteria used in the selection of the varieties for this study (Sadras and Lawson, 2011). In addition, neither tillage system, nor its interaction with variety, altered crop phenology, hence, time-trends in the present study were independent of phenological development.

4.4.2 Senescence dynamics

Our collection of varieties differed in the parameters describing senescence, while tillage system modified the dynamics of senescence. Maximum NDVI reflects the peak canopy size, usually attained a few days before flowering, while the minimum NDVI shows the residual foliage at maturity. Canopy senescence is captured by the decline in NDVI, and represents both the whole plant senescence and the greenness of the flag leaves.

Tillage system had no impact on maximum NDVI but crops grown under NT had higher minimum NDVI compared with those under CT. Onset (EC90) and time to 50% senescence (EC50) were largely unresponsive to variety × tillage interaction, but there was a slight delay in senescence under NT. The reason for delayed senescence and higher minimum NDVI under NT is unknown. However, in some but not all environments, NT may enhance soil water storage (Verhulst et al., 2011; Kirkegaard et al., 2014), thus increased water availability might account for part of the differences. Effect of water conservation on delayed senescence was observed in sorghum grown in deep soils with high water-holding capacities (Jordan et al., 2012) and in wheat that had limited N supply at sowing (Zhou et al., 2017). Often, stay-green is associated with yield increases (Gregersen et al., 2013; Christopher et al., 2016), but both EC90 and EC50 were unrelated to yield, suggesting that the extended greenness may not have been functional.

Decline in maximum NDVI between 1958 and 2011 could be attributed to changes in plant architecture, including plant height and canopy closure. Indeed, the present study identified a positive correlation between plant height and maximum NDVI. The chronological decline in maximum NDVI corroborates shifts from tall to modern short-stature varieties (Sadras and Lawson, 2011), which coincides with the introduction of *Rht* dwarfing genes in the 1970s (Fischer, 2011). In fact, plant height declined from 1958 to 1973, then remained constant onwards, as observed by Sadras and Lawson (2011). Based on previous work with these varieties (Sadras and Lawson, 2011; Sadras et al., 2012), the low peak maximum NDVI in modern varieties compared with older varieties might reflect more open canopies in the new varieties. The open canopies may have had better distribution of radiation throughout the profile, thus enhanced photosynthetic efficiency (Sadras et al., 2012), which may be related to yield increases in modern varieties. In the present study, we detected no changes in plant biomass, in contrast with Sadras and Lawson (2011).

Higher minimum NDVI among the modern varieties compared with older counterparts could be due to improvements in N nutrition. Consistent with the high NDVI at maturity, modern varieties maintained greener leaves throughout the crop cycle compared with the old varieties. This information supports previous findings that observed increases in N uptake in Australian wheats (Sadras and Lawson, 2013; Aziz et al., 2016; Sadras et al., 2016a), despite a reduction in root length density and root biomass (Aziz et al., 2016).

The rate of post-flowering senescence was faster in modern varieties compared with old varieties. In addition, the rate of senescence was faster under NT compared with CT, which could have been as a result of higher demand for N due to more grain under NT. Monocarpic plants such as wheat demonstrate a developmental senescence pattern which involves the successive death of old leaves and finally of the whole plant (Schippers et al., 2015). This age-related process is linked to the development of reproductive structures (Gregersen et al., 2013; Schippers et al., 2015), while sink strength is reported to influence the rate of senescence (Borrell et al., 2001; Xie et al., 2016). Higher demand for N by the high grain number in modern varieties could partly account for the accelerated rate of senescence (Wu et al., 2012). Previous studies associate fast rates of senescence with improved grain yield in wheat (Montazeaud et al., 2016) as a result of enhanced grain filling rates (Xie et al., 2016).

Taken together, a putatively more open canopy structure and greener leaves of the modern varieties may enhance radiation use efficiency, while a fast rate of senescence at the whole-canopy level could be partially compensated by re-allocation to, and maintenance of, greenness in flag leaf. This is in contrast with delayed senescence (stay-green) as a yield enhancing trait (Christopher et al. 2016). We found no relationship between grain N content and the rate of senescence, an outcome that contradicts the notion that a fast rate of senescence increases the remobilisation efficiency of N to the grain (Wu et al., 2012).

Greener leaves and extended greenness under NT potentially increased yield compared with CT (Verhulst et al., 2011; Gregersen et al., 2013; Christopher et al., 2016). Large and closed canopies (high NDVI at flowering) of the old varieties in the present study may be counterproductive compared with small and open canopies of the modern varieties. For modern varieties, increases in biomass can be modulated by a more open canopy that allows more light into the profile, and increases radiation use efficiency (Sadras et al., 2012; Richards et al., 2014). Similar responses would be obtained under non-limiting nitrogen conditions, which enhance canopy growth. Results of the present study indicate that senescence patterns may play a regulatory role in the adaptation of wheat to no-till, which deserves further investigation.

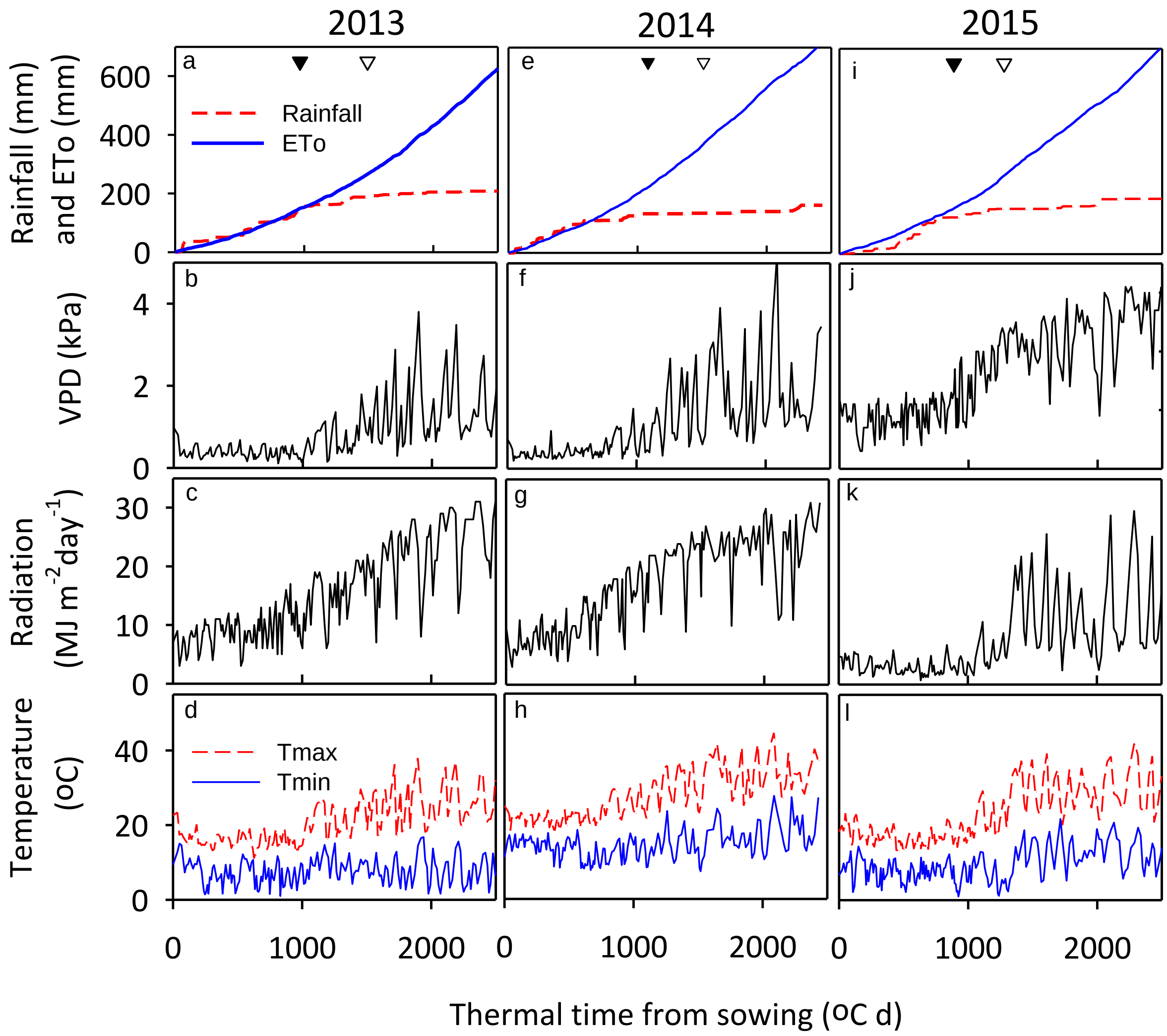

Figure 4.1. Growing conditions for wheat crops in 2013, 2014 and 2015 at Roseworthy, South Australia, including cumulative rainfall and reference evapotranspiration (ETo) (a, e, i), vapour pressure deficit (VPD) estimated at the time of daily maximum temperature (b, f, j), daily radiation (c, g, k) and daily maximum (Tmax) and minimum (Tmin) temperature (d, h, j). Closed arrowheads denote stem elongation while the open arrowheads denote flowering, averaged across varieties and tillage system. Data was obtained from the Australian Bureau of Meteorology (Bureau of Meteorology 2015).

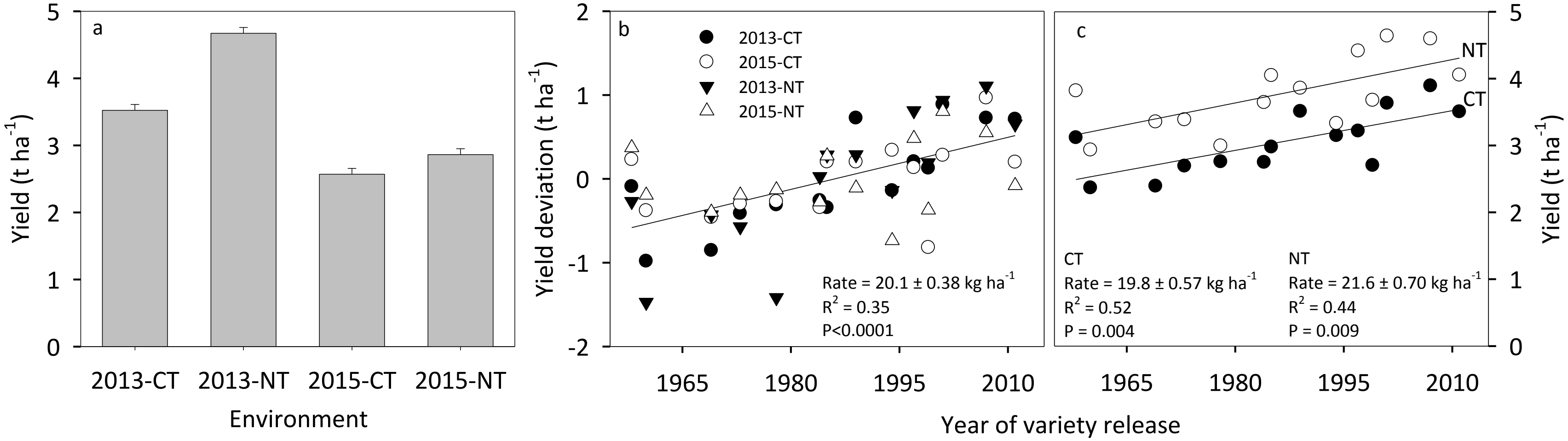

Figure 4.2. Environmental mean yield of Australian wheat varieties released between 1958 and 2011 (a). Error bars are 1 standard error of mean. The environments are a combination of two growing seasons and two tillage systems. Yield deviation as a function of year of release (b), and yield across both seasons under conventional tillage (CT) and no-till (NT) as function of year of release (c). Solid lines are least square linear regressions with slopes different from zero.

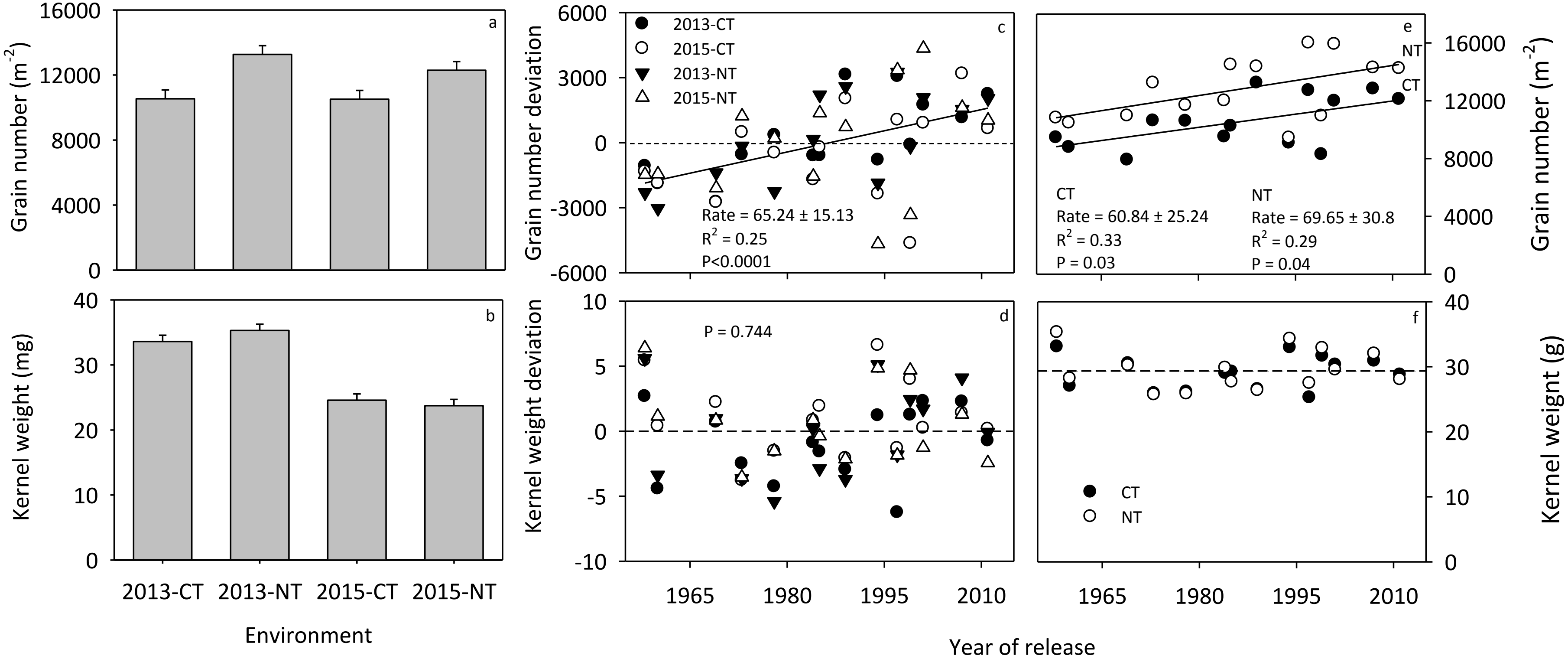

Figure 4.3. Environmental mean grain number (a) and kernel weight (b) of Australian wheat varieties released between 1958 and 2011, and grown in four environments. The environments are a combination of two growing seasons and two tillage systems, including conventional tillage (CT) and no-till (NT). Error bars are 1 standard error of mean. Grain number (c) and kernel weight deviation (d) as a function of year of release. Grain number (e) and kernel weight (f) as a function of year of release, of wheat varieties grown under CT and NT. Solid lines are least square linear regressions with slopes different from zero. Dashed lines denote y = 0 (c, d) or the mean value of the population when regression slope is not different from zero (f).

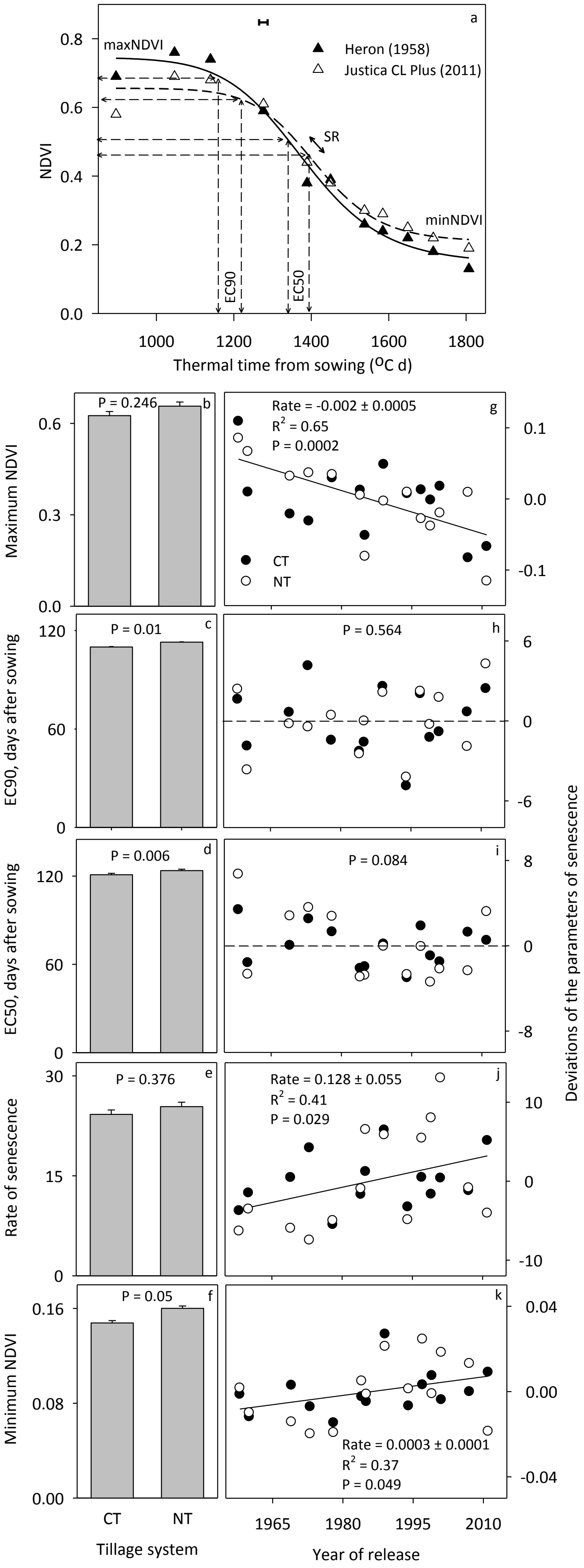

Figure 4.4. An illustration of an NDVI fitted time-course for the oldest variety (1958) and a modern variety (2011) released in Australia (a). NDVI: normalised vegetative index; maxNDVI: maximum NDVI; minNDVI: minimum NDVI; EC90: onset of senescence; EC50: time to loss of 50% of maximum NDVI; SR: senescence rate. Bar shows phenostage flowering. Conventional tillage (CT) and no-till (NT) means (b, c, d, e, f). Error bars are 1 standard error of mean. Parameters of senescence deviations g, h, i, j and k, with the closed symbols denoting CT and the open symbols representing NT. Solid lines are linear regressions with slopes different from zero. Dashed lines denote y=0.

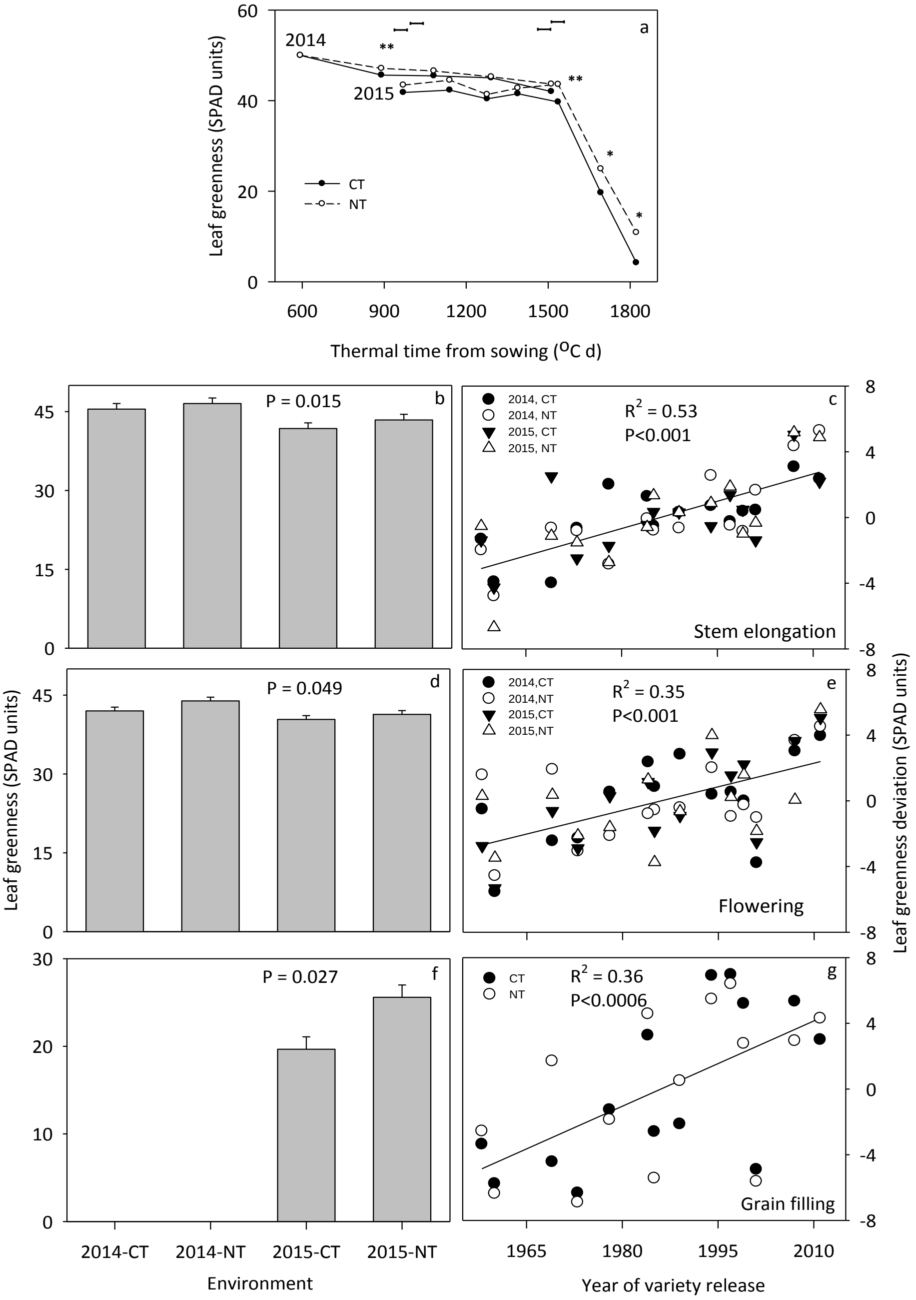

Figure 4.5. Leaf greenness of the uppermost fully expanded leaf of Australian wheat varieties released between 1958 and 2011. Effect of tillage system as a function of thermal time from sowing (a). Bars show phenostage stem elongation and flowering, with the top pair representing 2014 and the bottom pair representing 2015. *significant at 0.05% and ** significant at 0.01%. Environmental means of leaf greenness at stem elongation, flowering and grain filling stages (b, d, f). Error bars are 1 standard error of mean. Environments are a combination of two cropping seasons and two tillage systems. (c, e, g) Deviations of leaf greenness at stem elongation, flowering and grain filling. Solid lines are least square linear regressions with slopes different from zero.

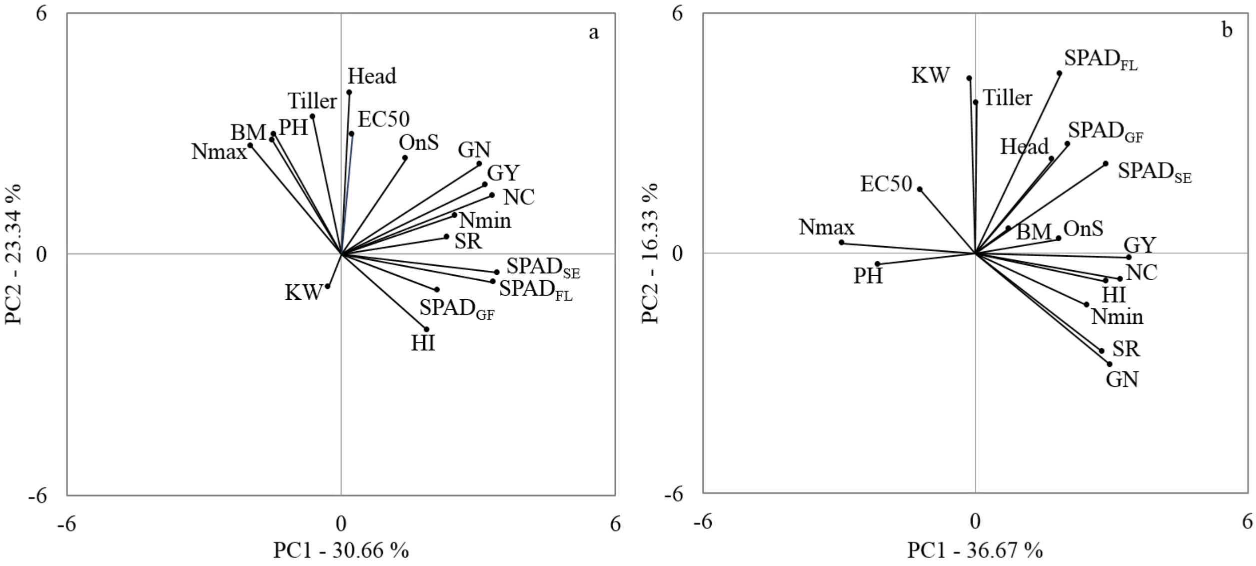

Figure 4.6. Biplots from principal component analyses showing correlations between yield components and senescence traits (n = 14) in South Australian wheat varieties released between 1958 and 2011 grown under conventional tillage (CT) (a) and no-till (NT) (b). Traits included grain yield (GY), grain number (GN), kernel weight (KW), tiller number (Tillers), head number (Heads), plant height (PHT), biomass (BM), harvest index (HI), % grain nitrogen content (%NC), leaf greenness at stem elongation ($\mathrm{SPAD}_{\mathrm{SE}}$), leaf greenness at flowering ($\mathrm{SPAD}_{\mathrm{FL}}$), leaf greenness at grain filling ($\mathrm{SPAD}_{\mathrm{GF}}$), minimum NDVI (minNDVI), maximum NDVI (maxNDVI), onset of senescence (OnS or EC90), time to lose 50% of the maximum NDVI (EC50), senescence rate (SR).

Statement of Authorship

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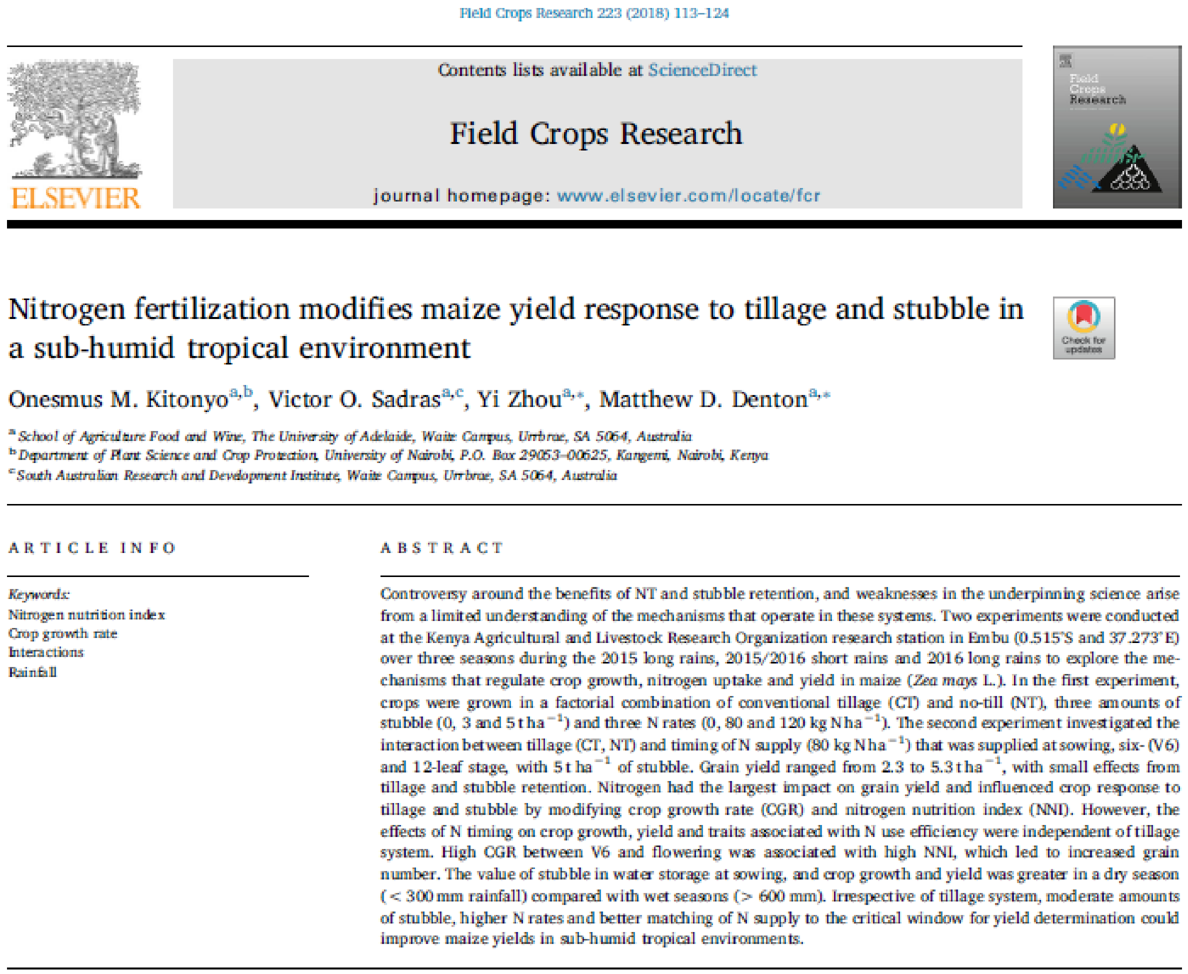
Chapter 5 Nitrogen fertilization modifies maize yield response to tillage and stubble in a sub-humid tropical environment



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Nitrogen fertilization modifies maize yield response to tillage and stubble in a sub-humid tropical environment

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ABSTRACT

Controversy around the benefits of NT and stubble retention, and weaknesses in the underpinning science arise from a limited understanding of the mechanisms that operate in these systems. Two experiments were conducted at the Kenya Agricultural and Livestock Research Organization research station in Embu (0.515°S and 37.273°E) over three seasons during the 2015 long rains, 2015/2016 short rains and 2016 long rains to explore the mechanisms that regulate crop growth, nitrogen uptake and yield in maize (*Zea mays* L.). In the first experiment, crops were grown in a factorial combination of conventional tillage (CT) and no-till (NT), three amounts of stubble (0, 3 and 5 $t\ ha^{-1}$) and three N rates (0, 80 and 120 $kg\ N\ ha^{-1}$). The second experiment investigated the interaction between tillage (CT, NT) and timing of N supply (80 $kg\ N\ ha^{-1}$) that was supplied at sowing, six- (V6) and 12-leaf stage, with 5 $t\ ha^{-1}$ of stubble. Grain yield ranged from 2.3 to 5.3 $t\ ha^{-1}$, with small effects from tillage and stubble retention. Nitrogen had the largest impact on grain yield and influenced crop response to tillage and stubble by modifying crop growth rate (CGR) and nitrogen nutrition index (NNI). However, the effects of N timing on crop growth, yield and traits associated with N use efficiency were independent of tillage system. High CGR between V6 and flowering was associated with high NNI, which led to increased grain number. The value of stubble in water storage at sowing, and crop growth and yield was greater in a dry season (< 300 mm rainfall) compared with wet seasons (> 600 mm). Irrespective of tillage system, moderate amounts of stubble, higher N rates and better matching of N supply to the critical window for yield determination could improve maize yields in sub-humid tropical environments.

5.1 Introduction

The benefits of no-till (NT) and stubble retention in the improvement of water and nitrogen use efficiency, and grain yield in sub-humid environments are controversial (Giller et al., 2009). In addition, the underpinning science is only partially understood (Giller et al., 2015). These uncertainties raise questions as to the circumstances where these practices improve yield and how physiological mechanisms regulate crop growth and yield under these conditions (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Some of the limitations concern the fertilizer N rates that are required to increase yield and counter possible N immobilization by cereal stubble, the minimum amount of stubble required to provide the benefits of mulching where there are trade-offs in stubble allocation between soil cover and livestock feeding, and potential avenues to increase N use efficiency (Giller et al., 2009; Giller et al., 2011).

A key attribute of NT and stubble retention is water conservation, an important driver for yield, increases in many dryland systems (Rusinamhodzi et al., 2011; Scott et al., 2013; Thierfelder et al., 2013). Stored subsoil moisture allows for early sowing and supports post-flowering growth when grain filling is sensitive to water deficit (Kirkegaard and Hunt, 2010; Sadras et al., 2012a). However, the contribution of NT and stubble retention depends on rainfall pattern, evaporative demand and soil type (Kirkegaard, 1995; Monzon et al., 2006; Kirkegaard and Hunt, 2010; Verburg et al., 2012).

Insufficient use and inappropriate management of fertilizer N limits not only the productivity of NT and stubble retention systems but is a widespread challenge in smallholder systems sub-Saharan Africa (Sommer et al., 2014; Vanlauwe et al., 2014). Yield declines under NT and stubble retention systems are larger without N addition in sub-humid environments than in drylands (Pittelkow et al., 2015b). Based on co-limitation principles, yield is maximized when both water and N are equally limiting (Sadras, 2005; Cossani et al., 2010; Riar et al., 2016). Sadras et al. (2012) discuss how N is critical to capture the benefits of water conservation and the requirement for an adequate water supply to capture the benefits of N supply. Knowledge is limited, however, on the rate and timing of N supply required to capture the benefits of water conservation, and on the means to counter possible N-immobilisation by cereal stubble to increase grain yield in NT and stubble retention systems (Giller et al., 2009; Giller et al., 2011).

Nitrogen use efficiency (NUE), the efficiency with which available N is absorbed and converted into grain (Dobermann, 2007), is frequently low in NT and stubble retention systems, due largely to N immobilisation in stubble (Grahmann et al., 2013). There is a need to adjust the rate and timing of N supply (Dobermann, 2007; Verhulst et al., 2014), and to reduce losses through leaching and denitrification (Angás et al., 2006; Verachtert et al., 2009). Improving both N uptake and utilization efficiency could increase yield and grain quality of maize (Ciampitti and Vyn, 2012). N uptake involves N recovery by the crop and agronomic efficiency of the applied N, while N use is facilitated through physiological efficiency and increasing N harvest index (Dobermann, 2007; Setiyono et al., 2010; Ciampitti and Vyn, 2012). In SSA, the soils are inherently infertile and have limited response to NT and stubble retention practices under current low N rates, which have stagnated since 1960s (Dimes et al., 2015).

Nitrogen economy is a critical driver for biomass accumulation and grain production (Sadras and Lemaire, 2014), and the assessment of crop N nutrition is a prerequisite for the interpretation of agronomic data (Gastal et al., 2015). Crop N nutrition can be quantified by nitrogen nutrition index (NNI), a ratio of actual N concentration to critical N concentration required to achieve maximum biomass (Gastal et al., 2015). On the other hand, understanding of the mechanisms that regulate crop growth, N uptake and use efficiency, and grain yield in maize would improve options for better N management.

In light of the constraints to the application of NT and stubble in sub-humid environments, this paper reports on two studies that evaluate the effects of tillage, stubble amount and nitrogen on crop growth, N nutrition and yield. The first study aims to understand the contribution of the management practices and their interactions by exploring underlying physiological mechanisms that regulate crop growth, N nutrition and yield. The second study provides an understanding of how the interaction between tillage and timing of N supply impact crop growth, N and yield in NT and stubble retention systems. In these studies we hypothesise that (i) the effect of tillage and stubble retention on water conservation and yield in sub-humid environments is dependent on seasonal rainfall, and that (ii) both the rate and timing of N supply will modify crop growth, N use and yield response to NT and stubble retention.

5.2 Materials and methods

5.2.1 Site

Field experiments were conducted at the Kenya Agricultural and Livestock Research Organisation Research Station at Embu, 0.515 ^{o}S and 37.273 ^{o}E, 1425 m above sea level. The site is sub-humid with mean temperature of 22 ^{o}C (Jaetzold et al., 2006). Rainfall is bimodal, with a long rains season from April to August and a short rains season from October to February (Jaetzold et al., 2006). Soils are deep (> 2.5 m) highly weathered humic nitisols with low exchangeable bases, relatively high P-sorption, and with medium to low fertility (Jaetzold et al., 2006). Table 5.1 presents initial soil characterisation at 0-15 cm and 15-30 cm depth.

At the onset of the experiments during 2015 long rains, soils were sampled at 0-15 and 15-30 cm layers in each replicate, bulked and analysed for pH (1:2.5, soil/water), organic carbon, total N, mineral N, potassium, calcium, magnesium, phosphorus and cation exchange capacity (CEC). Organic carbon was extracted using acidified dichromate while total N was determined by wet oxidation using the Kjeldahl method (Dai et al., 2013). Calcium and magnesium were extracted using 1 N KCl and determined using a spectrophotometer while phosphorus and potassium were determined using a modified Olsen method (Okalebo et al., 2002).

5.2.2 Treatments and experiment design

5.2.2.1 Experiment 1

Two tillage systems (conventional tillage, CT and no-till, NT), three amounts of stubble (0, 3 and 5 t ha^{-1}) and three fertilizer N rates (0, 80 and 120 kg N ha^{-1}) were evaluated under continuous maize cropping for three consecutive seasons. The experiment was laid out in a split-split-plot design with three replications. Tillage system was allocated to the main plots, stubble amount was assigned to the sub-plots while N rate formed the sub-sub plots. Main plot size was 31 m × 12.25 m, the sub-plots were 28 m × 3.75 m and sub-sub plot size was 7 m × 3.75 m.

Nitrogen was supplied as urea and provided as ⅓ at sowing and ⅔ at six leaf stage (V6), for both 80 and 120 kg N ha^{-1}. Top dressing applications were banded around plants, prior to sufficient amounts of rainfall to promote movement of urea into soil.

5.2.2.2 Experiment 2

Treatments were control (no fertilizer; N0), and 80 kg N ha^{-1} applied at sowing (N1) or applied as ⅓ at sowing and ⅔ at six-leaf stage (N2), ⅓ at sowing, ⅓ at six-leaf and ⅓ at 12-leaf stage (N3), and ½ at six-leaf and ½ at 12-leaf stage (N4). These treatments were evaluated under both CT and NT with the application of 5 t ha^{-1} of stubble. The experiment was laid out in a split-plot design with three replications. Tillage system was allocated to the main plots while N supply formed the sub-plots. Main plots measured 31 m × 12.25 m while the sub-plots were 7 m × 3.75 m.

5.2.3 Management

Prior to the establishment of both experiments, a pre-crop of maize was grown to even-out the experimental block and the soils were not tilled. To mine soil N, closely spaced maize was sown during the short rains season of 2014, without the addition of N fertilizer.

Tillage and stubble treatments were applied two weeks before sowing in the same plot every season. Exact amounts of stubble were maintained at the onset of each season, whereby additional stubble allowed for undecomposed material. Conventionally tilled plots were prepared by digging to 15 cm depth to thoroughly disturb the soil. Under CT, maize stubble was allocated at prescribed rates, chopped into less than 5 cm long pieces and incorporated into the soil when digging. No-till plots were left undisturbed and stubble mulch was spread on the soil surface at the prescribed rates. In all plots, sowing was done manually by opening 5 cm deep holes to hold seed and fertilizer. All plots received basal fertilizer of triple super phosphate at the rate of 60 P kg ha^{-1} which was side banded on the sowing rows.

A locally adapted hybrid of maize DeKalb (DK) 8031 was used in both experiments. Crops were sown at the onset of rains: on 25th March for 2015 long rains season, 19th October for 2015/2016 short rains season and 3rd April for 2016 long rains season. Seed was sown in rows 0.75 m apart with 0.25 m between holes in a row. Two seeds were sown per hole and thinned at the three leaf stage (V3) to one plant per station, to achieve a plant population density of approximately 5.3 plants m^{-2}.

Weeds were controlled with 1.5 L ha-1 of Roundup® (glyphosate) before sowing and 1.5 L ha^{-1} Dual Gold® (960 g L^{-1} S-metolachlor) after sowing in both tillage systems. In-crop weeds were removed by hoe-weeding in CT plots but with Twiga 2, 4-D® (Dimethylamine salt and 2, 4-diclorophenoxy acetic acid) in NT plots. The reason was to minimise soil disturbance in NT and to increase tillage in CT treatments. Insect pests were controlled with Thunder® (100 g L^{-1} imidacloprid) at 300 mL ha^{-1}.

5.2.4 Measurements

Daily rainfall, temperature and reference evaporation were obtained from a meteorological station located about 200 m from the experiments. Relative humidity and radiation data were obtained from the NASA Prediction of World Energy: Resource Climatology Resource for

Agro-climatology (NASA, 2017). Vapour pressure deficit was calculated from relative humidity and temperature.

During 2015 long rains and 2015/2016 short rains, gravimetric water content was measured at 20-cm intervals within 0-140 cm depth of the soil profile at sowing, flowering and maturity. Soil samples were taken in the middle of two central rows in each plot. Soil water content was not determined in 2016 long rains. The gravimetric water content was converted to volumetric water content by multiplying with the soil bulk density at each sampling layer and actual water content in millimetres was determined. Water use was estimated as evapotranspiration (ET), as the change in water content between sowing and maturity plus rainfall during the same period (French and Schultz, 1984). This study assumed that run-off and deep drainage would be negligible.

A phenological scale (CIMMYT, 2017) was used to monitor maize development and to guide the application of fertilizer treatments. Emerged plants were counted daily from day five through to 14 days after sowing. Days after sowing to 50% pollen shed were recorded but anthesis silking intervals were not determined. Shoot biomass was sampled from three plants per plot at V6 and R1 and five plants at harvest during 2015 long rains and 2015/2016 short rains. Samples were oven dried at 60 °C for 72 hours to determine dry mass and crop growth rate between V6 and R1.

Harvest area for both experiment 1 and 2 was 14.63 m^2 after the exclusion of border rows. Five plants were separated for biomass and ears. Yield and yield components were collected for all seasons while biomass and harvest index were measured in 2015 long rains and 2015/2016 short rains only. Ear length was determined with a tape measure while the diameter was measured with vernier callipers at the middle of the ear. Ears were threshed manually and a sub-sample was used for 100 kernel weight and grain protein determination. Grain protein content (%) was measured by near infra-red spectroscopy using FOSS Infratec® 1241 grain analyser during 2015/2016 short rains and 2016 long rains only. In 2015 long rains, grain was damaged by insects to allow for the analysis of protein content. The protein analyser was calibrated to maize grain (Kitonyo et al., 2017).

Nitrogen in shoots was determined at flowering and maturity during 2015 long rains and 2015/2016 short rains. A sub-sample was obtained from five plants per plot and milled through a 0.5 mm sieve, and analysed for N content using the Kjeldahl method (Dai et al., 2013). Shoot N content was used in the computation of N nutrition index, N remobilization efficiency, N harvest index and other traits associated with NUE as described below.

5.2.5 Computation and data analysis

Crop growth rate between V6 and flowering was calculated as the difference in biomass yield divided by days between the two stages. Nitrogen nutrition index (NNI) at flowering was calculated as the ratio between the actual N concentration of the above ground biomass and the critical N concentration at the same crop mass (Gastal et al., 2015). Critical N concentration is the minimum N concentration required to maximise biomass. Critical N concentration (Nc) was computed as shown in Eq. 5.1, where DM is the actual crop biomass in t ha^{-1} (Justes et al., 1994; Plénet and Lemaire, 1999).

$$\mathrm{Nc} = 3.4 * (\mathrm{DM})^{-0.37} \tag{5.1}$$

Grain protein was converted to grain N by dividing the protein content by 5.7 (Herridge, 2013). Nitrogen uptake and indices of use efficiency were computed (Dobermann, 2007; Ciampitti and Vyn, 2012). Nitrogen uptake (NU) was computed as the sum of N in the shoot biomass

(NUs) and in the grain (NUg). Nitrogen agronomic efficiency (AE) was calculated as shown in Eq. 5.2, Nitrogen recovery efficiency (RE) (Eq. 5.3), Nitrogen internal efficiency (IE) (Eq. 5.4), Nitrogen physiological efficiency (PE) (Eq. 5.5), N remobilization efficiency (NRE %) (Eq. 5.6), and Nitrogen harvest index (NHI %) (Eq. 5.7).

$$\mathrm{AE\ (kg\ kg^{-1}\ N)} = \frac{\text{yield with fertilizer} - \text{yield without fertilizer}}{\text{amount of fertilizer N applied}} \tag{5.2}$$

$$\mathrm{RE\ (kg\ kg^{-1}\ N)} = \frac{\text{N uptake with fertilizer} - \text{N uptake without fertilizer}}{\text{amount of fertilizer N applied}} \tag{5.3}$$

$$\mathrm{IE\ (kg\ kg^{-1}\ N)} = \frac{\text{grain yield}}{\text{N uptake}} \tag{5.4}$$

$$\mathrm{PE\ (kg\ kg^{-1}\ N)} = \frac{\text{grain yield with fertilizer} - \text{grain yield without fertilizer}}{\text{N uptake with fertilizer} - \text{N uptake without fertilizer}} \tag{5.5}$$

$$\mathrm{NRE\ (\%)} = \frac{\text{N in shoot at flowering} - \text{N in shoot at harvesting}}{\text{N in shoot at flowering}} \tag{5.6}$$

$$\mathrm{NHI\ (\%)} = \frac{\text{grain N content}}{\text{N uptake}} \tag{5.7}$$

Water use efficiency (WUE) was calculated as the ratio of grain yield to seasonal evapotranspiration (French and Schultz, 1984). A boundary line representing the water-limited yield potential in the sub-humid environments of sub-Saharan Africa was used to compute yield gaps. Parameters of the boundary line were: x-intercept at 60 mm and slope 9.5 kg ha^{-1} mm^{-1} based on the highest historical water use efficiency for maize in these environments (Dimes et al., 2015).

Analysis of variance (ANOVA) was used to assess the experimental sources of variation for all traits using GenStat 18th Edition (VSN International Ltd., Hertfordshire, UK) SAS 9.2 for windows. Data conformed to the requirements of ANOVA. Residuals for all measured variables were checked for normal distribution, and no transformations were required. For individual season analysis, split-split plot design was used where tillage × stubble × N rate were used in the treatment structure, and treatments were assigned to the main, sub-plot and sub-sub plots as described in the design of this study. When across season analysis was performed, season × tillage × stubble × N rate were used in the treatment structure. As season was not a factor to be controlled, it was considered as the random factor in the analysis. Differences between treatments were compared and separated using Fisher's Least Significant difference (LSD) test at 0.05 probability (Gomez and Gomez, 1984). Relationships between variables were examined by correlations and regression analysis.

5.3 Results

5.3.1 Growing conditions

Figure 5.1 summarises the growing conditions. Rainfall between sowing and harvest was 635 mm for 2015 long rains season, 600 mm for 2015/2016 short rains and 290 mm for 2016 long rains. Based on long-term averages for this environment, 2015 long rains and 2015/2016 short rains would occur in 10% years while season 2016 long rains would happen in about 30% of years. Vapour pressure deficit (VPD) was lower during the first season compared with the second and third seasons. There were no extremes in temperature and radiation.

5.3.2 Experiment 1

5.3.2.1 Phenology

Stubble amount affected plant emergence ($P < 0.001$) but there were no effects of tillage or its interaction with stubble or N rate (data not shown). Eight days after sowing in 2015 long rains, 3 plants m^{-2} had emerged under stubble compared with 2 plants m^{-2} on bare ground. In 2015/2016 short rains and 2016 long rains seasons, the application of stubble reduced emergence to 1 plants m^{-2} compared with 3 plants m^{-2} on plots without stubble. Despite the differences in early emergence, the final plant densities were similar across the treatments.

Season ($P = 0.062$), tillage ($P = 0.463$), stubble amount ($P = 0.100$) and their interactions did not affect the reproductive phenological development of maize. However, lack of N delayed the occurrence of 50% pollen shed (R0) by three days compared with fertilised crops ($P < 0.001$), but there were no significant effects on phenology between the application of 80 and 120 kg N ha^{-1}.

5.3.2.2 Grain yield and yield components

Across seasons, season ($P < 0.001$), tillage ($P < 0.001$), N rate ($P < 0.001$) and season × tillage × stubble × N rate interactions ($P = 0.003$) affected grain yield. At the same scale of analysis, grain yield was unaffected by stubble ($P = 0.409$) but its effects varied with season ($P < 0.001$) and tillage ($P = 0.002$) while stubble × N rate interactions had no effects. P values, means and LSDs for main effects and interactions are presented in appendices Table 5.A1, Table 5.A2, Table 5.A3 and Table 5.A4.

Grain yield ranged from 2.3-5.3 t ha^{-1}. Although seasonal variations in grain yield are reported, results of the present study could not comprehensively quantify the effects of rainfall on crop responses. If we do not consider interactions, NT reduced grain yield by 5% compared with CT but yields varied with season. During 2015 long rains and 2015/2016 short rains, tillage did not affect grain yield. In 2016 long rains, NT produced 4.0 t ha^{-1} of grain compared with 4.3 t ha^{-1}, which represented 7% yield decline (Figure 5.2 a). Across seasons, stubble did not affect grain yield but its effects varied with season, whereby in 2015 long rains, yield increased by 5% with 3 t ha^{-1} of stubble but decreased by 10% under 5 t ha-1 of stubble (Figure 5.2 a). In 2015/2016 short rains, both 3 and 5 t ha^{-1} of stubble reduced yield by 7% compared with bare ground while during the 2016 long rains season, addition of 5 t ha^{-1} of stubble increased grain yield by 6% compared with both bare ground and 3 t ha^{-1} of stubble (Figure 5.2 b, c).

Across seasons, three-way interactions between tillage × stubble × N rate impacted grain yield ($P = 0.013$) and shoot biomass ($P < 0.001$), and the supply of N ameliorated the yield-reducing effects of both NT and the addition of stubble. Across seasons, when stubble was combined with the shortage of N supply, there were little differences in grain yield between both CT and NT. However, under N shortage, the addition of stubble reduced shoot biomass by 1.4 t ha^{-1} (23%) under NT compared with CT. There were no significant differences in grain yield and biomass between CT and NT with the addition of N.

Looking at individual seasons, stubble × N rate interactions ($P < 0.009$) were consistent and dominated the interactions between other treatments (Table 5.A2). However, three-way interactions between tillage × stubble × N rate varied with season, implying that rainfall effects were important. Considering the main effects of N rate, on average grain yield increased by 38% with N supply compared with the lack of fertilizer, while few differences were measured between 80 and 120 kg N ha-1. Similar effects were measured for kernel number, kernel weight, shoot biomass and harvest index (Figure 5.2 d-m).

Grain yield was correlated with kernel number ($R^2 = 0.90$, $P < 0.0001$) but weakly with kernel weight ($R^2 = 0.46$, $P < 0.0001$). Also, grain yield was positively correlated with shoot biomass

($R^2 = 0.57$, $P < 0.0001$) and harvest index ($R^2 = 0.43$, $P = 0.002$) but there was no relationship between biomass and harvest index ($R^2 = 0.01$, $P = 0.500$).

5.3.2.3 Crop growth rate

Four-way interactions between season × tillage × stubble × N rate did not affect crop growth rate (CGR) between V6 and flowering ($P = 0.340$) but this trait was affected by tillage × stubble × N rate ($P = 0.005$). P values, means and LSDs for main effects and interactions are presented in appendices Table 5.A1, Table 5.A3 and Table 5.A4. The pooled analysis between 2015 long rains and 2015/2016 short rains showed that NT and the retention of stubble reduced CGR by 0.6 g m^{-2} day^{-1} compared with both CT and bare ground. The effects of N rate on CGR were dominant ($P < 0.001$), while NT and stubble addition modified CGR in response to N supply. Shortage of N reduced CGR by 40% compared with N supply but there were little effects on this trait between the supply of 80 and 120 kg N ha-1. Stubble reduced CGR in unfertilized crops by 10% compared with bare ground (Figure 5.3 a, b). Kernel number, the main driver of variation in grain yield, was proportional to CGR (Figure 5.3 c, d). In turn, CGR was proportional to N nutrition index at flowering (NNI), as presented in Figure 5.3 e and f, and discussed below.

5.3.2.4 Nitrogen traits

Most N traits were determined for 2015 long rains and 2015/2016 short rains while in 2016 long rains only grain N concentration was measured. In 2015 long rains and 2015/2016 short rains, only stubble and N rate ($P < 0.001$) affected NNI at flowering and there were no treatment interactions ($P > 0.05$) (Appendix Table 5.A1). In these two seasons, N remobilization efficiency from the shoot to grain (NRE), was affected by the four-way interactions between season × tillage × stubble × N rate ($P < 0.001$) and three-way interactions between tillage × stubble × N rate ($P < 0.001$) but NRE was unaffected by tillage (Appendix Table 5.A1).

Nitrogen uptake in shoot and grain and agronomic efficiency were predominantly impacted by N rate, and consequently N supply modified the effects of tillage and stubble, while treatment interactions were few.

Table 5.2 presents N traits. Application of stubble reduced NNI by 8% compared with crops on bare ground while N supply improved this trait by 60% compared with the unfertilized control. However, NNI for both 80 and 120 kg N ha^{-1} were similar and close to 1. The supply of nitrogen increased N uptake in the shoot and grain by 80% during 2015/2016 short rains, and by more than 100% in the grain during 2016 long rains, compared with unfertilised control (Table 5.2). N uptake was positively correlated with grain yield (Figure 5.4 a), biomass (R^2 = 0.57, $P < 0.0001$) and CGR (R^2 = 0.47, P = 0.004). A positive but weak correlation was measured between grain yield and grain protein (R^2 = 0.26, P = 0.037).

Grain yield was proportional to NRE (Figure 5.4 b), and in turn, NRE was positively correlated with kernel number (R^2 = 0.58, $P < 0.0001$) and grain protein (R^2 = 0.55, $P < 0.0001$) but weakly associated with kernel weight (R^2 = 0.38, P = 0.017). In addition, NRE was correlated with both N uptake (R^2 = 0.48, P = 0.0002) and NNI (Figure 5.4 c). In these relationships, however, the scatter of data was largely dependent on N rate, which clustered as two groups, fertilized and unfertilized.

Nitrogen agronomic efficiency (AE) ranged from 11 to 26 kg kg^{-1} N. No-till reduced AE by 23% compared with CT while the effects of stubble were less. The supply of 120 kg N ha^{-1} reduced AE by 40% compared with 80 kg N ha^{-1} (Table 5.2). Tillage system did not affect N internal efficiency (IE) but the application of stubble improved this trait by 7% compared with stubble removal. Lack of N supply increased IE by 12% compared with N fertilization but there were no significant differences in IE between 80 and 120 kg N ha^{-1} (Table 5.2).

Nitrogen harvest index (NHI) ranged from 52-66%, and was neither affected by tillage nor stubble amount. However, fertilization increased NHI by 26% compared with the lack of N supply. Increased NHI was associated with high grain harvest index (Figure 5.4 d), high grain yield ($R^2 = 0.51$, $P < 0.0001$), and high N uptake ($R^2 = 0.48$, $P < 0.0001$) and NRE ($R^2 = 0.50$, $P < 0.0001$).

5.3.2.5 Storage of soil water, evapotranspiration and yield gaps

In addition to CGR and NNI, other potential mechanisms that led to variations in treatment effects on grain yield were water capture and storage at sowing, seasonal evapotranspiration and water use efficiency (WUE). Application of stubble increased rain water storage in 0-140 cm profile at sowing by 40 mm during 2015 long rains and 50 mm in 2015/2016 short rains, compared with bare ground. On bare ground, NT reduced water storage by 40 mm (10%) compared with CT in 2015/2016 short rains but tillage × stubble interactions were not measured in 2015 long rains ($P = 0.251$) (Table 5.3). Tillage, stubble and N rate did not affect evapotranspiration. In 2015/2016 short rains, when stubble was removed, NT reduced evapotranspiration by 6% compared with CT. WUE ranged from 3-8 kg ha^{-1} mm^{-1}. Tillage did not affect WUE but this trait increased with the addition of up to 3 t ha-1 of stubble but decreased by 25% on both bare ground and with the addition of 5 t ha^{-1} of stubble. The supply of N increased WUE by 33% during 2015 long rains and by 78% during 2015/2016 short rains compared with unfertilized control. WUE was strongly correlated with grain yield ($R^2 = 0.85$, $P < 0.0001$).

Large gaps were found between water-limited yield potential and actual yield. Yield gaps ranged from -0.79 to -3.4 t ha^{-1}, and N supply ($P > 0.001$) was the most effective in reducing these gaps. Application of stubble reduced yield gaps by 22% compared with stubble removal but there were no tillage effects ($P = 0.329$).

5.3.3 Experiment 2

5.3.3.1 Grain yield, crop N status and growth rate

Across 2015 long rains and 2015/2016 short rains, timing of N supply ($P < 0.001$) affected crop N nutrition as reflected by NNI (Figure 5.5 a). Crop growth rate was directly correlated with NNI (Figure 5.5 b), and CGR explained most of the variation in kernel number (Figure 5 c), which in turn explained 97% of the variation in grain yield (Figure 5.5 d). Tillage ($P = 0.769$) or its interaction with N timing ($P = 0.312$) did not affect grain yield (Figure 5.5 d). Timing of N supply as treatment N2 out-yielded the unfertilized control by 62%, and larger sowing applications (N1) by 20% and delaying N supply to later stages by 15% for N3 and 27% for N4.

5.3.3.2 Nitrogen traits

Nitrogen uptake and traits associated with N use efficiency were strongly affected by the timing of N supply but the effects of tillage or its interaction with N supply were small (Table 5.4). Treatment N1, N2 and N3 increased N uptake, NRE and grain protein compared with the unfertilized control and marginally with treatment N4 (Table 5.4). Treatment N2 had the highest AE at 22 kg kg^{-1} N while treatments N1 and N4 produced the least efficiency at 11 kg kg^{-1} N. In turn, N internal efficiency (IE) was 5% higher with phased N supply compared with the sowing application. Phasing N supply did not affect N harvest index (NHI) and the efficiency with which the acquired N was transformed into grain (PE) but the unfertilized control reduced NHI by 24%.

5.4 Discussion

This study provides new knowledge relevant to NT and stubble retention in maize-based cropping systems in sub-humid tropical environments, and provides insights on crop physiology and agronomy. The effects of N were dominant, and modified crop response to tillage and stubble. Nitrogen effects are to be expected, as they have been more widely documented in in smallholder systems in sub-Saharan Africa (Giller et al. 2009; Rusinamhodzi et al., 2011; Dimes et al., 2015). Increases in grain yield due to N application arose from increases in grain number, and grain number was proportional to CGR between V6 and flowering, the critical period for yield determination. CGR and NNI were some of the mechanisms that regulated crop growth and yield, in addition to water capture and storage, water use efficiency and traits associated with NUE. Treatment interactions or lack of interactions are discussed. As a pre-crop, maize did not increase disease and pest incidence.

5.4.1 Dominant effects of N on yield

Whilst poor soil fertility and low fertilization rates are wide-spread in SSA (Tittonell and Giller, 2013; Sommer et al., 2014; Vanlauwe et al., 2014; Pittelkow et al., 2015a), fertilizer N use has stagnated since the 1960s (Tittonell and Giller, 2013; Dimes et al., 2015). In the present study, N supply not only increased yield but modified crop response to both NT and stubble application, potentially by reducing N-immobilisation by the cereal stubble (Grahmann et al., 2013; Lundy et al., 2015). However, the application of more than 80 kg N ha^{-1} did not increase yield.

Interactions between N and tillage and stubble suggests that N influenced crop response to tillage and stubble in this environment. In some cases these interactions were not consistent over years (appendix Table 5.A2), with both positive and negative effects observed as stubble increased, implying that rainfall effects were important. In the drier 2016 long rains, the supply of N increased yield as stubble increased (Figure 5.2 c) but in the wetter seasons, the contribution of N to increase yield under stubble was limited (Figure 5.2 a and b). Thus, in maize-based NT and stubble retention systems in the sub-humid environments of Kenya, benefits of higher N rates would be obtained with low rainfall. However, timing of N supply on grain yield was generally not impacted by tillage system.

Explaining crop performance requires the understanding of mechanisms that regulate growth and yield, a case that is rarely reported in previous studies on NT and stubble retention systems (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Gastal et al. (2015) and Sadras and Lemaire (2014) demonstrate the robustness of NNI in the quantification of crop N status and interpretation of agronomic data. NNI close to 1 suggest that the crop's N concentration is sufficient to achieve maximum biomass, while NNI greater than 1 indicate luxury consumption of N, and those below 1 indicate N deficiency. In the present study, unfertilised crops were N deficient, as evident in the NNI of 0.6, while both 80 and 120 kg N ha^{-1} produced NNI close to 1 which suggests that N was non-limiting under these treatments.

The similarity in crop N nutrition between 80 and 120 kg N ha^{-1} explains why there were no significant differences in crop growth and yield between the two N rates, hence lower N rates could maximise yield in these environments (Kihara et al., 2012; Lundy et al., 2015). The positive relationship between CGR, grain yield and kernel number in the present study is consistent with theory and experiments (Andrade et al., 2005). In addition to N rate, better timing of N supply at sowing and V6 improved NNI and CGR hence higher yield compared with large sowing applications and delayed N supply.

5.4.2 NUE components

Tillage × stubble × N timing interactions on the measured variables imply that options for improving NUE in maize systems depend on higher N rates. However, the effect of timing of the supply of the same N rate (experiment 2) on grain yield and many traits associated with N use efficiency was independent of tillage system. With reference to the concept advanced by

Vanlauwe et al. (2014) whether fertilizer N should be included as a fourth principle of conservation agriculture in SSA, the present results suggest that NT and stubble retention do not require different N management strategies compared with conventional practices. Thus, in support of Sommer et al. (2014), present results demonstrate adequate N rates and better management of N supply are universally important in all cropping systems.

The ability to improve N uptake is the first step to increase the traits associated with N use efficiency (Gastal et al., 2015; Rossini et al., 2018). Crop growth rate regulates N uptake, but N uptake also controls CGR as demonstrated in the present relationship between CGR and NNI. In this study, high CGRs were associated with high NNI at flowering. At the same crop mass, critical N concentration in maize did not change with the increase of N rate from 80 to 120 kg N ha^{-1}, which reaffirms that there were little differences in N uptake and yield between the two N rates. However, optimal N rates and other avenues to improve NUE are necessary.

Nitrogen agronomic efficiencies (AE) in the present study were comparable to efficiencies in other parts of Africa (Vanlauwe et al., 2011). The 23% reduction in AE under NT compared with CT supports evidence that NUE is often low in NT systems (Grahmann et al., 2013). Universally, AE decreases with increasing N rates (Dobermann, 2007), and the present study demonstrates that in our study environment the supply of more than 80 kg N ha^{-1} may lead to N losses (Abril et al., 2007; Al-Kaisi and Kwaw-Mensah, 2007; Hickman et al., 2014) but timing N supply at sowing and V6 increased recovery efficiency. While N uptake is partly regulated by CGR, the present results, in agreement with others, suggest that N supply should be timed just before V6, when rapid crop growth begins (Gastal et al., 2015). However, providing a fraction of N at sowing might improve early vigour and weed competition (Kaur et al., 2018). For the short maturity DK8031 hybrid used in the present study, treatment N3 which supplied N uniformly at sowing, V6 and V12 did not appear to be as useful, most likely due to the delayed fraction of N supplied at V12.

The present study found a linear correlation between N uptake and grain yield, as have others (Setiyono et al., 2010; Ciampitti and Vyn, 2012). This relationship could be attributed to the positive relationship between grain HI and NHI, which implied that the allocation of N between the stover and the grain components was, to a large extent, dependent on the partitioning of mineral nutrients to the grain (Ciampitti and Vyn, 2012; Gastal et al., 2015). Grain HI positively associated with grain yield ($R^2 = 0.43$, $P = 0.013$), and the supply of N was the key driver of yield increases. Therefore, in addition to increased N uptake and recovery efficiency, the deployment of hybrids with high HI might be useful in increasing NUE in NT and stubble retention systems. The cost of fertilizer, which is two to six times higher in Africa than in Europe, the Americas and Oceania (Sanchez, 2002; Kelly et al., 2003), is an obstacle that should be addressed, along with consistent supply of the input to farmers. Future research should evaluate the effects of different N timing treatments at an economic optimum N rate, rather than the arbitrary treatment rate of 80 kg N ha^{-1}.

5.4.3 Tillage and stubble effects on yield

Tillage effects only appeared in the third season, whereby NT reduced grain yield by 6% compared with CT, indicating that the yield-reducing effects by N immobilization in NT develop soon after its implementation. Tillage × stubble interactions were observed but differences only appeared in treatments where stubble was removed, and the effects of stubble were dependent on seasonal rainfall. The reduction in grain yield and biomass by 10% under NT compared with CT supports previous evidence that the yield-reducing effects of NT are exacerbated when stubble is removed (Govaerts et al., 2009a; Rusinamhodzi et al., 2011; Kihara et al., 2012; Pittelkow et al., 2015a), due to increased surface run-off in NT soils compared with higher surface roughness on tilled soils (Gicheru et al., 2004; Guto et al., 2012). We did not measure rainfall infiltration rates but when stubble was removed, NT had on average 8% reduced water storage at sowing, compared with CT.

The application of 3 or 5 t ha^{-1} of stubble did not alter water capture and storage at sowing and neither did the interaction between these amounts of stubble and tillage systems. This implying that the benefits of stubble in water conservation could be maximised at 3 t ha^{-1} of stubble, irrespective of tillage system. Reinforcing this critical threshold of soil cover, WUE increased with addition of 3 t ha^{-1} of stubble but reduced with 5 t ha^{-1} of stubble, particularly during 2015/2016 long rains. Yield response to stubble was influenced by seasonal rainfall, with low grain yield when stubble was added during the first two wetter seasons but yield increased due to stubble addition during the comparatively drier third season. Previous studies show that the effect of stubble on water conservation depends on rainfall patterns, and its effects are negligible in both extremely dry or extremely wet environments (Monzon et al., 2006; Kader et al., 2017).

In southern Africa environments, when annual rainfall was lower than 600 mm, maize yield increased under NT and stubble retention compared with conventional practices but yield decreased with >1000 mm rainfall (Rusinamhodzi et al. 2011). In sub-humid environments of eastern Africa, the application of more than 1 t ha^{-1} stubble did not improve maize yield (Baudron et al. 2014) but stubble rates of up to 4 t ha^{-1} increased maize grain yield in drylands of eastern (Baudron et al., 2014) and southern (Mupangwa et al., 2007; Mupangwa et al., 2012) Africa. In the present study, rainfall exceeded evaporation during the first two seasons, while the third season was fairly dry, whereby rainfall matched evaporation only up to a few days before flowering. In our study environment, the drier season would happen in about 30% of years, whereas the wetter seasons would occur in less than 10% years.

Giller et al. (2015) summarised the results of (Heenan et al., 1994) and (Kirkegaard et al., 1994) to show that yield response to stubble largely depends on rainfall in the dryland wheat systems of southern Australia. The yield response to stubble in these systems varied with rainfall amount, whereby in wetter seasons (> 300 mm) stubble reduced yield compared with bare ground but in many occasions stubble did not have effects on grain yield when rainfall was < 250 mm (Heenan et al., 1994; Kirkegaard et al., 1994). In the present study, yield decline under stubble was associated with reduced CGR and NNI, compared with treatments lacking stubble, due to N immobilization (Giller et al., 2011), poor drainage (Rusinamhodzi et al., 2011) and low soil temperature (Cai and Wang, 2002). Mulch reduced soil temperature by 2-6.8 ^{o}C in maize systems in China (Cai and Wang 2002) and by 5-7 ^{o}C in wheat systems in southern Australia (Zhou et al., 2016), compared with bare ground, a condition that led to reduced vegetative growth in both systems.

5.4.4 Yield gaps

In this study, large gaps between actual yield and water-limited yield potential were measured. Lack of N supply and the removal of stubble led to large yield gaps. Global studies benchmark water-limited yield potential for maize at 20 kg ha^{-1} mm^{-1} (van Ittersum et al., 2013). This high efficiency is not comparable to the efficiencies typical of SSA due to variable distribution of rainfall, poor soil fertility and non-commercial production systems. A benchmark of 9.5 kg ha^{-1} mm^{-1} was used (Dimes et al., 2015), which is a realistic water-limited yield potential given the prevailing agro-ecological and socio-economic conditions in this region.

Closing grain yield gaps could simultaneously increase biomass yield, hence reduced competition for stubble allocation between soil cover and livestock feed (Jaleta et al., 2012; Valbuena et al., 2012; Baudron et al., 2015). However, the frequent lack of site-specific recommendations on the minimum amount of stubble that provides the benefits of soil protection and water conservation, and maximise yield, limits the scope for stubble allocation among competing uses (Giller et al., 2011; Paul et al., 2013; Kirkegaard et al., 2014).

Taken together, the relative value of stubble in water storage and low WUE with 5 t ha-1 of stubble, implies that grain yield in sub-humid environments of Kenya could be maximised at moderate amounts of stubble (~3 t ha^{-1}), hence amounts over this limit could be allocated to alternative uses. In dryland wheat systems of southern Australia, Scott et al. (2013) and Hunt et al. (2016) recommend 2-3 t ha^{-1} of stubble to maximise soil water infiltration and yield, and trade-offs between soil protection and grazing or stubble removal for livestock feed.

5.5 Conclusions

There was a strong interaction between rainfall and nitrogen supply modulating the effects of tillage and stubble on maize yield in a sub-humid tropical environment. Across all sources of variation, the nitrogen nutrition index explained most of the variation in crop growth rate in the critical window of yield determination, and this trait accounted for most of the variation in kernel number and yield. This emphasises the importance of interpreting crop agronomic responses in the light of physiological principles.

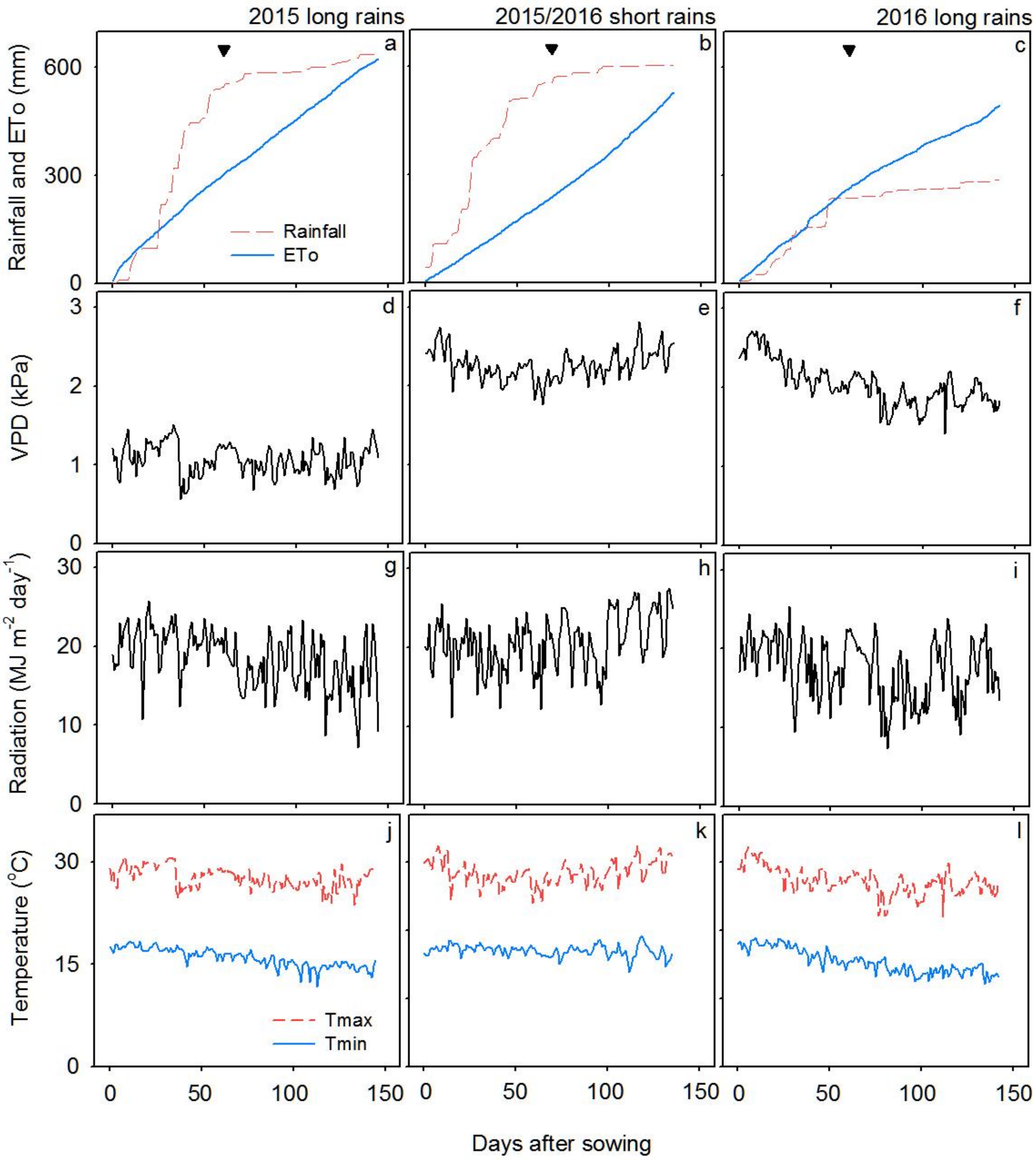


Figure 5.1. Growing conditions for maize crops in 2015 long rains (a, d, g, j), 2015/2016 short rains (b, e, h, k) and 2016 long rains (c, f, i, l) at Kenya Agricultural and Livestock Research Organisation, Embu research station. Cumulative rainfall and reference evapotranspiration (ETo) (a–c), vapour pressure deficit (VPD) estimated at the time of maximum temperature (d–f), daily radiation (g–i) and daily maximum (Tmax) and minimum (Tmin) temperature (j–k). Arrow heads indicate anthesis at 50% shedding of pollen. Data obtained from the Department of Meteorology, Embu research station.

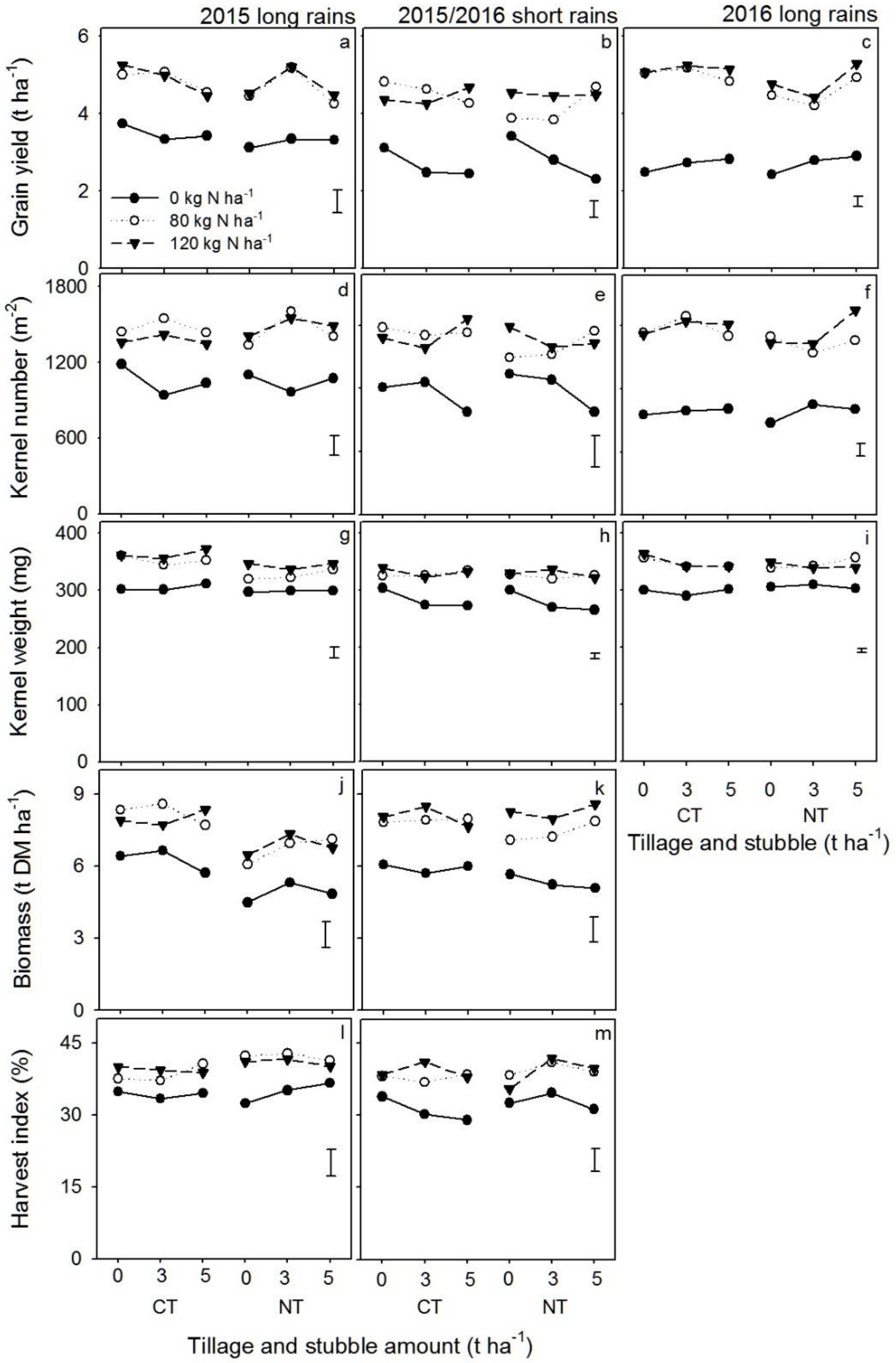


Figure 5.2. Grain yield (a-c), kernel number (d-f), kernel weight (g-i), shoot biomass (j, k) and harvest index (m, n) of maize grown under conventional tillage (CT) and no-till (NT), three amounts of stubble and three fertilizer N rates during the 2015 long rains (a, d, g, j, m), 2015/2016 short rains (b, e, h, k, n) and 2016 short rains (c, f, i) at the Kenya Agricultural and Livestock Research Organisation, Embu research station. From left to right, vertical bars are LSD at 0.05 probability to compare means for three-way interactions between tillage × stubble × N rate.

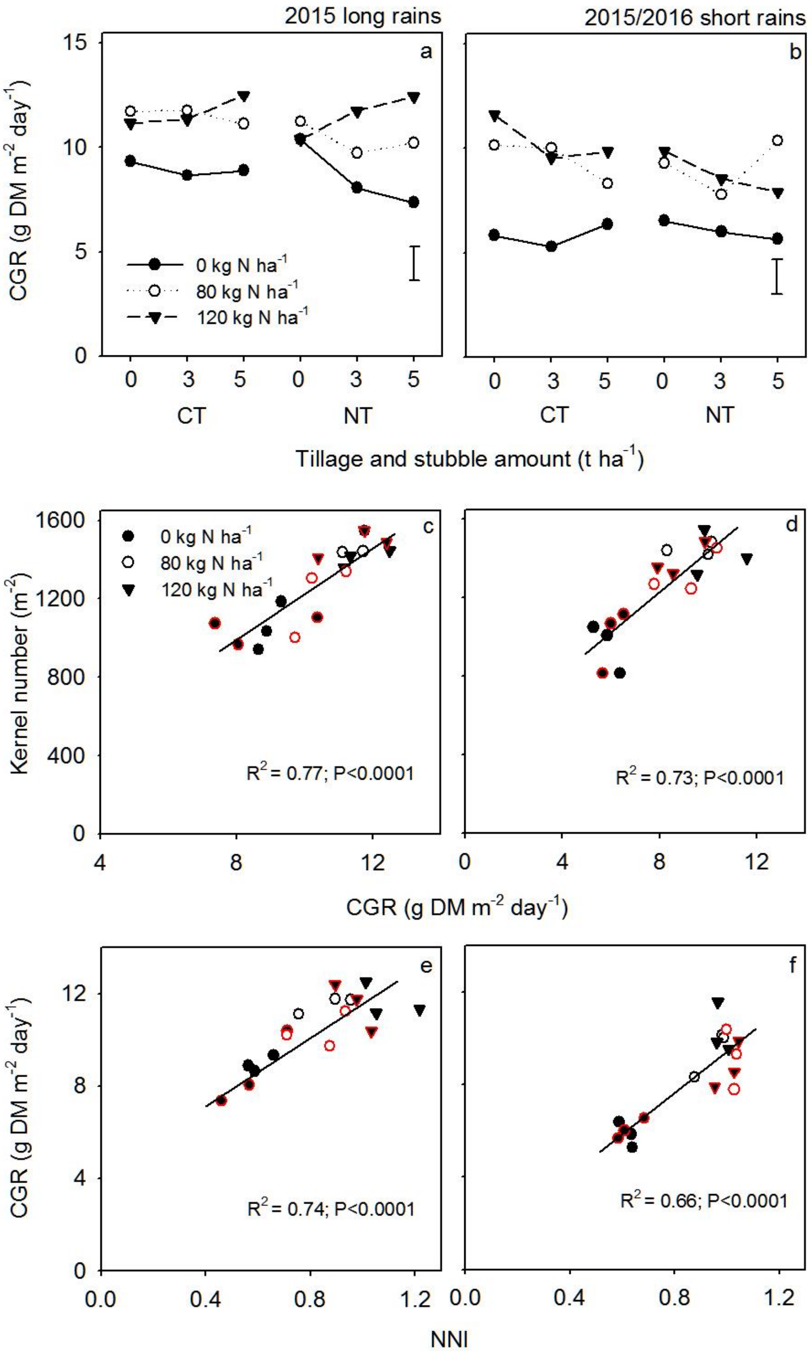


Figure 5.3. Crop growth rate (CGR), kernel number and nitrogen nutrition index (NNI) of maize grown under conventional tillage (CT) and no-till (NT), three amounts of stubble and three N rates during 2015 long rains (a, c, e) and 2015/2016 short rains (b, d, f) at the Kenya Agricultural and Livestock Research Organisation, Embu research station. CGR between six-leaf stage and flowering (a, b). Relationship between CGR and kernel number (c, d). Relationship between NNI and CGR (e, f). In ‘a’ and ‘b’, vertical bars are LSD at 0.05 probability to compare means for three-way interactions between tillage × stubble × N rate. In c-f, data were pooled across tillage, stubble and N rate. Symbols with dark edges are CT while symbols with red edges are NT. Lines are least square linear regressions.

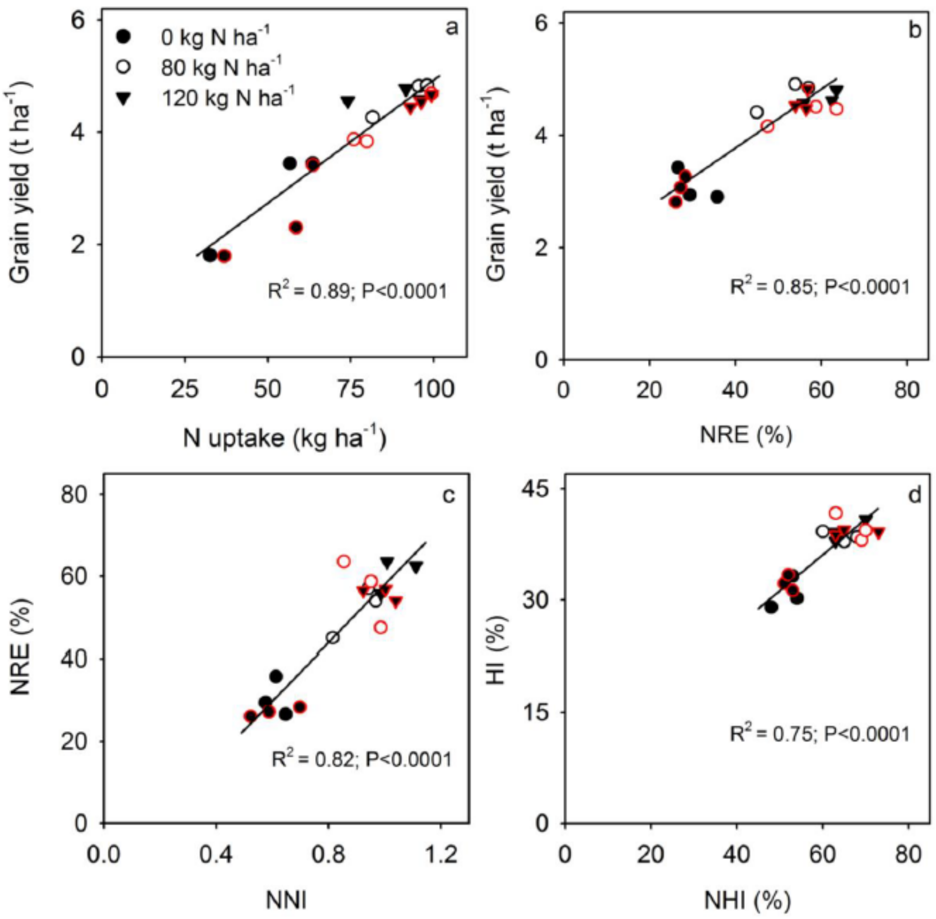


Figure 5.4. Relationships between grain yield and N use efficiency traits of maize grown under conventional tillage (CT) and no-till (NT), three amounts of stubble and three N rates during 2015 long rains and 2015/2016 short rains at Kenya Agricultural and Livestock Research Organisation, Embu research station. Relationship between N uptake and grain yield (a). Relationship between N remobilization efficiency and grain yield (b). Relationship between N remobilization and NNI (c). Relationship between N harvest index and grain HI (d). Symbols with dark edges are CT while symbols with red edges are NT. Lines are least square linear regressions.

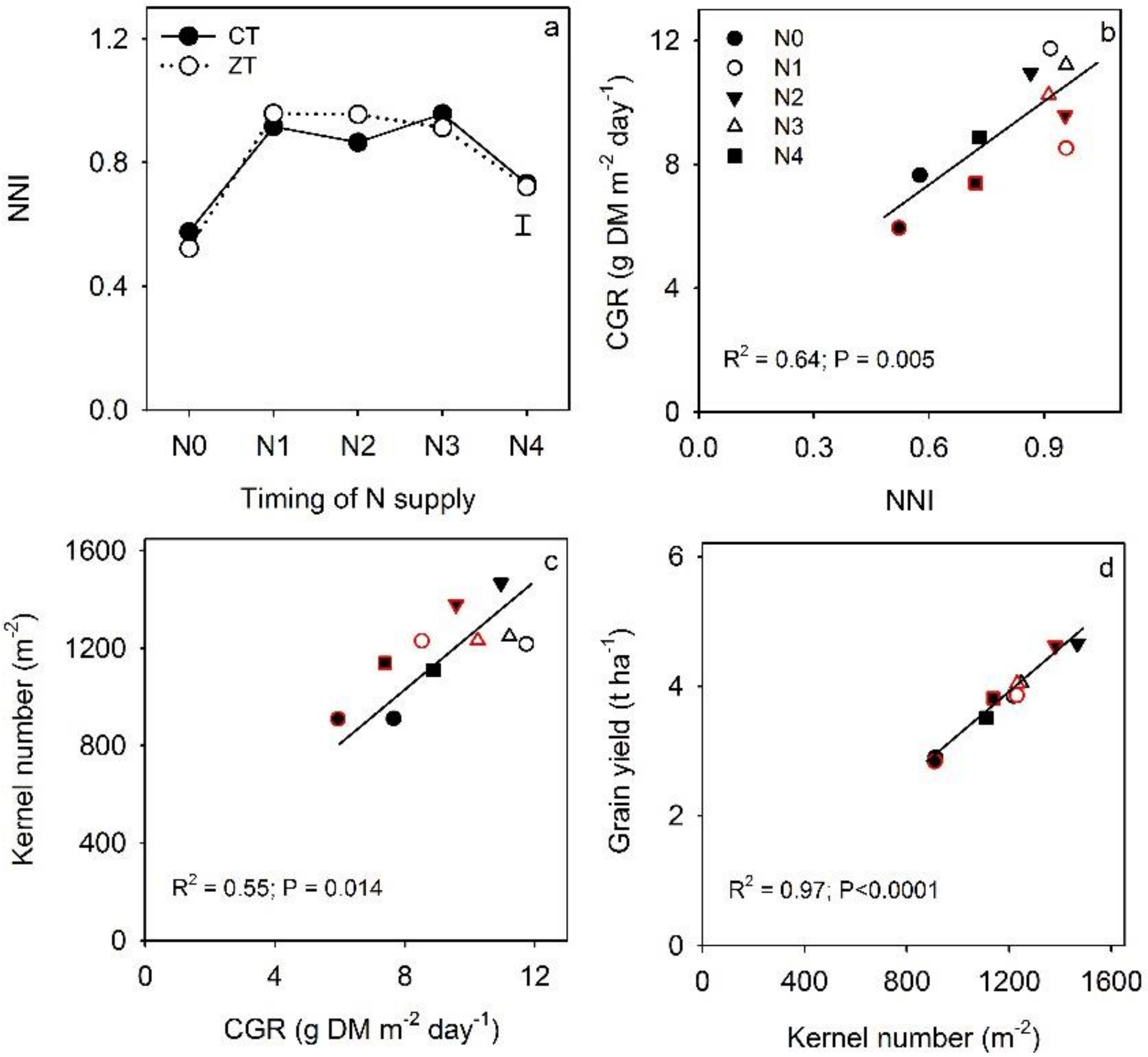


Figure 5.5. Crop N status, crop growth rate (CGR) and yield of maize grown under conventional tillage (CT) and no-till (NT) and five timings of N supply at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Crop N nutrition index (NNI); data pooled for 2015 long rains and 2015/2016short rains (a). Relationship between CGR and NNI (b). Relationship between CGR and kernel number (c). Relationship between kernel number and grain yield. In Figure a, vertical bar is LSD at 5% probability to compare means for N timing, where 80 kg N ha^{-1} was supplied as, N0: unfertilized control; N1: sowing application; N2: ⅓ at sowing and ⅔ at six-leaf stage (V6); N3: ⅓ at sowing, ⅓ at V6 and ⅓ at 12-leaf stage (V12); N4: ½ V6 and ½ V12. In b-d, lines are least square linear regression. Symbols with dark edges are CT while symbols with red edges are NT.

Table 5.1. Soil characterisation before trial establishment during 2015 long rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station.

Depth (cm)	Bulk density (g cm^{-3})	pH (H_2O)	OC%	NH_4 (kg ha^{-1})	$N0_3$ (kg ha^{-1})	Total N (kg ha^{-1})	K (mg kg^{-1})	Ca (ppm)	Mg (mg kg^{-1})	CEC (meq/100g)	P (mg kg^{-1})
0 - 15	1.17	4.7	2.5	1.1	20.7	21.8	5.8	2.4	2.4	17.0	35.3
15 - 30	1.04	4.6	2.4	1.0	23.8	24.8	5.2	2.3	2.3	16.0	30.1

Table 5.2. Indices of nitrogen use efficiency for maize grown under conventional tillage (CT) and no-tillage (NT), three amounts of stubble and three N rates during 2015 long rains, 2015/2016short rains and 2016 long rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Data from experiment 1.

Treatments	2015 long rains				2015/2016short rains							2016 long rains		
	NNI	NUs	AE	NRE	NNI	NUsg	AE	IE	NHI%	NRE	Grain P	NUg	AE	Grain P
Tillage														
CT	0.86a	13a	14a	45a	0.85a	77a	19a	54a	61a	50a	8.9a	69a	25a	9.1a
NT	0.80a	12a	15a	46a	0.89a	78a	15b	51a	62a	47a	9.8a	67a	20b	9.4a
Stubble														
0 t ha^{-1}	0.89a	13a	14b	44a	0.89a	77a	12c	53b	62a	47a	8.9b	67a	25a	9.3a
3 t ha^{-1}	0.85a	12a	19a	48a	0.88a	79a	17b	57a	63a	52a	9.4a	67a	21b	9.2a
5 t ha^{-1}	0.73b	13a	11b	45a	0.83b	82a	22a	56a	60a	48a	9.7a	71a	22b	9.2a
N rate														
0 kg N ha^{-1}	0.59c	12a		27b	0.62b	52b		57a	52b	31b	8.5b	39b		8.4b
80 kg N ha^{-1}	0.86b	13a	17a	51a	0.98a	88a	20a	50b	65a	57a	9.7a	80a	26a	9.6a
120 kg N ha^{-1}	1.03a	12a	12b	58a	0.99a	92a	14b	50b	66a	59a	9.7a	85a	19b	9.8a
ANOVA for interactions														
Tillage × stubble	0.651	0.096	ns	0.047	0.505	0.096	0.001	0.663	0.002	0.011	0.097	0.346	0.001	0.006
Tillage × N rate	0.531	0.026	ns	0.013	0.513	0.038	**	0.581	0.006	0.091	0.321	0.082	*	0.213
Stubble × N rate	0.678	0.437	ns	0.439	0.962	0.001	ns	0.001	0.133	0.099	0.083	0.494	ns	0.507
Tillage × stubble × N rate	0.871	0.192	ns	0.714	0.845	0.003	0.001	0.468	0.019	0.001	0.242	0.190	ns	0.684

NNI: N nutrition index (unitless); NUs: N uptake in the shoot (kg N ha^{-1}); NUg: N uptake in the grain (kg N ha^{-1}); NUsg: N uptake in the grain and shoot (kg N ha^{-1}); AE: agronomic efficiency (kg kg^{-1}); IE: internal efficiency (kg kg^{-1}), NHI: N harvest index (%); NRE: N remobilization efficiency (%); Grain P: grain protein content (%). Within a column, means followed by the same letter are not significantly different at 0.05 probability. NNI and NRE were not determined in 2016 long rains while grain protein content was not determined in 2015 long rains. IE and NHI were determined in 2015/2016 short rains only.

Table 5.3. Soil water storage, evapotranspiration and water use efficiency (WUE) for maize grown under conventional tillage (CT) and no-tillage (NT) and three amounts of stubble during 2015 long rains and 2015/2016 short rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Data from experiment 1.

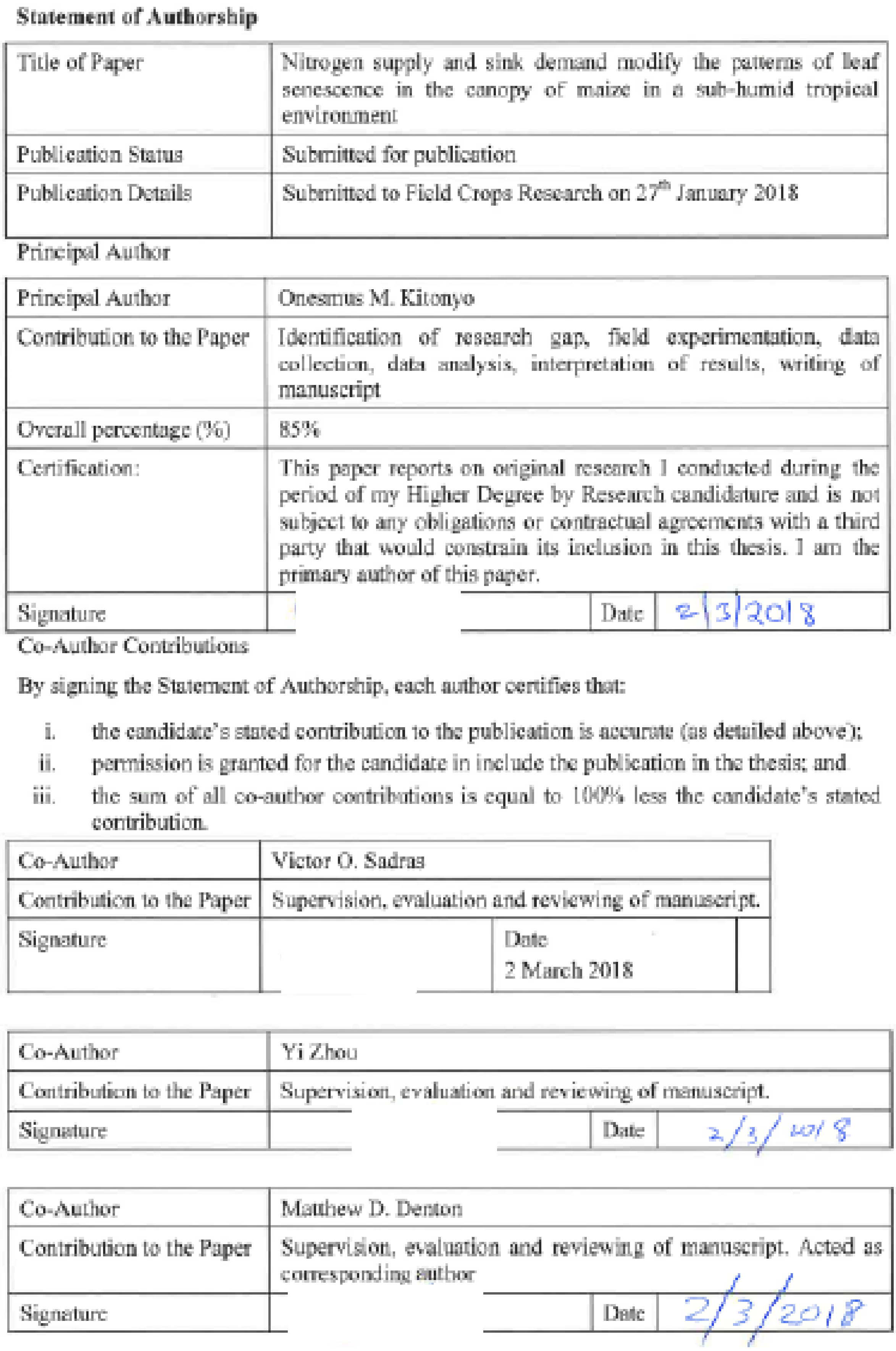
Amount of stubble	Soil water storage at sowing (mm)				Evapotranspiration (mm)				WUE (kg ha^{-1} mm^{-1})			
	2015 long rains		2015/2016 short rains		2015 long rains		2015/2016 short rains		2015 long rains		2015/2016 short rains	
	CT	NT	CT	NT	CT	NT	CT	NT	CT	NT	CT	NT
0 t ha^{-1}	656a	617b	419b	379c	761a	750a	576b	541c	4.9b	4.3b	5.4b	6.1b
3 t ha^{-1}	659a	675a	460a	450a	785a	832a	612a	585ab	6.6a	6.2a	7.4a	6.9a
5 t ha^{-1}	678a	682a	446a	464a	750a	758a	595ab	619a	5.4a	5.1a	5.8b	5.7b

Within a column, means followed by the same letter are not significantly different at 0.05 probability.

Table 5.4. Indices of nitrogen use efficiency for maize grown under conventional tillage (CT) and no-tillage (NT) and timing the supply of 80 kg N ha^{-1} during 2015 long rains, 2015/2016short rains and 2016 long rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Data from experiment 2.

Treatments	2015 long rains			2015/2016short rains								2016 long rains		
	NUs	AE	NRE	NUsg	AE	RE	IE	PE	NHI	NRE	Grain P	NUg	AE	Grain P
Tillage														
CT	54a	8a	41a	116a	21a	61a	51a	54a	62a	48a	9.2b	60a	14a	9.1a
NT	53a	8a	47a	124a	25a	66a	46a	66a	64a	53a	9.9a	59a	13a	9.0a
N supply														
N0	47b		25c	73b			45b		52b	31c	9.4a	41c		8.2b
N1	62a	8ab	50a	123a	19b	52b	48b	55a	62a	49ab	9.3a	58b	8b	9.4a
N2	56a	13a	51a	144a	28a	78a	50a	58a	65a	57ab	9.7a	81a	25a	9.5a
N3	58a	8b	54a	138a	25ab	69a	50a	63a	69a	63a	9.9a	62b	13b	9.3a
N4	54a	4b	37b	121a	19b	54b	51a	65a	65a	53ab	9.5a	56b	10b	9.0a
ANOVA														
Interaction	0.135	0.602	0.061	0.111	0.912	0.079	0.028	0.156	0.074	0.298	0.418	0.557	0.864	0.524

N0: unfertilized control; N1: sowing application; N2: ⅓ at sowing and ⅔ at six-leaf stage (V6); N3: ⅓ at sowing, ⅓ at V6 and ⅓ at 12-leaf stage (V12); N4: ½ V6 and ½ V12; NUs: N uptake in the shoot (kg N ha^{-1}); NUg: N uptake in the grain (kg N ha^{-1}); NUsg: N uptake in the grain and shoot (kg N ha^{-1}); AE: agronomic efficiency (kg kg^{-1}); RE: recovery efficiency (kg kg^{-1}); IE: internal efficiency (kg kg^{-1}); PE: physiological efficiency (kg kg^{-1}); NHI: N harvest index (%); NRE: N remobilization efficiency (%); Grain P: grain protein content (%). Within a column, means followed by the same letter are not significantly different at 0.05 probability.



Statement of Authorship

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Principal Author

Principal Author	Onesmus M. Kitonyo		
Contribution to the Paper	Identification of research gap, field experimentation, data collection, data analysis, interpretation of results, writing of manuscript		
Overall percentage (%)	85%		
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	2/3/2018

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.

Co-Author	Victor O. Sadras	
Contribution to the Paper	Supervision, evaluation and reviewing of manuscript.	
Signature		Date 2 March 2018

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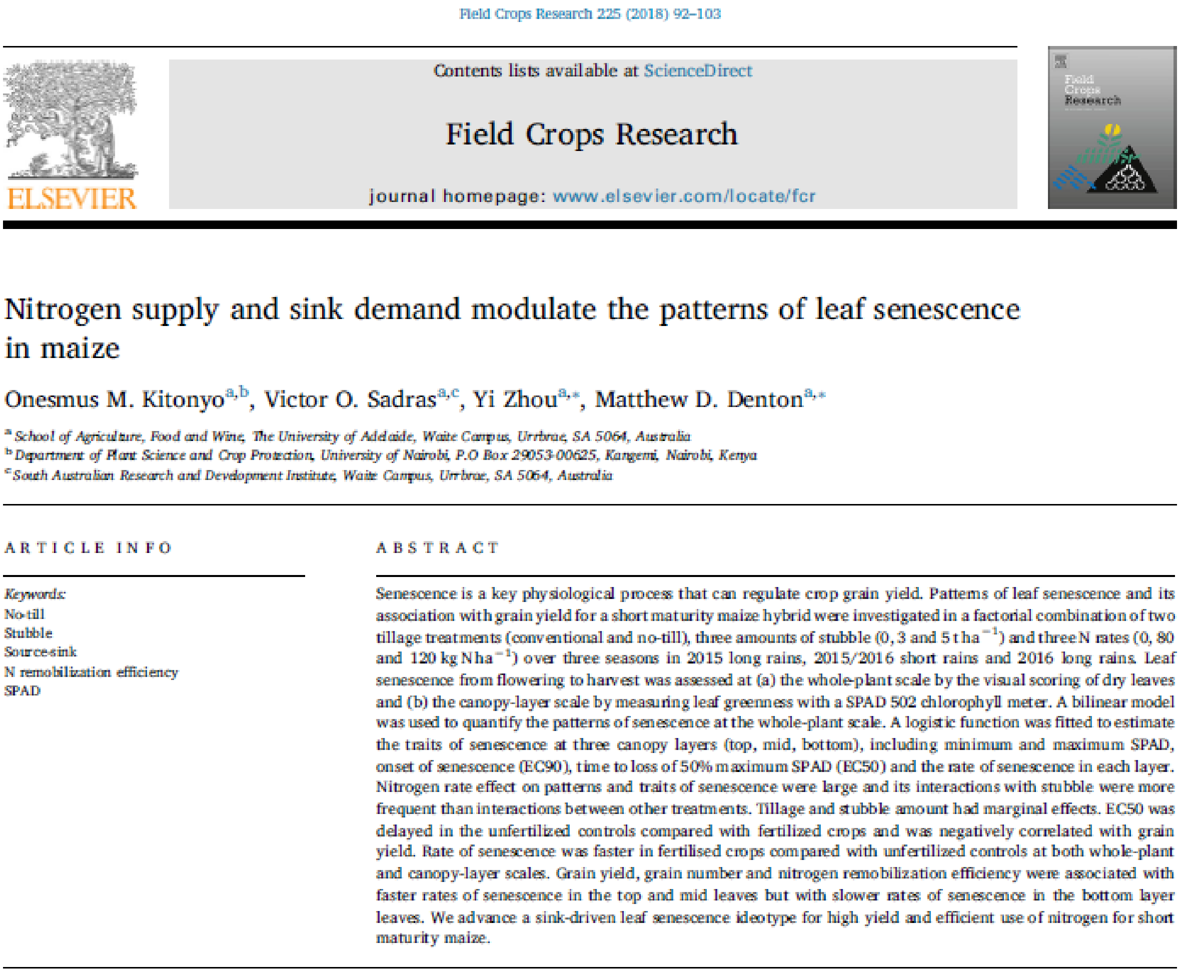
Co-Author	Matthew D. Denton		
Contribution to the Paper	Supervision, evaluation and reviewing of manuscript. Acted as corresponding author		
Signature		Date	2/3/2018

Chapter 6 Nitrogen supply and sink demand modulate the patterns of leaf senescence in maize



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Nitrogen supply and sink demand modulate the patterns of leaf senescence in maize

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Stubble
Source-sink
N remobilization efficiency
SPAD

ABSTRACT

Senescence is a key physiological process that can regulate crop grain yield. Patterns of leaf senescence and its association with grain yield for a short maturity maize hybrid were investigated in a factorial combination of two tillage treatments (conventional and no-till), three amounts of stubble (0, 3 and 5 t ha^{-1}) and three N rates (0, 80 and 120 kg N ha^{-1}) over three seasons in 2015 long rains, 2015/2016 short rains and 2016 long rains. Leaf senescence from flowering to harvest was assessed at (a) the whole-plant scale by the visual scoring of dry leaves and (b) the canopy-layer scale by measuring leaf greenness with a SPAD 502 chlorophyll meter. A bilinear model was used to quantify the patterns of senescence at the whole-plant scale. A logistic function was fitted to estimate the traits of senescence at three canopy layers (top, mid, bottom), including minimum and maximum SPAD, onset of senescence (EC90), time to loss of 50% maximum SPAD (EC50) and the rate of senescence in each layer. Nitrogen rate effect on patterns and traits of senescence were large and its interactions with stubble were more frequent than interactions between other treatments. Tillage and stubble amount had marginal effects. EC50 was delayed in the unfertilized controls compared with fertilized crops and was negatively correlated with grain yield. Rate of senescence was faster in fertilised crops compared with unfertilized controls at both whole-plant and canopy-layer scales. Grain yield, grain number and nitrogen remobilization efficiency were associated with faster rates of senescence in the top and mid leaves but with slower rates of senescence in the bottom layer leaves. We advance a sink-driven leaf senescence ideotype for high yield and efficient use of nitrogen for short maturity maize.

6.1 Introduction

No-till (NT) management and stubble retention protects the soil from water and soil erosion, improves soil water capture and storage, and promotes soil chemical and physical properties, which leads to higher yields (FAO, 2015). Previous studies on the impact of these practices on crops and cropping systems are restricted to crop growth and yield, water and nutrient economy, with little emphasis on physiological processes (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Kitonyo et al. (2018) or Chapter 5 of this thesis concluded that nitrogen (N) modifies crop response to NT and stubble retention in a sub-humid tropical environment, by altering N nutrition index (NNI), which explained most of the variation in crop growth rate in the critical window of yield determination. Crop growth rate in turn accounted for most of the variation in kernel number and yield while grain yield was linearly correlated with N remobilization efficiency (NRE), which is defined as the difference in shoot N at flowering and harvesting (Kitonyo et al., 2018). The manipulation of patterns of leaf senescence that impact photosynthesis, harvest index and N remobilization, and potentially N use efficiency has received little attention in cropping systems (Masclaux-Daubresse et al., 2010; Wu et al., 2012).

In monocarpic plants such as maize, leaf senescence is a developmental process that involves the gradual loss of green leaf area in the older leaves and finally the whole plant (Gregersen et al., 2013). High yield potential in maize has been achieved through the extension of photosynthetic duration and increased harvest index, two traits that are related with leaf senescence (Bänziger et al., 2002). Genetic and environmental factors trigger and regulate senescence (Gregersen et al., 2013; Thomas and Ougham, 2015). There is considerable genetic variation in the patterns of senescence in maize (Gregersen et al., 2013). Broadly, senescent hybrids senesce earlier irrespective of growing conditions while the “stay-green” phenotypes show prolonged green leaf area duration (Gregersen et al., 2013).

The genetic control of senescence is complex and involves both programmed cell death and hormonal regulators (Wilkinson and Davies, 2002; van Doorn and Woltering, 2004; Liu et al., 2005; Lim et al., 2007). Hormonal signals such as abscisic acid, ethylene, cytokinins and jasmonic acid regulate senescence in response to stress and source-sink ratios (Harding et al., 1990; Staswick, 1992; Schippers et al., 2007; Davies and Gan, 2012). Environmental factors like water, nutrient stress and temperature modulate senescence (Gregersen, 2011). Both leaf area duration and green leaf area proportionally impact grain yield (Gregersen et al., 2013).

The ratio of assimilate supply (i.e., source) to demand (i.e., sink) during grain filling also regulates senescence, and impacts nutrient fluxes from the senescing leaves to the grain (Feller et al., 2007; Wei et al., 2018). In some species, for example tomato, low source:sink ratio favours senescence but in maize the response of senescence to source:sink ratio varies with hybrid (Crafts-Brandner and Poneleit, 1987; Sadras et al., 2000).

The translocation of N from senescing tissues to the grain indirectly impacts N use efficiency (NUE) (Masclaux-Daubresse et al., 2008; Gregersen, 2011). At the crop level, NUE, the ratio between grain yield and fertilizer supplied (Dobermann, 2007), depends on N uptake from the soil, internal utilization and the subsequent partitioning and remobilization of N to the grain (Masclaux-Daubresse et al., 2010). Nitrogen remobilisation is fundamental for crop N economy since it controls a large part of N fluxes from sources to sinks (Masclaux-Daubresse et al., 2008). N remobilization efficiency (NRE) accounted for 85% variation in grain yield in both maize (Kitonyo et al., 2018) and wheat (Barraclough et al., 2014). Despite the fundamental role played by N remobilization in crop N economy (Yang and Udvardi, 2017), patterns of leaf senescence have been least explored for the improvement of NUE in NT and stubble retention systems.

In the model advanced by Christopher et al. (2014), the key traits of senescence are quantified: the minimum leaf greenness before harvesting, maximum greenness before the onset of senescence, the onset of senescence, and the progression and rate of senescence. Profiles of leaf senescence vary within the spatial arrangement of leaves, which affects light interception and attenuation, thus shaded leaves often senesce earlier than unshaded ones (Maddonni et al., 2001). In addition, carbon assimilation and N transfer from senescing leaves to the grain varies with leaf position (Feller et al., 2007). The middle leaves and top leaves are a source of N for maize grain filling while the bottom leaves export more N to the roots than to the grain (Feller et al., 2007).

This study investigated the patterns of leaf senescence in maize and their association with yield in a context of NT and stubble retention. Our aims were to (i) characterize the time-course of post-flowering leaf senescence under conventional tillage and NT, and with three stubble and three N rates, and (ii) establish relationships between senescence and grain yield, yield components, crop N status quantified as NNI, as well as traits related to nitrogen use efficiency.

6.2 Materials and methods

The experiments are fully described in Chapter 5. Here we briefly summarise treatments and experimental design, and focus on measurements and analysis of senescence.

6.2.1 Site

A field study was conducted at the Kenya Agricultural and Livestock Research Organisation, Embu research station (0.515 ^{o}S, 37.273 ^{o}E, 1425 masl), for three consecutive seasons during the 2015 long rains, 2015/2016 short rains and 2016 long rains. Embu is in the upper midland zone three (UM3) and has a sub-humid climate with mean annual temperature of 22 ^{o}C (Jaetzold et al., 2006). In this environment, there are two five-month rainy seasons; the long rains that occur between April and August, and the short rains season from October to February. Soils are deep (> 2.5 m) well-weathered humic nitisols with low exchangeable bases and relatively high P-sorption, and of medium to low fertility (Jaetzold et al., 2006).

6.2.2 Treatments and experiment design

Effects of conventional tillage (CT) and no-till (NT), three amounts of maize stubble (0, 3 and 5 t ha^{-1}) and three fertilizer N rates (0, 80 and 120 kg N ha^{-1}) were evaluated under continuous maize cropping over three seasons during 2015 long rains, 2015/2016 short rains and 2016 long rains. Tillage and stubble treatments were applied two weeks before sowing in the same plot in all seasons. Prescribed amounts of stubble were supplied in the first season while in the next two seasons, additional stubble allowed for undecomposed material. In CT plots stubble was chopped to small pieces and incorporated into the soil by digging to 15 cm depth while the NT treatments were not disturbed and stubble was surface applied without cutting. Fertilizer N was sourced from urea (46% N) and side-banded on the sowing rows in the fractions of ⅓ at sowing and ⅔ at six-leaf stage. All plots received 60 P kg ha^{-1} of basal fertilizer as triple super phosphate that was side banded in the sowing rows.

Experiments were laid out as split-split plot design with three replications. Tillage systems formed the main plots, stubble amount the sub-plots and N rate formed the sub-sub plots. The main plots measured 31 m long and 12.25 m wide, sub-plots were 28 m x 3.75 m while the sub-sub plots were 7 m × 3.75 m. In all plots, sowing was done manually by opening 5 cm deep holes with a sharp machete to hold seed and fertilizer.

A locally adapted short-maturity DeKalb (DK) 8031 maize hybrid was used. DK 8031 has a fast dry-down syndrome and has a yield potential of 5-8 t ha^{-1}, and is frequently used as a commercial check in breeding studies in Kenya (Abate et al., 2017; Beyene et al., 2017). Crops were sown at the onset of rains: on 25th March for 2015 long rains season, 19th October for 2015/2016 short rains season and 3rd April for 2016 long rains season. Crops were sown with 0.75 m between rows and 0.25 m within rows to give an approximate density of 5.3 plants m^{-2}. Weeds were controlled with Roundup® (glyphosate) before sowing and Dual Gold® (960 g L-1 S-metolachlor) after sowing in both tillage systems while in-crop weeds were removed by hoe-weeding in CT plots but with Twiga 2, 4-D® (Dimethylamine salt and 2, 4-diclorophenoxy acetic acid) in NT plots. Insect pests were controlled with Thunder® (100 g L-1 imidacloprid) at 300 mL ha^{-1} (see Chapter 5 or Kitonyo et al., 2018).

6.2.3 Measurements

A phenological scale (CIMMYT, 2017) was used to determine flowering as 50% shedding of pollen. Growing degree days (^{o}C d) were computed as the mean day temperature minus 10 oC, which is the base temperature for maize (Bonhomme, 2000). Timing of maize maturity was determined by dislodging kernels and observing the development of a black layer at the point of kernel attachment to the cob.

Five plants per plot were tagged for the assessment of leaf senescence at the whole-plant scale. Senescence was scored visually from a few days after flowering through to maturity by recording leaves that presented more than 50% green leaf area. At the same phenological range, vertical profiles of leaf greenness were measured from two tagged plants per plot. From top to bottom leaves, leaf greenness was measured using SPAD 502 chlorophyll meter (Konica Minolta, Japan), at several points of the whole-leaf length and the mean SPAD unit was recorded. Leaf counts and SPAD measurements were sampled at least every two weeks. Even though rare for DK8031, in the circumstances where a plant produced two ears, the lower ear was removed.

Kitonyo et al. (2018) described yield collection and computations for traits related to N use efficiency. Briefly grain yield was measured from a harvest area of 14.6 m^2, and kernel number m-2 and 1000 kernel weight were determined in all seasons. Grain protein was measured by near infra-red spectroscopy using FOSS Infratec® 1241 grain analyser during 2015/2016 short rains and 2016 long rains only. Nitrogen nutrition index at flowering was calculated as the ratio between the actual N concentration of the shoot biomass and the critical N concentration at the same crop mass (Gastal et al., 2015). Critical N concentration (N_c), the minimum N concentration required to maximise biomass, was computed as: Nc = 3.4 * (DM)-0.37; where DM is the actual crop biomass in t ha^{-1} (Justes et al., 1994; Plénet and Lemaire, 1999). N remobilization efficiency (NRE) was calculated as (N content at flowering – N content at maturity)/N content at flowering.

6.2.4 Analysis of senescence

At the whole-plant level, rate of senescence was quantified by fitting a bilinear model of leaf counts against thermal time from flowering using the piece-wise routine of SigmaPlot version 10.0 (Systat Software, Inc., San Jose California USA, www.systatsoftware.com) (Eqs. (6.1 a) and (6.1 b)). This model was used to describe monocarp senescence in fruit (Bonada et al., 2013), and estimated slope 1 (Eq. (6.1 a)), slope 2 (Eq. (6.1 b)) and a breakpoint thermal time at the transition from the first to the second slope.

$$Slope\ 1 = \frac{y_1(T-t)+y_2(t-t_1)}{T-t_1} \qquad \text{For, } T > t_1 \qquad (6.1\text{ a})$$

$$Slope\ 2 = \frac{y_2(t_1-t)+y_3(t-T)}{t_1-T} \qquad \text{For, } T < t_1 \qquad (6.1\text{ b})$$

In Eqs. (6.1 a) and (6.1 b), y_1 is number of green leaves at the onset of senescence, y_2 is the number of green leaves at harvesting, y_3 is the number of green leaves at breakpoint, T is the breakpoint (^{o}C d), t is onset of senescence (^{o}C d) and t_1 is the end of senescence (^{o}C d). The bilinear model was fitted for each plot.

The profiles of leaf greenness were separated into three canopy layers: the mid layer of which comprised the ear leaf, one leaf below the ear leaf and two leaves above the ear leaf. The top and the bottom layers consisted of the leaves above and below the mid layer, respectively. A logistic regression function was adopted to fit a time-course of leaf senescence to quantify the traits of senescence at each canopy layer using SigmaPlot (Christopher et al., 2014; Kitonyo et al., 2017) (Eq. 6.2).

$$y = SPAD_{min} + \frac{SPAD_{max} - SPAD_{min}}{1 + (\frac{x}{EC50})^{SR}} \tag{6.2}$$

Eq. 6.2 estimated four parameters, including the minimum SPAD before harvesting ($SPAD_{min}$), maximum SPAD before the onset of senescence ($SPAD_{max}$), time to loss 50% of $SPAD_{max}$ (EC50) (^{o}C d) and the rate of leaf senescence (SR) (SPAD units ^{o}C d^{-1}). A fifth parameter, the onset of senescence (EC90) (^{o}C d) was calculated. The logistic function was fitted for each plot but some trajectories lacked end tail, so $SPAD_{min}$ was unreliable and not analysed.

A senescence ideotype for a short maturity hybrid was designed to allow for the comparison of patterns of senescence as a consequence of grain yield. In the three leaf-layers and across the three seasons, leaf greenness was plotted against thermal time from a few days after flowering through to maturity. The patterns of senescence were regulated by grain yield and the ideotype was driven by either high yield under the application of fertilizer or low yield when fertilizer was not added.

As detailed in Kitonyo et al. (2018), water use was estimated as seasonal evapotranspiration, the change in soil water content between sowing and harvesting plus rainfall during the same period (French and Schultz, 1984). A correlation matrix was used to analyse the impact of evapotranspiration on the patterns of leaf senescence.

Analysis of variance (ANOVA) was conducted to assess the experimental sources of variation for all traits including parameters of fitted curves using GenStat 18th Edition (VSN International Ltd., Hertfordshire, UK) SAS 9.2 for windows, at $P \leq 0.05$ probability. Split-split plot design in GenStat was used, and tillage × stubble × N rate were used as the treatment structure. Treatments were assigned the main (tillage), sub-plots (stubble) and sub-sub plots (N rate), as described in our experimental design. Leaf layers were not randomly assigned in the ANOVA. Residuals for all measured variables were checked for normal distribution, and transformations were not required. For across season or canopy layer analysis, a design in GenStat was selected, where season (or leaf layer) × tillage × stubble × N rate were set up as treatment structure. Differences between treatment means were compared and separated using Fisher's least significant difference (LSD) test at $P \leq 0.05$ (Gomez and Gomez, 1984). Relationships between variables were examined by correlations and regression analysis.

6.3 Results

6.3.1 Post-flowering growing conditions

Figure 6.1 summarises post-flowering rainfall, mean daily temperature and evapotranspiration. Accumulated rainfall was 75 mm in 2015 long rains and rain events intensified as the crops aged. In 2015/2016 short rains, 50 mm was received, where larger events occurred a few days after flowering and rainfall tapered-off as crops aged. Post-flowering rainfall was evenly distributed during the 2016 long rains, which received 50 mm. There were no large within-season variations in evapotranspiration and temperature but evapotranspiration was lower during the third season. Detailed growing conditions from sowing to flowering are reported in Kitonyo et al. (2018).

6.3.2 Grain yield and yield components

We reported grain yield, yield components and N traits in Kitonyo et al. (2018). Briefly, grain yield varied with season and ranged from 2.3-5.3 t ha^{-1} but tillage and stubble effects were small. N rate effects were large, and, on average, N fertilization increased grain yield by 40% compared with the unfertilized control but there were no significant differences in grain yield between 80 and 120 kg N ha^{-1}. Grain yield was a function of kernel number (R^2 = 0.90, P < 0.001) and kernel weight (R^2 = 0.46, P < 0.001). NRE accounted for 85% (P < 0.001) variation in grain yield. NRE was proportional to NNI at flowering (R^2 = 0.85, P < 0.001). Grain protein was weakly correlated with grain yield (R^2 = 0.26, P = 0.037), and marginally with kernel weight (R^2 = 0.11, P = 0.047). Fertilized crops had 15% higher grain protein than unfertilized controls but with little differences between 80 and 120 kg N ha^{-1}.

6.3.3 Time-course of leaf senescence at the whole-plant level

Figure 6.2 shows the time-course of leaf senescence at the whole-plant level, and Table 6.1 the fitted parameters. The progression of leaf senescence followed a two-phase pattern (Eq, 1). Across seasons, season (P < 0 .001) and N rate (P = 0.003) affected the rate of senescence, and the effects were larger for slope 2 compared with slope 1. Tillage (P > 0.050) did not affect rate of senescence while stubble amount impacted slope 1 (P = 0.010) but not slope 2 (P = 0.102). At the same scale of analysis, season (P < 0.001), tillage (P < 0.001), stubble (P = 0.005) altered the breakpoint between the slope 1 and slope 2 but for individual season analysis, the effects of tillage, stubble and many interactions were small. Overall, N rate effects on the breakpoint were absent (P = 0.98). However, when seasons were analysed separately lack of N delayed the breakpoint compared with N supply (Table 6.1). On average, the breakpoint was delayed by 86 ^{o}C d (~ 7 days) in the unfertilized crops compared with fertilized counterparts but there were no significant differences in this trait between 80 and 120 kg N ha^{-1}. This was concomitant with the fast rate of senescence in fertilized crops compared with unfertilized controls, particularly during 2016 long rains.

6.3.4 Time-course of leaf senescence in the canopy layers

Figure 6.3, 6.4 and 6.5 show the time-course of leaf senescence at three canopy layers. N rate effects were large throughout the canopy layers (Figure 6.3). The unfertilized crops had reduced leaf greenness compared with their fertilized counterparts. However, there were no significant differences in leaf greenness in crops supplied with 80 and 120 kg N ha^{-1}, except for greener bottom leaves at 120 kg N ha^{-1} compared with 80 kg N ha^{-1} in the first season. During the third season, N rate did not alter the pattern of senescence in the middle and bottom-layer leaves.

Stubble effects were not observed in the first two seasons (Figure 6.4). However, in the third season, mid-layer leaves of crops on bare ground had reduced greenness compared with crops with stubble. Tillage system did not alter leaf greenness at any of the three canopy layers (Figure 6.5).

6.3.5 Traits of senescence

Figure 6.6 shows the leaf senescence traits in canopy layers, as defined by the parameters of the logistic function (Eq. 6.2). Senescence patterns displayed a sequential loss of leaf greenness: first in bottom leaves, then the top leaves and eventually the leaves in the mid layer. On average, $SPAD_{max}$ was 48 for top, 55 for mid and 38 for the bottom layers (Figure 6.6 a, b, c). Tillage did not affect $SPAD_{max}$ ($P > 0.05$) at any of the three canopy layers. Often, stubble reduced leaf greenness compared with crops on bare ground. Tillage and stubble, and interaction effects are presented in Table 6.A1.

EC90 was not impacted by N rate, but large effects on EC50 were observed ($P < 0.001$) (Figure 6.6 d, e, f). In the top and mid layers, unfertilized controls retarded EC50 compared with N fertilization. In contrast, fertilization prolonged leaf greenness in the bottom leaves compared with the unfertilized control.

Across seasons, season did not affect EC90 in the top- (P = 0.067) and middle-layer leaves (P = 0.610) but large effects were observed in the bottom leaves (P < 0.001). On the other hand, season effects on EC50 were large (P < 0.001) in all canopy layers. In tandem with the maize senescence patterns, EC90 varied across the canopy layers (P < 0.001), and was neither affected by tillage (P = 0.526) nor N rate (P = 0.357) but was marginally affected by stubble (P = 0. 043). EC90 was earlier in the bottom leaves, then the top leaves and the last to initiate senescence were the ear leaves. Similarly, EC50 varied across the canopy layers (P < 0.001) but unlike EC90, this trait was impacted by tillage (P = 0.013), N rate (P = 0.008) and many treatment interactions.

Rate of leaf senescence was altered by N rate (P < 0.05) across the canopy layers but differences were large in 2015 long rains and marginal during 2015/2016 short rains and 2016 long rains (Figure 6.6 g, h, i). In fertilized crops, rate of senescence was higher in the top and mid-layer leaves, and slower in the bottom layer only when N was applied. In the unfertilized controls, rate of senescence was lower in the mid layer compared with both the top and bottom leaves, during the second and third season. There were no marked differences in the rate of senescence across the canopy layers during the first season. Overall, rate of senescence was faster in the top and mid layers (18-20 SPAD units $^{o}C\ d^{-1}$) and slower in the bottom layer (10 SPAD units $^{o}C\ d^{-1}$).

6.3.6 Relationship between traits of senescence and grain yield, yield components and N traits

At the whole-plant level, slope 1 and 2 and the breakpoint between the two slopes was not correlated with grain yield and yield components or N traits (P > 0.05).

Table 6.2 presents correlations between senescence parameters for canopy layers, yield components and N traits. Grain yield, yield components and N traits were strongly and positively correlated with SPAD_{max}. On the other hand, yield and N traits were weakly and inconsistently correlated with EC90. Strong negative correlations were observed between EC50 and grain yield and NNI and NRE traits, mostly in the mid and top layer leaves. In the bottom layer, EC50 positively correlated with grain yield in two of the three seasons.

Grain yield and kernel number were associated with a faster rate of senescence in the top and mid layer leaves and slower rate of senescence in the bottom leaves (Table 6.2). The patterns and traits of senescence and their relationship with grain yield could be summarised in a sink-driven senescence ideotype for a short maturity maize hybrid (Figure 6.7). Here, SPAD_{max} and a fast rate of senescence were associated with high yield. Low grain yield was associated with prolonged leaf greenness and slow rate of senescence in the top and mid layer leaves (Figure 6.7 a, b). In the bottom leaves, N fertilization prolonged leaf greenness while the shortage of N supply (small sink) induced early leaf senescence (Figure 6.7 c).

In the present study, evapotranspiration did not alter the traits of senescence. In addition, crops were protected with fungicides and insecticides, thus disease and pest damage did not affect this study. Moreover, apart from varying rates of N supply, crop deficiency from other nutrients were not observed.

6.4 Discussion

The improvement of N economy in NT and stubble retention systems requires multiple approaches to increase N uptake, internal utilization and partitioning to the grain (see Chapter 5 or Kitonyo et al., 2018). The present study demonstrates strong links between layered patterns of leaf senescence, grain yield and NRE in maize. Senescence was sink-driven and the patterns of leaf senescence modulated N fluxes from the senescing leaves to the grain. On the other hand, sink size was dependent on N supply while the effects of tillage, stubble and many treatment interactions, and seasonal evapotranspiration were small.

6.4.1 Onset and progression of senescence

The pattern of leaf senescence in this study was typical, whereby loss of greenness commenced from the bottom leaves, then the top leaves, while the last remaining green leaves were the mid ones (Valentinuz and Tollenaar, 2004; Escobar-Gutiérrez and Combe, 2012). Irrespective of canopy layer, the onset of senescence (EC90) was independent of growing season and management practice, and was rarely correlated with grain yield or N traits, which is consistent with the strong genetic control of this trait (Noodén et al., 1997). On the other hand, EC50 was altered by growing conditions, whereby leaf greenness persisted during the long rain seasons but crops senesced earlier during the short rains season.

The progression of senescence was similar at both the whole-plant and canopy layer scales in response to N supply. At the whole plant level, the breakpoint between slope 1 and 2 occurred earlier in the fertilized crops compared with unfertilized controls. Likewise, at canopy layer level, EC50 was delayed in the unfertilized crops compared with fertilized counterparts. This outcome could be attributed to sink strength, which regulated the rate of senescence, as illustrated in the senescence ideotype (Figure 6.7), and discussed below.

6.4.2 Senescence and the modulation of grain yield and N traits

The regulation of senescence by genetic and environmental factors is complex. The present study neither focussed on genetics nor comprehensively analysed the environmental effects on leaf senescence. However, the remobilization of N from the senescing organs to the grain, which was quantified by NRE in the present study, is modulated by the patterns of senescence in crop plants (Masclaux-Daubresse et al., 2008; Gregersen, 2011; Wu et al., 2012). Our results showed an increase in the rate of senescence with increases in both grain yield and NRE. The amount of N remobilized increased with N supply but there were no significant differences between 80 and 120 kg N ha^{-1} grain (see Chapter 5 or Kitonyo et al., 2018). This suggests that the sink strength regulated the rate of senescence, and in turn NRE. In wheat, the rate of senescence increased with grain yield (Xie et al., 2016; Kitonyo et al., 2017), and a high rate of grain filling was associated with faster rate of senescence (Xie et al., 2016).

In the source-sink transition, demand for N by the grain could have accelerated leaf senescence (Sinclair et al., 1990) but the role of crop genetics cannot be excluded. Our test variety DK8031, is an early maturity maize hybrid and has a fast dry-down syndrome. In short maturity hybrids, grain yield is often restricted by sink strength, compared with yield in long maturity counterparts (Capristo et al., 2007). In addition, short maturity hybrids have limited post-flowering N uptake from the soil, hence shortfalls in N supply may be compensated by accelerated rates of senescence and remobilization of N to the grain (Borrell et al., 2001). On the other hand, “stay-green” phenotypes have higher post-flowering N uptake and accumulate more biomass after flowering but the biomass is retained in the stems (Borrell et al., 2001).

Leaf senescence explained 42% of the variation in tropical maize grain yield under limiting N conditions (Bänziger and Lafitte, 1997). When abiotic and biotic stresses are limited, sink strength has been shown to regulate the rate of senescence, in sorghum (Borrell et al., 2001), wheat (Biswas and Mandal, 1986; Xie et al., 2016) and maize (Sadras et al., 2000). Lack of grain delayed leaf senescence in maize (Wolfe et al., 1988; Antonietta et al., 2016) and sunflower (Ho and Below, 1989; Sadras et al., 2000). Other reports show accelerated leaf senescence in response to low grain yield in maize, potentially due to hormonal and nutritional signals in the regulation of senescence (Sadras et al., 2000). Enhanced concentrations of cytokinins, for example, may delay leaf senescence in maize (He et al., 2005) but the hormone’s association with reduced sink size in maize is poorly understood. Nonetheless, senescence is more nuanced in maize as it depends on hybrid (Crafts-Brandner and Poneleit, 1987). The persistence of green leaf area in the unfertilized controls in the present study could be related to reduced N fluxes to the grain due to small sink size.

The source-sink relationship in the present study could be restricted to the top and middle layer leaves but not in the bottom layer, where rate of senescence was negatively correlated with grain yield and NRE. This outcome corroborates the delay in the senescence of bottom leaves in fertilized crops compared with the unfertilized controls. This implies that the bottom leaves were less important in the remobilization of N to the grain. This observation is consistent with previous studies, where the senescence of the bottom leaves starts during the vegetative phase as the stem expands and most nutrients are exported to the roots (Pommel et al., 2006; Gregersen et al., 2013; Schippers et al., 2015). In addition to age, the early senescence of bottom leaves could be attributed to shading by the upper leaves (Maddonni et al., 2001; Borrás et al., 2003; Pommel et al., 2006). It appears that the senescence signal could have been triggered by a threshold in grain filling or a decrease in leaf N (Pommel et al., 2006).

The effects of tillage, stubble and N management practices on the patterns of leaf senescence and the associated effects on grain yield have received little attention, especially as a pathway to the improvement of NUE in maize. In wheat, NT increased SPAD_{max} compared with CT but tillage system did not affect EC90, EC50 or the rate of senescence for individual varieties (Kitonyo et al., 2017). The timing and progression of senescence not only affects yield but also the nutritional quality of grain (Schippers et al., 2015). Despite the weak correlations between rate of senescence and grain protein in the present study, fast rates of senescence are shown to associate with grain protein in cereals (Xie et al., 2016). A potentially negative consequence of delayed senescence is reduced grain protein content (Masclaux-Daubresse and Chardon, 2011).

6.4.3 Leaf senescence ideotype

A senescence ideotype for a short maturity maize hybrid, driven by sink size, is proposed from the present study. This ideotype had high $SPAD_{max}$ in all leaf layers, which potentially associates with higher photosynthesis (Martin et al., 2005). In the top and mid layer leaves, the onset of senescence was regulated by sink size but N fertilization delayed senescence in the bottom layer. The early onset of leaf senescence in the top and mid-layer leaves was coupled with a fast rate of senescence. While high yielding hybrids should present a delay in the onset of senescence to extend photosynthetic duration, a fast rate of senescence hastens nutrient remobilization to the grain (Wu et al., 2012). The present results contradict the delayed onset of senescence trait but high $SPAD_{max}$ suggests the maintenance of high photosynthetic rate. Direct measurements of leaf photosynthesis are required to test this proposition.

Biochemical regulators may have strongly regulated the onset of senescence in our test hybrid (Crafts-Brandner and Poneleit, 1987). Maize derives 35-55% kernel N from post-flowering soil N uptake, while the rest is remobilised from senescing organs (Hirel et al., 2007; Gregersen et al., 2013). Increased soil N could have prolonged leaf greenness in the fertilized crops compared with the unfertilized controls (Rajcan and Tollenaar, 1999). Traits that promote water conservation (such as early maturity) or increase water and nutrient uptake, and high harvest index could complement the proposed senescence ideotype for a short-maturity maize hybrid (Sadras and Richards, 2014).

6.5 Conclusion

Understanding the factors affecting yield formation in maize is important in the management of tillage, stubble retention and N fertilization practices. In the present study, tillage and stubble retention did not affect the senescence of maize canopy. However, N was the dominant factor, and interacted with stubble in driving leaf senescence. A senescence ideotype demonstrated sink-driven patterns of leaf senescence, in which faster rates of senescence associated with N supply and high yield while slower rates of senescence were concomitant with low grain yield. Nonetheless, these patterns of senescence could be restricted to short maturity maize hybrids. Further work on a wide range of senescent and “stay-green” hybrids under contrasting tillage systems and stubble amounts, and different rates and timing of N supply is required.

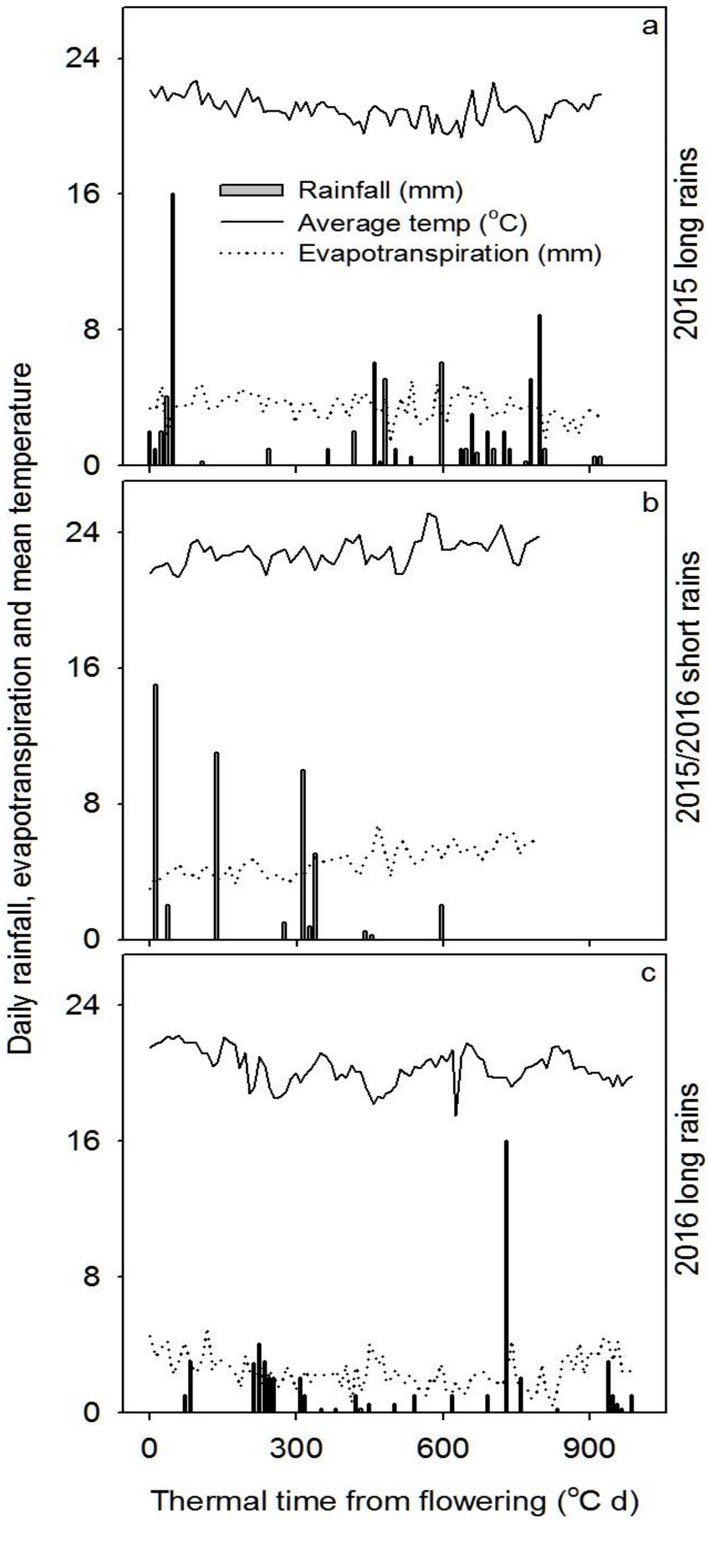

Figure 6.1. Growing conditions from flowering (50% pollen shedding) to harvesting of maize during 2015 long rains (a), 2015/2016 short rains (b) and 2016 long rains (c) at the Kenya Agricultural and Livestock Research Organisation, Embu research station

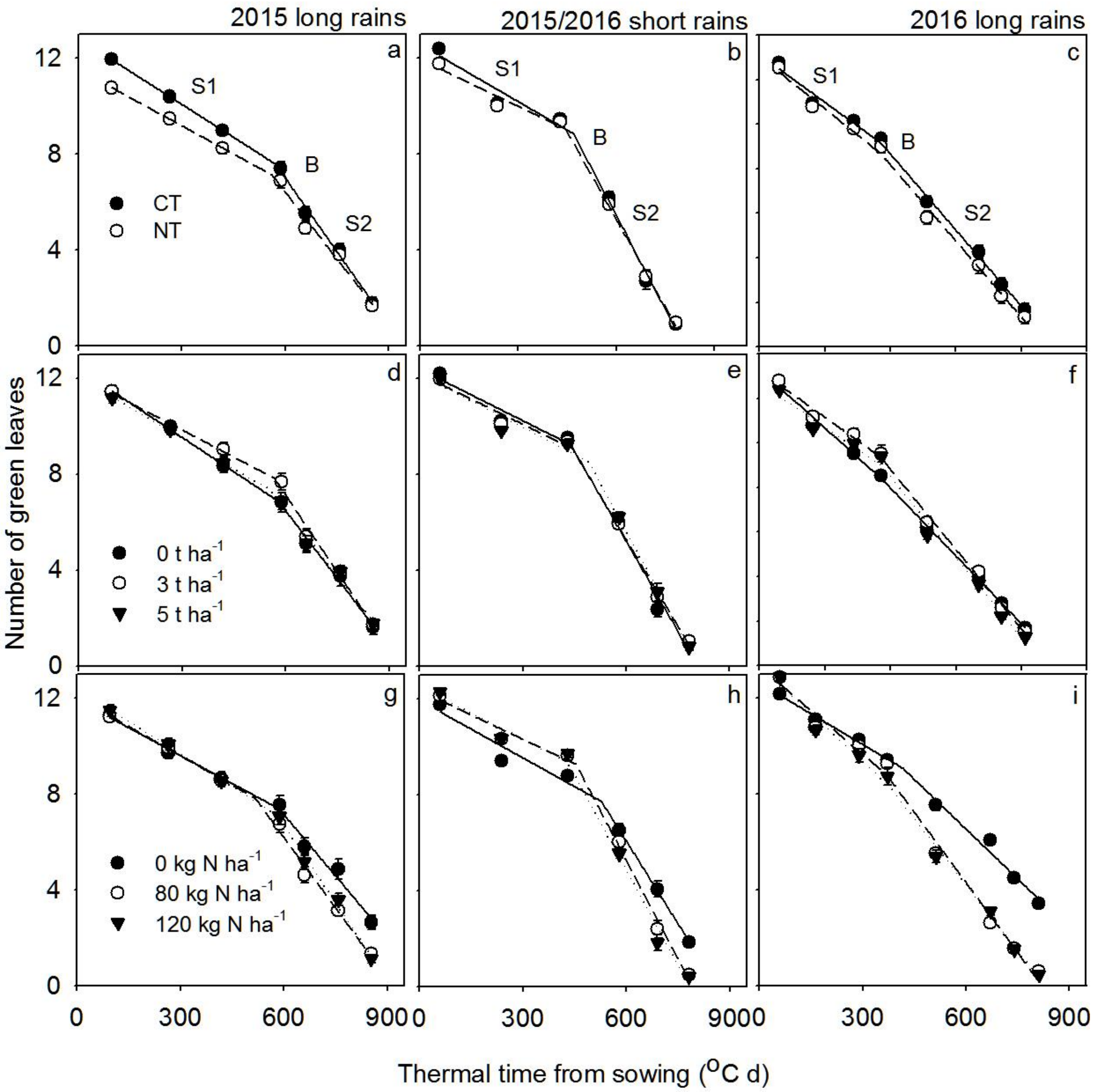

Figure 6.2. Time-course of leaf senescence of maize grown under conventional tillage (CT) and no-till (NT) (a-c), three amounts of stubble (d-f) and three N rates (g-i) during the 2015 long rains (a, d, g), 2015/2016 short rains (b, e, h) and 2016 long rains (c, f, i) at Kenya Agricultural and Livestock Research Organisation, Embu research station. Slope S1 and S2 are the rate of senescence. The breakpoint and slopes are summarised in Table 6.1.

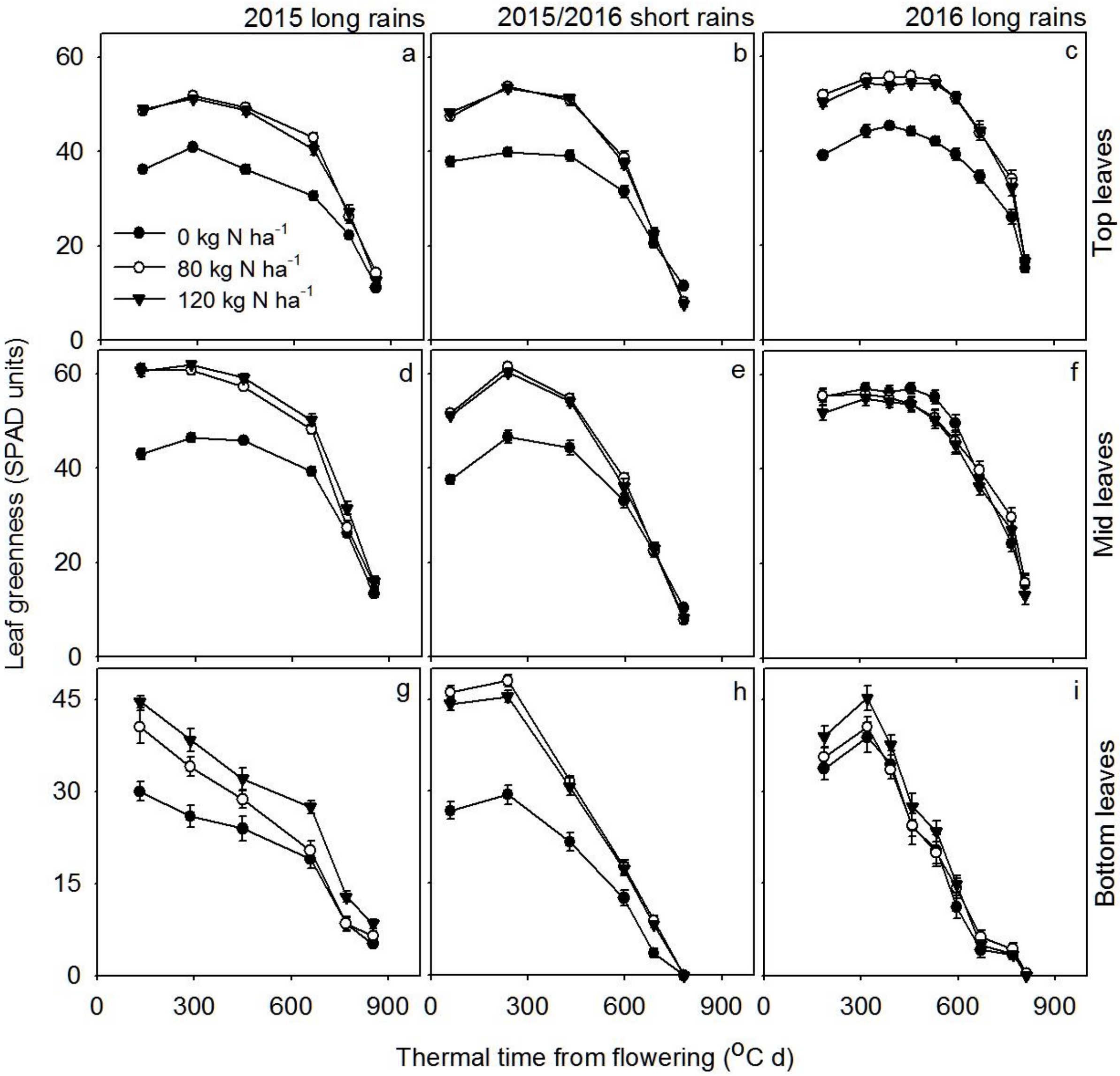

Figure 6.3. The effect of N rate on leaf senescence of maize at three canopy layers during 2015 long rains (a, d, g), 2015/2016 short rains (b, h, h) and 2016 long rains (c, f, i) at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Error bars are 1 standard error of the mean.

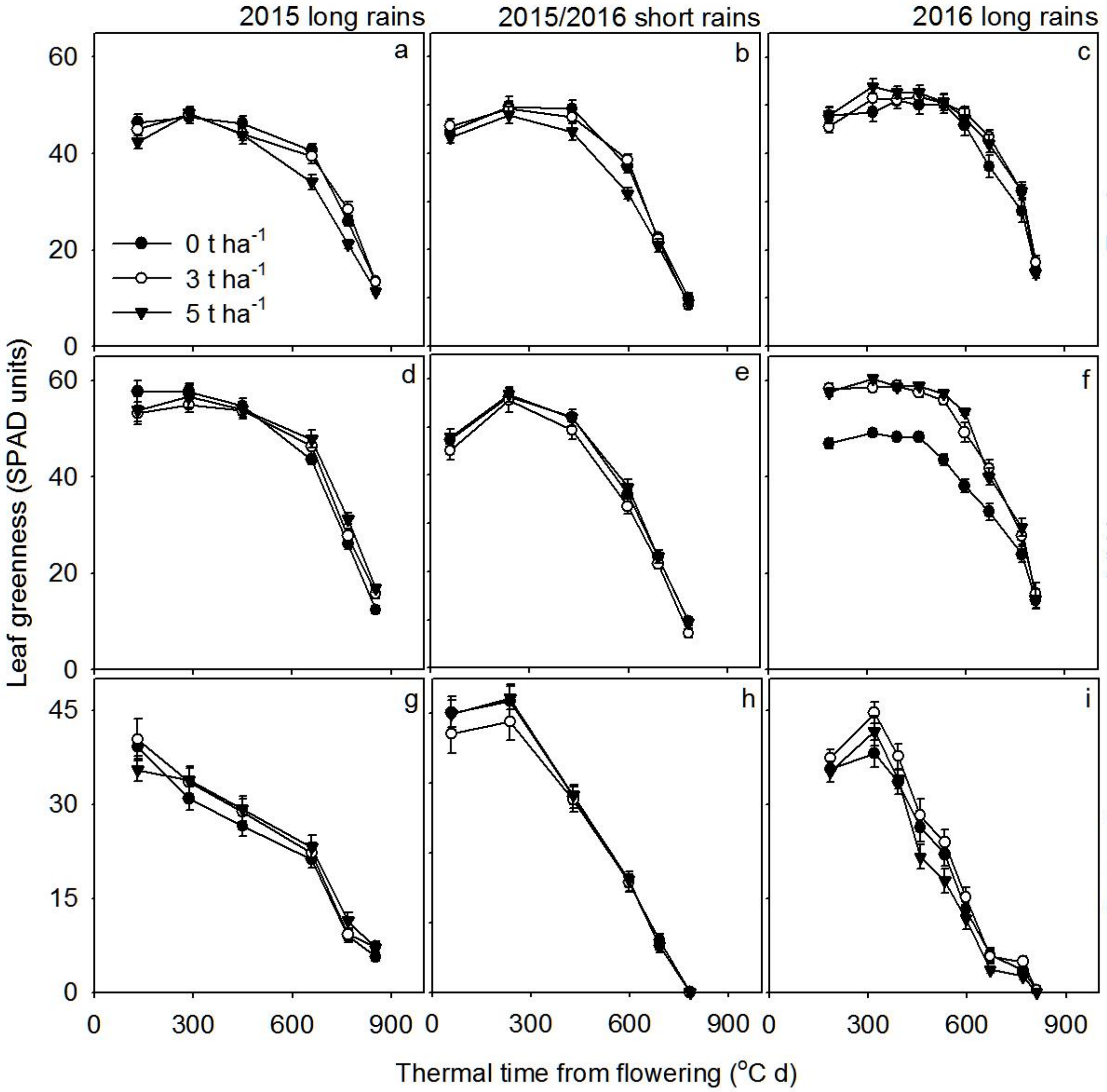

Figure 6.4. The effect of stubble amount on leaf senescence of maize at three canopy layers during 2015 long rains (a, d, g), 2015/2016 short rains (b, h, h) and 2016 long rains (c, f, i) at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Error bars are 1 standard error of the mean.

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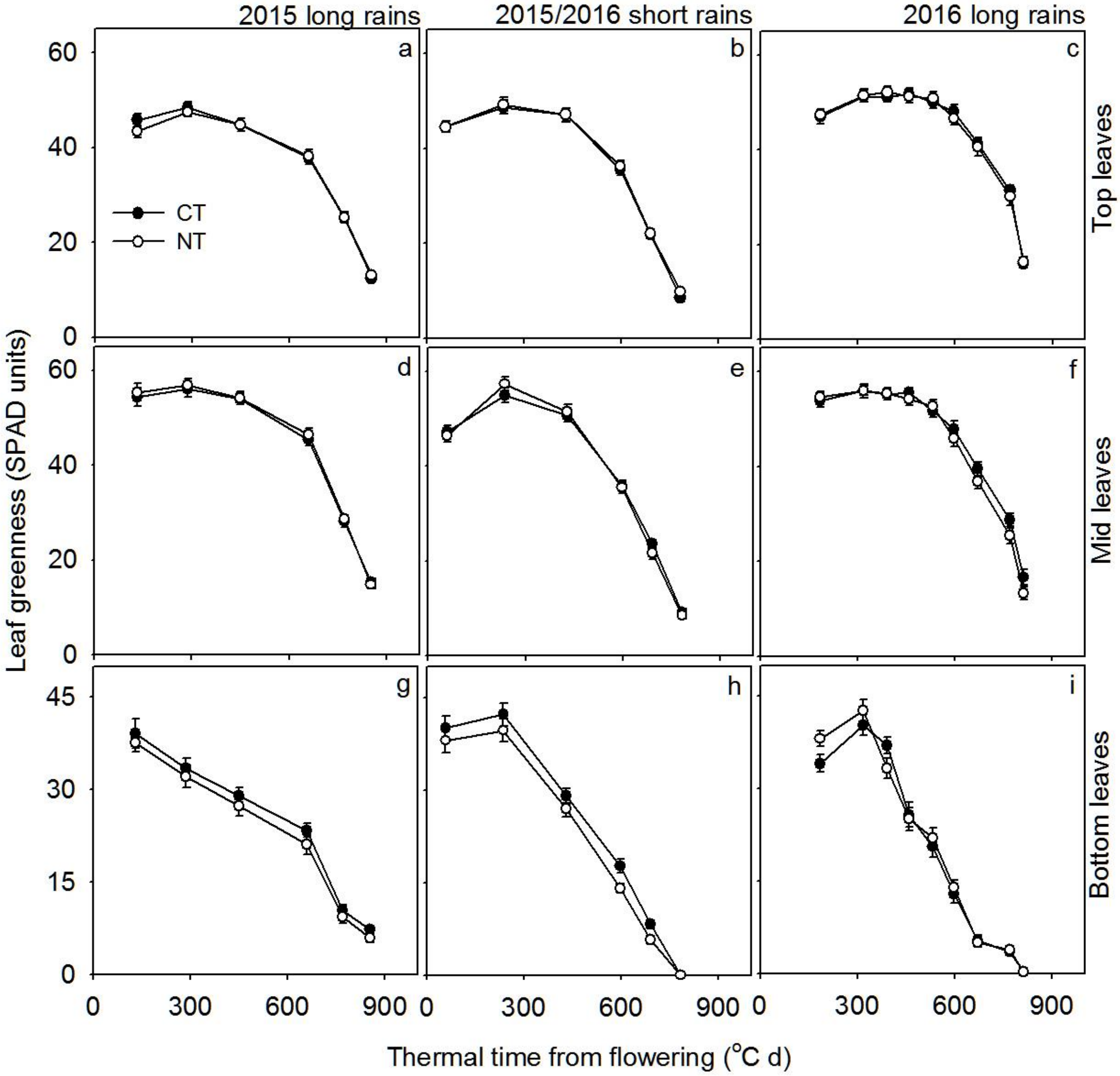

Figure 6.5. The effect of tillage system on leaf senescence of maize at three canopy layers during 2015 long rains (a, d, g), 2015/2016 short rains (b, h, h) and 2016 long rains (c, f, i) at the Kenya Agricultural and Livestock Research Organisation, Embu research station. Error bars are 1 standard error of the mean.

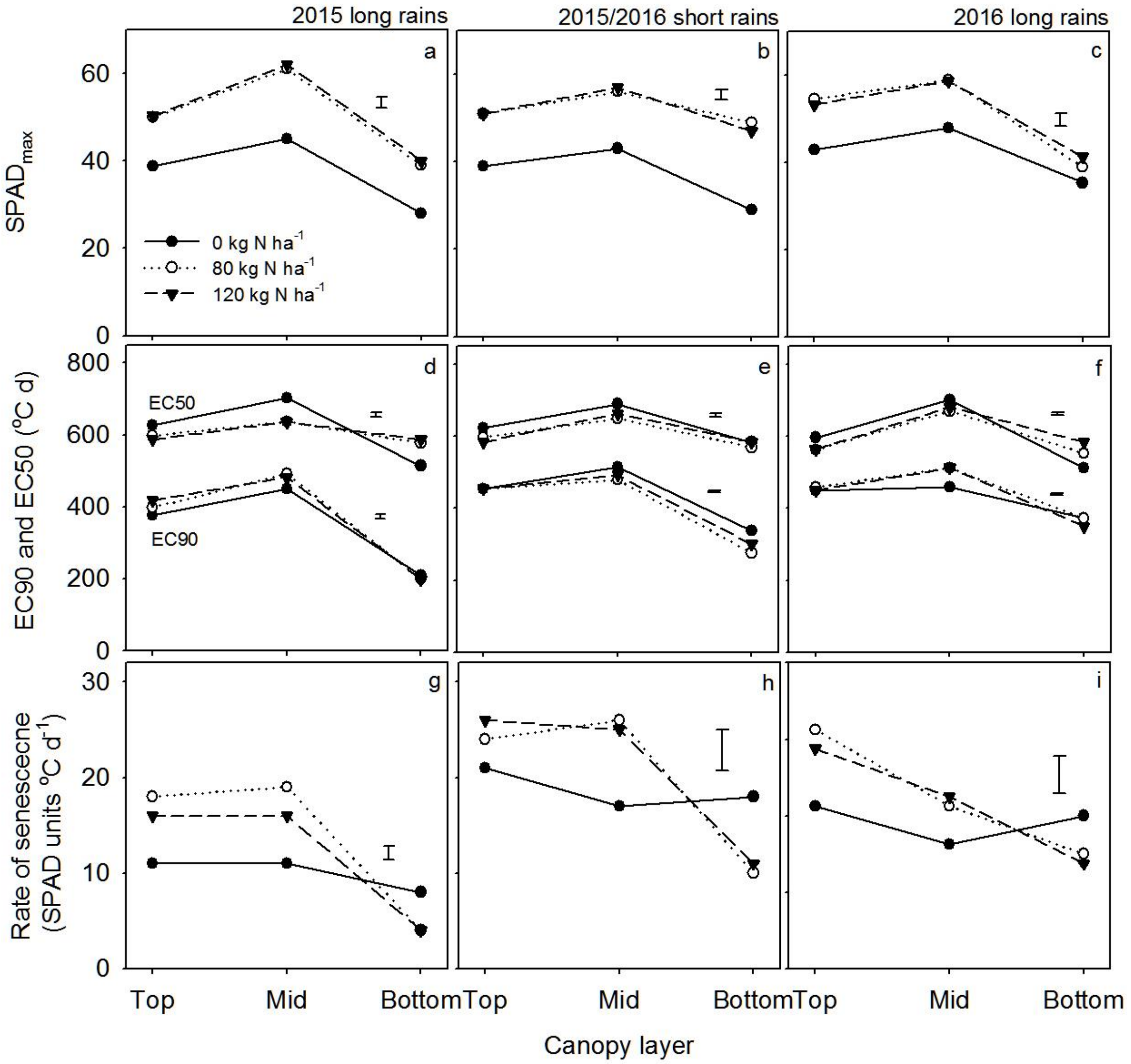

Figure 6.6. Nitrogen-driven traits of leaf senescence at different layers of maize canopy grown at the Kenya Agricultural and Livestock Research Organization, Embu research station during 2015 long rains (a, d, g), 2015/2016 short rains (b, e, h) and 2016 long rains. Vertical bars are LSD at 5% probability. Data was pooled for tillage systems and stubble amounts.

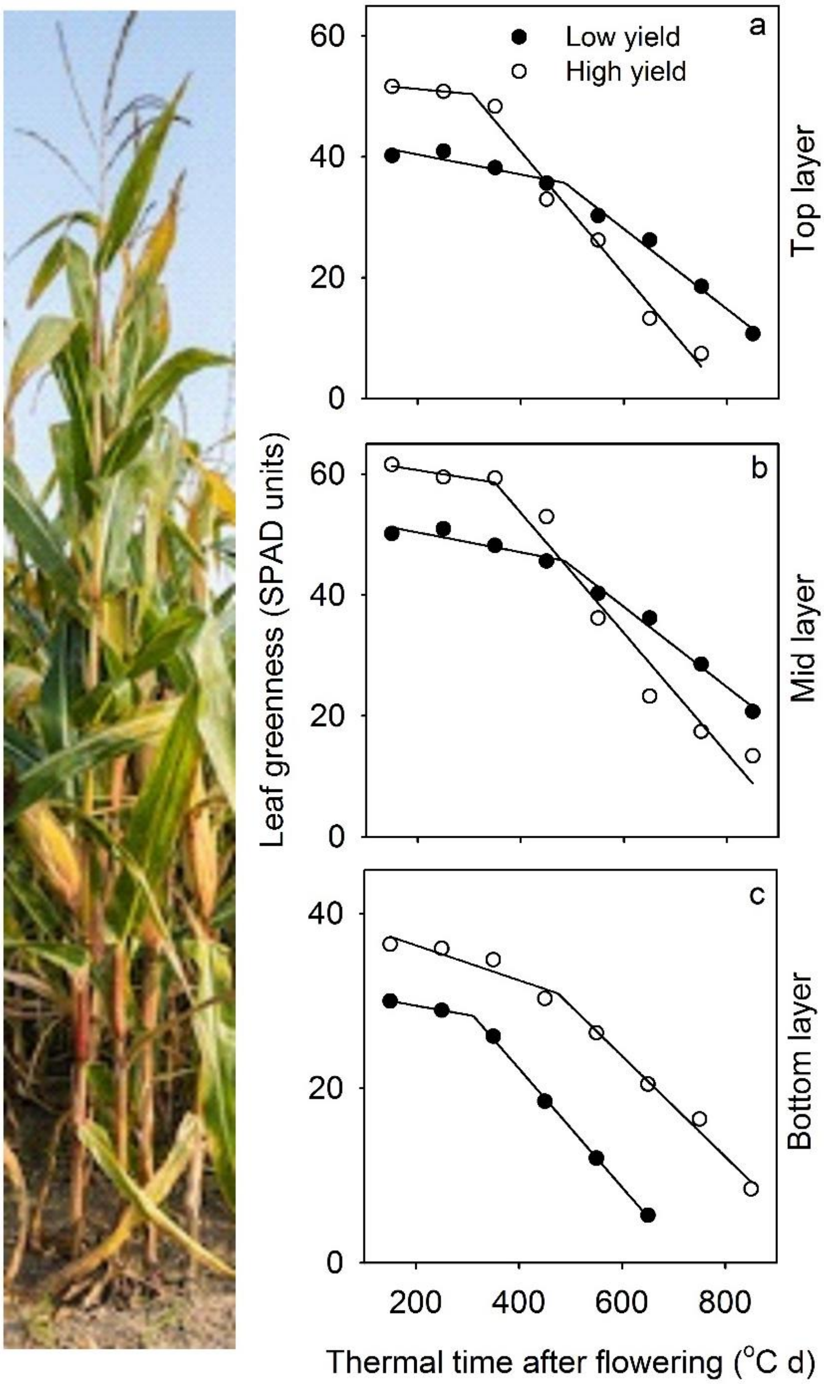

Figure 6.7. Sink-driven leaf senescence ideotype of a short maturity maize hybrid. Data points are actual SPAD units pooled across treatments in the three seasons. High yield is grain yield with the addition of fertilizer N while low yield is grain yield without the addition of N. The photo is maize at dough stage (R4) when kernels are half filled with solid starch.

Table 6.1. Traits of leaf senescence at the whole-plant level of maize grown under conventional tillage (CT) and no-till (NT), three amounts of stubble and three N rates during 2015 long rains, 2015/2016 short rains and 2016 long rains at Kenya Agricultural and Livestock Research Organisation, Embu research station. Slopes 1 and 2 are the rate of senescence (number of green leaves °C d^{-1}) and the breakpoint (°C d) is the transition between the two slopes. The breakpoint and slopes were estimated by fitting Eq. 6.1 'a' and 6.1 'b'.

Treatment	2015 long rains			2015/2016 short rains			2016 long rains		
	Breakpoint	Slope 1	Slope 2	Breakpoint	Slope 1	Slope 2	Breakpoint	Slope 1	Slope 2
Tillage									
CT	571a	-0.009a	-0.022a	480a	-0.008a	-0.028a	434a	-0.011a	-0.018a
NT	570a	-0.007a	-0.020a	472a	-0.007a	-0.027a	391a	-0.011a	-0.018a
Stubble									
0 t ha^{-1}	575a	-0.009a	-0.019a	449a	-0.007a	-0.026a	430a	-0.013a	-0.016b
3 t ha^{-1}	580a	-0.007a	-0.023a	482a	-0.007a	-0.028a	403a	-0.010b	-0.019a
5 t ha^{-1}	557a	-0.009a	-0.020a	498a	-0.008a	-0.029a	405a	-0.010b	-0.019a
N rate									
0 kg N ha^{-1}	614a	-0.008a	-0.019b	526a	-0.008a	-0.027a	491a	-0.009b	-0.016b
80 kg N ha^{-1}	527c	-0.008a	-0.022a	442b	-0.007a	-0.027a	355b	-0.012a	-0.020a
120 kg N ha^{-1}	570b	-0.009a	-0.022a	460b	-0.007a	-0.028a	392b	-0.013a	-0.019a
Interactions ANOVA									
Tillage x stubble	ns	ns	ns	ns	ns	ns	ns	**	ns
Tillage x N rate	ns	ns	ns	ns	ns	ns	ns	***	**
Stubble x N rate	**	ns	***	ns	ns	ns	ns	***	*
Tillage x stubble x N rate	**	ns	*	ns	ns	ns	ns	*	ns

Within a column, means followed by the same letter are not significantly different at 0.05 probability. *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$; ns: not significant.

Table 6.2. Correlation coefficients between senescence traits and grain yield, yield components and N traits in three canopy layers of maize grown under conventional tillage and no-till, three amounts of stubble and three N rates during 2015 long rains, 2015/2016 short rains and 2016 long rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station.

Traits	2015 long rains				2015/2016 short rains				2016 long rains			
	SPADmax	EC90	EC50	SR	SPADmax	EC90	EC50	SR	SPADmax	EC90	EC50	SR
Top layer												
Grain yield	0.83	0.29	-0.50	0.40	0.81	0.05	-0.45	0.21	0.86	0.06	-0.54	0.31
Kernel number	0.70	0.35	-0.50	0.45	0.70	0.05	-0.40	0.13	0.87	0.07	-0.54	0.34
Kernel weight	0.40	-0.08	-0.07	-0.08	0.46	0.12	-0.26	0.29	0.14	-0.05	-0.11	-0.04
Grain protein					0.46	-0.10	-0.33	0.08	0.64	0.12	-0.39	0.36
NNI	0.68	0.18	-0.52	0.24	0.84	0.14	-0.45	0.38				
NRE	0.81	0.25	-0.58	0.31	0.80	0.14	-0.34	0.23				
N uptake	-0.17	-0.02	0.15	-0.02	-0.05	0.03	-0.03	0.15	0.17	-0.18	-0.12	-0.10
NAE	-0.02	0.21	-0.06	0.37	-0.35	-0.24	0.27	-0.32	-0.09	0.06	0.01	0.12
Mid layer												
Grain yield	0.73	0.32	-0.52	0.54	0.85	-0.38	-0.32	0.63	0.82	0.24	-0.55	0.31
Kernel number	0.68	0.17	-0.63	0.48	0.64	-0.31	-0.25	0.55	0.84	0.26	-0.55	0.30
Kernel weight	0.26	0.06	-0.08	0.14	0.71	-0.21	-0.28	0.40	0.09	-0.15	-0.07	0.01
Grain protein					0.60	-0.15	-0.27	0.30	0.69	0.15	-0.27	0.22
NNI	0.68	0.00	-0.58	0.27	0.83	-0.42	-0.36	0.66				
NRE	0.82	0.11	-0.62	0.40	0.77	-0.47	-0.26	0.51				
N uptake	-0.33	0.01	0.17	-0.02	0.07	0.18	-0.15	0.04	0.02	-0.15	0.15	-0.12
NAE	-0.33	0.32	0.20	0.35	-0.31	0.07	-0.02	-0.41	0.11	-0.12	-0.27	-0.05
Bottom layer												
Grain yield	0.70	-0.01	0.74	-0.50	0.82	-0.03	-0.44	-0.53	0.33	-0.01	0.42	-0.49
Kernel number	0.62	-0.03	0.68	-0.43	0.64	-0.08	-0.43	-0.54	0.33	-0.06	0.42	-0.48
Kernel weight	0.24	0.15	0.34	-0.22	0.64	0.05	-0.16	-0.26	0.07	0.12	0.04	-0.08
Grain protein					0.45	-0.11	-0.14	-0.21	0.35	0.01	0.36	-0.30
NNI	0.64	-0.06	0.66	-0.52	0.78	0.03	-0.34	-0.51				
NRE	0.67	-0.15	0.77	-0.61	0.72	-0.03	-0.33	-0.43				
N uptake	-0.19	-0.20	-0.35	0.12	-0.06	0.09	-0.23	-0.06	0.09	-0.32	-0.26	0.01
NAE	0.18	0.03	-0.02	0.26	0.12	-0.25	-0.02	-0.13	-0.14	0.16	0.09	0.01

SPAD$_{max}$, maximum SPAD; EC90, onset of senescence; EC50, loss of 50% maximum SPAD; SR, rate of senescence; NNI, nitrogen nutrition index at flowering; NRE, nitrogen remobilization efficiency; NAE, nitrogen agronomic efficiency; Increasing colour intensity indicates P value for positive (blue) and negative (red) correlations; uncoloured coefficients had P > 0.05. n = 54.

Colour legend			
	🟦	$P < 0.05$	🟧
	🟦	$P < 0.01$	🟧
	🟦	$P < 0.001$	🟧

Chapter 7 General discussion

7.1 Introduction

This thesis provides new insights on crop physiology and agronomy in both wheat systems in southern Australia and maize systems in Kenya. Despite differences in biophysical and socio-economic circumstances between the two cropping systems, this study found unifying responses to the components. In both crop systems, the supply of N had the largest impact on yield compared with tillage and stubble retention. Nitrogen influenced crop response to both tillage and stubble retention. In addition, applying the majority of N at sowing led to a large initial canopy in both crops which caused small crop growth rates during the critical window for yield determination, hence low grain yield compared with delayed N supply. In both crop systems, tillage did not affect yield, even across seasons, and its effects were worsened when both stubble and N were not supplied. Applying high amounts of stubble did not improve water capture and storage but reduced emergence, early growth and grain yield. It was apparent that both wheat and maize yield could be maximised at 2-3 t ha^{-1} of stubble, but this might vary with seasonal rainfall. However, the amount of stubble and the way in which it is applied influences how it might interact with N. The mechanisms that regulated grain yield, water and N use efficiency in the crop systems were dependent on crop growth rates during the critical period for grain set. Crop growth rate during this period impacted radiation use efficiency and N nitrogen nutrition index. Apparently, the rate of leaf senescence in both crops was sink driven, which appears to contradict established notions that patterns of leaf senescence drive yield. In all these traits, both crop systems responded similarly. Further details of these are summarised below and in Table 7.1.

7.2 Effect of management practices

7.2.1 Variety/breeds

Breeding of Australian wheats has improved yield, but has not provided greater adaptation to NT and stubble retention systems (Chapter 4). Between 1958 and 2011, grain yield increased at 21 kg ha^{-1} $year^{-1}$, which supports previous reports (Sadras and Lawson, 2011; Sadras and Lawson, 2013). Lack of variety × tillage interactions resonates with the marginal tillage × stubble interactions observed for both wheat (Chapter 3) and maize (Chapter 5). This implies that current wheat varieties are equally adapted to tillage systems, and there is an opportunity to enhance adaptation to NT systems. However, modern varieties are likely to have had better exposure to NT and stubble retention during their later stages of selection compared with older counterparts. As a result, there was a modest shift in grain yield under NT by 1.8 kg ha^{-1} $year^{-1}$ compared with CT (Figure 2 c in Chapter 4), which suggests that NT offered better growing conditions.

7.2.2 Nitrogen

A key question relating to crop N uptake and NUE is the rate and timing of N supply that is required to ameliorate the negative effects of NT and stubble retention on N cycling (Giller et al., 2009). C:N ratio in wheat and maize stubble is more than 30, thus the addition of stubble results in net N immobilization. Maize crops had 8% reduction in NNI at flowering when stubble was added compared with bare ground (Chapter 5). Delaying N supply in maize increased N uptake, nitrogen nutrition index (NNI) and traits associated with NUE compared with sowing application.

Nitrogen supply was important in modifying crop response to both tillage and stubble. Timing the supply of N at the critical periods for yield determination in both wheat and maize manipulated canopy development. In this case, delaying N supply initially produced a small and more open canopy, while high sowing applications favoured early growth. However, the initially small canopies produced large crop growth rates (CGR) during the critical period for grain set and led to higher radiation use efficiency (RUE) and NNI. Alteration of canopy development through the timing of N supply has been shown to improve WUE and NUE and grain yield and quality, while sowing applications inefficiently convert biomass and N into grain in the drylands of southern Australia (Hooper et al., 2015; Zhou et al., 2017).

The importance of N in NT and stubble retention has been recognised (Giller et al., 2009; Giller et al., 2011; Sadras et al., 2012c; Lundy et al., 2015), including considerations regarding whether to include N fertilization as a fourth principle in the definition of CA (Sommer et al., 2014; Vanlauwe et al., 2014). In maize, differences in NNI, CGR and grain yield between 80 and 120 kg N ha^{-1} were not detected and the same observation was made for other traits, while interactions were few. Intermediate nitrogen rates are required to refine the N rate at which grain yield, CGR, NNI and traits associated with NUE are maximised.

Economically optimal N rates and timing regimes are expected to vary with environment, quantity and quality of stubble, rainfall patterns and the desired yield. In SSA, N use has been static since 1960s (Tittonell and Giller, 2013), a constraint that needs to be addressed (Dimes et al., 2015). Some agronomic benefits of NT and stubble retention take a long time to accrue (Rusinamhodzi et al., 2011), thus higher rates of N supply may be required to bridge the lag phase. Immediate challenges to overcome in SSA are high costs, poor supply chains and counterfeit fertilizer. In wheat systems of southern Australia, variable rainfall patterns challenge N supply strategies, which can have significant implications (Hooper et al., 2015; Zhou et al., 2017).

7.2.3 Stubble

Under our experimental conditions, grain yield increased with the application of moderate amounts of stubble (~ 2-3 t ha^{-1}) but decreased with high quantities of stubble (~ 5 t ha^{-1}). This response was clearer in wheat than in maize systems. Water capture and storage increased with stubble but there were no significant differences between moderate and high amounts of stubble. Moreover, in the sub-humid tropical environment in Kenya, addition of stubble reduced maize grain yield in wetter seasons (> 600 mm) but positive effects were measured in a season with < 300 mm of rainfall.

The value of stubble in water conservation and potentially the final grain yield varies with rainfall amount, rainfall frequency and size of events, soil evaporative demand and type of soil (Monzon et al., 2006; Kirkegaard and Hunt, 2010; Verburg et al., 2012). When rainfall exceeded 600 mm in southern Africa environments, Rusinamhodzi et al. (2011) and Nyamangara et al. (2014) found that NT and stubble retention reduced maize grain yield compared with CT but grain yield increased once rainfall was less than 600 mm. Similarly, in dryland wheat systems of Australia, stubble reduced grain yield when rainfall exceeded 300 mm but its effects were negligible with < 250 mm (Heenan et al., 1994; Kirkegaard et al., 1994; Giller et al., 2015), which indicates the importance of seasonal effects.

7.2.4 Tillage

Tillage system marginally impacted crop growth and yield in both systems, and was independent of seasonal differences. Previous reports did not find seasonal differences in crop response to tillage, both in wheat (Muñoz-Romero et al., 2010) and maize (Thierfelder et al., 2013; Thierfelder et al., 2015). The present study measured inconsistent increases in grain yield under NT compared with CT in both systems, potentially due to factors that increased crop growth and the final yield. In the short-term, NT improves soil porosity which promotes gaseous exchange as well as water infiltration and storage (Palm et al., 2013; Paul et al., 2013). In the long-term, however, NT may reduce crop growth and yield due to soil compaction (Gicheru et al., 2004). In the short duration of the present study, yield increases were with NT, potentially because the yield-reducing constraints of continuous NT had not developed sufficiently.

The negative effects of NT were amplified when stubble was removed. For instance, in maize, when stubble was removed, NT reduced grain yield by 10% compared with CT under the same conditions. The yield reduction was matched by 8% reduction in water storage under NT compared with CT. Thus, sufficient soil cover is important in NT to promote water capture and storage, and grain yield (Govaerts et al., 2009a; Rusinamhodzi et al., 2011; Corbeels et al., 2014; Pittelkow et al., 2015a). The marginal effects of NT on crop growth and yield in the present study suggests the most important aspect of NT is the potential to reduce labour and fuel costs, timeliness of operations and ease of crop management (Kirkegaard et al., 2014).

7.3 Canopy development and yield determination

7.3.1 Crop growth rates

Grain yield correlated with crop growth rates during the critical period of grain set. In wheat, the critical period for yield determination falls between stem elongation and approximately 10 days after flowering (Slafer et al., 2014). Kernel number is determined between V6 and a few days after silking in maize (Andrade et al., 2005). In both crops, CGR during the critical period for yield determination was proportional to grain number, which reinforces empirical and theoretical evidence, and provides new insights into crop management.

In the highlands of Mexico, Verhulst et al. (2011) observed that wheat and maize crops under NT and stubble retention had slow initial growth but growth rates increased in later stages. The study claimed that there was net N immobilization by NT and stubble during the early stages but N was made available later in the season. In the present study, tillage and stubble amount marginally affected CGR, and their effects were modified by N supply. The implication of N timing on CGR has been discussed under section 7.2.2. In the regulation of CGR, high production of tillers with sowing application of N led to reduced crop growth rates and lower RUE compared with delayed N supply (Chapter 3).

In maize (Chapter 5), the consistent role played by N timing in altering crop growth rate, which in turn was proportional to NNI at flowering underscores the necessity to fine-tune crop developmental rates by matching N supply to crop demand to improve yield and increase NUE. There was poor synchrony between N availability and crop demand for N with large sowing applications, as reflected by 28% decrease in N uptake under sowing application compared with delayed application in maize (experiment 2 of Chapter 5).

7.3.2 Canopy greenness and patterns of senescence

Wheat canopy architecture changed from older taller varieties with closed canopies to modern short-stature varieties with more open canopies. Modern varieties had greener leaves compared with older ones but selection for yield did not alter the onset of senescence. Modern varieties had faster rates of senescence, apparently driven by the sink size. In maize, faster rates of senescence associated with high grain yield and higher efficiency in NRE. Patterns of leaf senescence in both crops, and the subsequent relationships between traits of senescence, grain yield and traits associated with NUE, suggests that senescence ideotypes are an integral part of crop yield improvement.

7.3.3 Grain number

Grain number largely accounted for variation in grain yield in both systems. Understanding the regulation of grain number is central for the development of management practices that improve yield (Andrade et al., 2005). End-of-season grain yield and yield components do not provide adequate information about the within-season fluctuations that impact yield formation. This impairs a full understanding of the impact of management practices (Verhulst et al., 2011; Brouder and Gomez-Macpherson, 2014). Examination of the physiological status of the crop during the critical window for yield determination will assist in the adjustment of rate and timing of input supply and the selection of right varieties in NT and stubble retention systems (Verhulst et al., 2011).

7.4 Environmental effects

7.4.1 Water-limited yield gaps

The estimation of water-limited yield identified that N was the most effective factor in reducing yield gaps in both wheat and maize. Tillage had no effect while moderate amounts of stubble reduced yield gaps compared with both bare ground and high amounts of stubble, by 15% in wheat and 44% in maize. This was in line with higher water storage and WUE under moderate amounts of stubble compared with bare ground, and the lack of differences observed under moderate and high amounts of stubble previously. In wheat systems of Australia, 2-3 t ha^{-1} of stubble provided about 70% soil cover, increased rainfall infiltration and improved grain yield (Scott et al., 2013; Hunt et al., 2016). Establishment of critical cover thresholds are particularly important in low yielding crop-livestock systems where competition for stubble allocation between soil mulch and livestock feed is a challenge (Giller et al., 2009; Baudron et al., 2015).

7.4.2 Rainfall and water use efficiency

Average water use efficiency (WUE) was higher in wheat, ranging from 6-8 kg ha^{-1} mm^{-1} compared with 3-8 kg ha^{-1} mm^{-1} in maize. van Ittersum et al. (2013) found higher WUE in wheat systems of southern Australia in Victoria that received 200 mm of rainfall compared with maize in sub-humid regions of western Kenya with 650 mm. High WUE in wheat systems in the Mediterranean environments has been associated with high water-N co-limitation (Sadras, 2005; Savin et al., 2015). In water-limited drylands of the Loess Plateau of China, WUE in maize ranged between 2.8-39.0 kg N ha^{-1} mm^{-1}, with higher efficiencies under NT and the application of either stubble or plastic mulch (Zhang et al., 2014). Tailoring N supply to rainfall and crop demand for N has been instrumental in these environments (Wang et al., 2012). The present study and that of van Ittersum et al. (2013) suggest that there are serious inefficiencies in the cropping systems of SSA, principally due to low N use (Dimes et al., 2015). Higher N rates and better timing of N supply with crop demand for N are required to benefit from NT, stubble retention and relatively high amounts of rainfall in this region.

7.5 A mechanistic approach for the application of tillage, stubble and N fertilizer

There are two ways to describe relationships between inputs and outputs in a cropping system: an empirical approach and a mechanistic approach (Acock and Acock, 1991). An empirical approach reports results in terms of nominal treatments, e.g. high vs low yield or curves relating yield and fertilizer rate; which are uninformative, of local interest and do not provide insights to underlying processes (Sadras and Lemaire, 2014).

A mechanistic approach, also called process-level approach, focuses on the process from the management of tillage, stubble retention and fertilizer N to yield variation in a specific environment. Mechanistic approaches have largely been ignored in probing the suitability of NT and stubble retention across diverse environments, potentially due to limited data collection of the physiological drivers for yield. A focus on physiological drivers could help in adapting management practices to local circumstances, diffuse current debates on NT and stubble retention (Giller et al., 2015) and improve pragmatism in the application of these practices (Kirkegaard et al., 2014).

Figure 7.1 provides a conceptual explanation of the physiological mechanisms that impacted wheat and maize yield in response to tillage, stubble retention and rate and timing of N supply. The physiological processes for yield formation in both systems were broadly an outcome of environmental conditions (rainfall), management practices and varieties. In a systems agronomy approach, yield improvement in NT and stubble retention systems should critically evaluate: (1) the cropping environment that is controlled by tillage, stubble and rainfall pattern; (2) canopy development to increase crop growth rates during the critical period of yield determination, which can be manipulated through the strategic supply of N; and (3) synergy between varieties and management which requires high yielding genotypes and additional traits such as patterns of senescence.

7.5.1 Manipulation of canopy development

Fine-tuning crop developmental rates can improve yield and WUE and NUE in NT and stubble systems. Under our experimental conditions, N supply was the most important strategy for managing crop development. Both rate and timing of N supply should seek to maximise key physiological processes, such as crop growth rate, N nutrition index, radiation use efficiency and N remobilization efficiency, as illustrated in Figure 7.1.

7.5.2 Environment

Decisions on how much stubble to retain should be based on rainfall patterns. Under our study conditions, the value of stubble in water storage and evapotranspiration was higher in dry environments compared with high rainfall environments. This was typical in Kenya, as the effect of stubble amount on maize grain yield was negligible in high rainfall seasons but increased yield in a dry season. In the drylands of Australia, applying high amounts of stubble did not improve water storage but reduced wheat grain yield compared with moderate amount of stubble.

7.5.3 Capturing the synergy between better varieties and improved agronomy

Yield gains arise from better varieties, improved agronomy and their synergy (Fischer, 2009). Broadly, wheat varieties and maize hybrids specifically bred for adaptation to NT and stubble retention are not available (Trethowan et al., 2012; Herrera et al., 2013). The modest shift in wheat grain yield suggests that NT and stubble offered better growing conditions. There is opportunity to enhance adaptation in these systems. Leaf senescence ideotypes with high peak leaf greenness coupled with faster rates of senescence will increase yield and NUE in these systems. Mechanisms regulating the patterns of senescence in these systems should be explored.

7.6 Conclusions

This research has provided new insights on the mechanisms that operate in NT and stubble retention systems.

Nitrogen was critical in modifying crop response to NT and stubble. Timing N supply manipulated canopy development which impacted water and N use efficiency and grain yield. N supply strategies that targeted the critical period for grain set improved crop growth rates, N nutrition index, radiation use efficiency, and provided higher grain yield compared with sowing applications of N. No-till reduced water infiltration and yield but these effects were ameliorated by the application of stubble. Water capture and storage, WUE and grain yield were maximised at moderate amounts of stubble, but the value of stubble depends on the amount of rainfall. Critical soil cover threshold ranged between 2-3 t ha^{-1} in both wheat and maize systems, irrespective of stubble architecture, whether standing or flattened in wheat.

Patterns of senescence in both wheat and maize were regulated by size sink. Faster rates of senescence associated with higher grain yield and higher efficiency in the remobilization of N to the grain. Senescence ideotypes with high peak photosynthetic capacity and faster rates of senescence can improve yield and N use efficiency in NT and stubble retention systems.

A shift from current debates on the value of NT and stubble retention, to understanding the conditions under which these practises maximise yield is required. In general, NT and stubble retention will increase yield under conditions of high rates and strategic N supply, while the value of stubble will depend on seasonal rainfall. Mechanisms outlined in this research should be targeted in the manipulation of canopy development to improve yield in NT and stubble retention systems.

7.7 Further research

- More research is required to design a systems approach for adapting NT and stubble retention practices tailored to site specific biophysical and socio-economic conditions
- Site specific critical soil cover thresholds should be developed to maximise water capture and infiltration and minimise trade-offs in stubble allocation between competing enterprises;
- Nitrogen supply modified crop response to tillage and stubble. Site specific and economically optimal N rates and strategies of N supply should be developed
- Scarcity of water and N will continue to limit productivity in NT and stubble retention systems. Attempts to simultaneously improve water and N use efficiency in these systems are required;
- Modeling crop growth, yield, water and N budget components under NT and stubble retention could have added value to the present research. This is an area for further research;

- Patterns of leaf senescence may vary across environments. More research is required under contrasting environments, diverse water and N management regimes as well as varieties.

Table 7.1.Thesis summary of key findings, implications and research gaps

Treatment	Key findings			Implications	Gaps
	Similarities between systems	Wheat systems	Maize systems		
Interactions	Most interactions were driven by N or season/environment			N modifies crop responses to tillage and stubble	Investigate why treatment interactions are few in these systems
	Crop response to tillage and stubble was modified by N supply				
	Tillage system was independent of season/environment				
N fertilization	Large effects of both rate and timing of N supply were measured on grain yield and crop growth rate	N timing as ¼ at sowing, ½ at tillering and ¼ at awn emergence increased grain yield	-There were little differences between 80 and 120 kg N ha^{-1}. -120 kg N ha^{-1} reduced N agronomic efficiency	Optimal N rates and fine-tuning application to critical growth stages maximises yield	Establish optimal N rates, especially in SSA
	Higher yield was gained by not applying majority of N at sowing		Timing N supply as ⅓ at sowing and ⅔ at V6 increased yield and traits associated with NUE		Evaluate different N timing treatments at an economic optimum rate
Stubble		Grain yield increased with moderate stubble but decreased with high amounts of stubble	Relationship between stubble amount and grain yield was not apparent	Grain yield and water conservation are maximised at critical soil cover thresholds	Establish site specific thresholds
	Stubble increased water conservation compared with bare ground	Stubble increased water conservation; there were no significant differences between moderate and high amounts of stubble	Stubble application increased water capture; no significant differences between 3 and 5 t ha^{-1} stubble	Critical soil cover thresholds will maximise trade-off between stubble for mulch and livestock feeding	Advance post-harvest stubble management such as cutting height, spreaders and seeding technologies
	High amounts of stubble either delayed or reduced emergence	High amounts of stubble reduced emergence; NT improved emergence under high stubble compared with CT	Stubble delayed emergence in 2 of the 3 seasons	Decrease in soil temperature under stubble retention leads to a delay in emergence	Economic analysis of the trade-off for retaining stubble vs. using for livestock feeding

Treatment	Key findings			Implications	Gaps
	Similarities between systems	Wheat systems	Maize systems		
		Stubble reduced soil surface temperature by 10-12 °C in the day time but 3-5 °C rise at night		Physical obstruction and stubble-borne phyto-toxic chemicals cannot be ruled out	
Tillage	Marginal effects on yield, crop growth, water storage and use, and NUE	Overall, 12% grain yield improvement under NT compared with CT	Only during the third season did CT increase grain yield by 6% compared with NT	No-till should be adopted based on its potential to reduce costs, timeliness of operations and ease of crop management	The risks associated with continuous NT, especially in SSA soils
		Selection for yield in Australian wheats has not approved adaptation to NT			Flexibility and extent of soil disturbance to remove the negative aspects of NT
Variety	A sink-driven pattern of leaf senescence was observed	Rate of senescence increased with increases in grain yield	Rate of senescence was sink-driven	Australian wheat varieties are equally adapted to NT and stubble retention	Adaptation of maize hybrids to NT and stubble retention
					Patterns of leaf senescence vary, more research is required using diverse water regimes and varieties
	Tillage and stubble had marginal effects on the patterns of senescence			Understanding relationships between patterns of leaf senescence and grain yield and traits related to NUE might guide the deployment of senescence ideotypes to improve grain yield and quality	Breed wheat varieties and maize hybrids with leaf senescence ideotypes that improve grain yield and quality

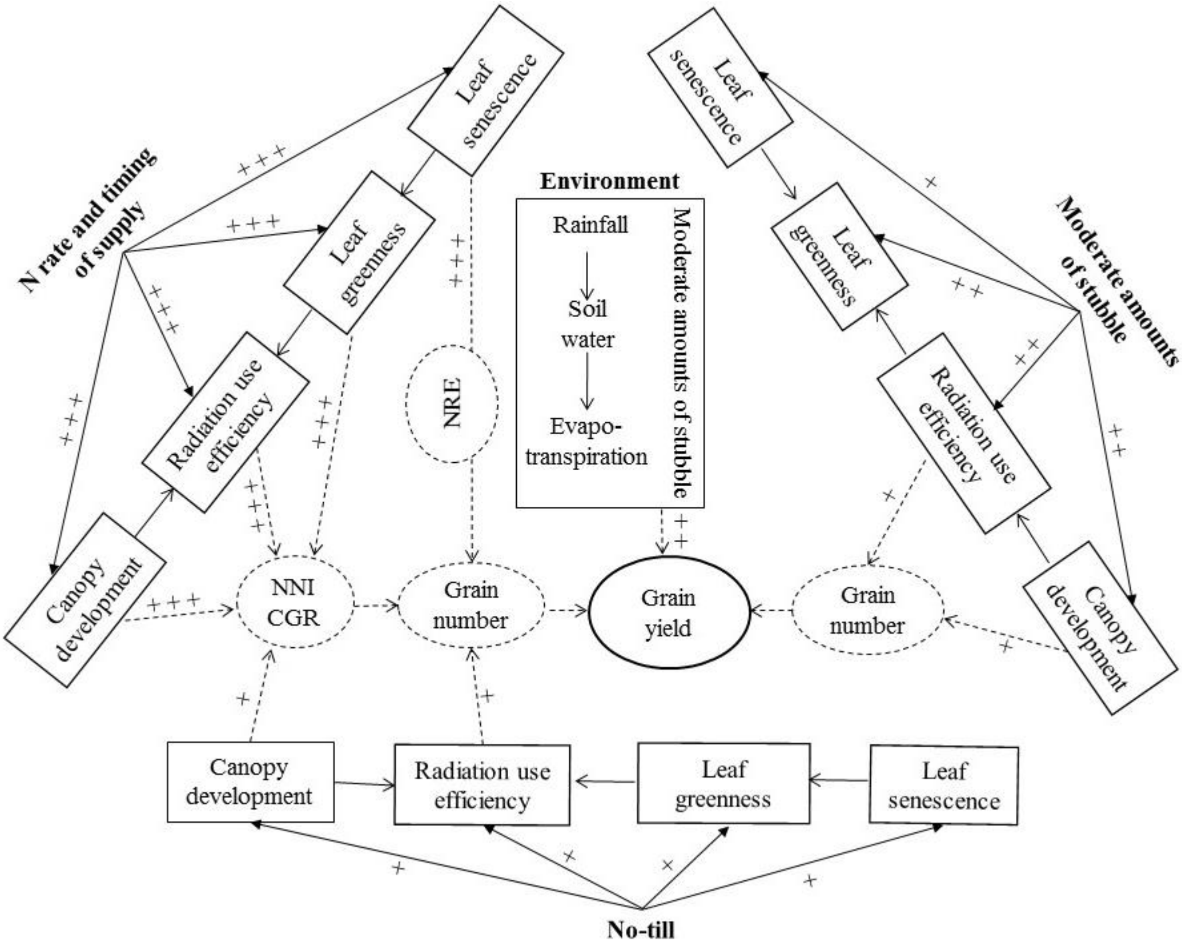

Figure 7.1. A conceptual explanation for the physiological mechanisms that impacted crop growth and yield due to environment, tillage, stubble retention and N supply. Crop growth rate (CGR), nitrogen nutrition index (NNI), nitrogen remobilization efficiency (NRE) and grain number are some of traits that mechanistically explained management effects. Dashed lines indicate physiological processes that were associated with grain yield. Minor (+) and major (+++) treatment effects and physiological processes are shown.

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Appendices

Table 4.A1. Mean grain yield (t ha^{-1}) of Australian wheat varieties released between 1958 and 2011 grown under conventional tillage (CT) and no-till (NT) in 2013 and 2015, and pooled data across the two seasons. Rank change is the difference between yield rank under NT and yield rank under CT. Ranking for yield was ordered from the lowest to the highest yielding variety. A nil rank change indicates that there was no change in ranking for a given variety between CT and NT, a negative rank change shows that the given variety ranked higher under CT compared with NT while a positive rank change indicates the vice versa. Rs is the Spearman's rank correlation coefficient between CT and NT. LSD is Fisher's least significant difference for comparing and separating means. * significant at $P \leq 0.05$; ** significant at $P \leq 0.01$; significant at $P \leq 0.001$; ^{ns} not significant at $P \leq 0.05$ probability levels.

Year of release and variety name	2013				2015				Pooled 2013 and 2015			
	CT	NT	Mean	Rank change	CT	NT	Mean	Rank change	CT	NT	Mean	Rank change
1958 Heron	3.43	4.40	3.92	3	2.80	3.24	3.02	6	3.12	3.82	3.47	0
1960 Gamenya	2.54	3.20	2.87	2	2.19	2.67	2.43	4	2.37	2.93	2.65	0
1969 Halbard	2.67	4.24	3.46	0	2.11	2.47	2.29	-2	2.39	3.35	2.87	2
1973 Condor	3.11	4.10	3.61	2	2.27	2.67	2.47	3	2.69	3.39	3.04	2
1978 Warigal	3.21	3.26	3.23	1	2.30	2.73	2.52	5	2.76	2.99	2.88	-4
1984 Spear	3.27	4.70	3.98	-2	2.23	2.59	2.41	-3	2.75	3.64	3.20	1
1985 Machete	3.18	4.96	4.07	6	2.77	3.14	2.96	1	2.98	4.05	3.51	3
1989 Janz	4.25	4.96	4.60	-3.5	2.77	2.76	2.76	-2	3.51	3.86	3.68	-3
1994 Frame	3.38	4.53	3.96	6	2.91	2.13	2.52	-5	3.15	3.33	3.24	-6
1997 Krichauff	3.73	5.48	4.61	-3	2.71	3.35	3.03	0	3.22	4.42	3.82	2
1999 Yitpi	3.65	4.86	4.26	-8	1.75	2.49	2.12	-5	2.70	3.68	3.19	3
2001 Wyalkatchem	4.41	5.61	5.01	-2	2.85	3.67	3.26	1	3.63	4.64	4.14	1
2007 Gladius	4.25	5.78	5.01	1.5	3.54	3.41	3.48	-1	3.89	4.60	4.24	-1
2011 Justica CL Plus	4.24	5.32	4.78	-3	2.77	2.78	2.78	-2	3.50	4.05	3.78	0
Mean	3.52	4.67	4.10		2.67	2.86	2.72		3.0	3.8	3.41	
LSD tillage	0.80*				0.39ns				0.28**			
LSD variety	0.61***				0.50***				0.39***			
LSD tillage × variety	0.92^{ns}				0.71^{ns}				0.57^{ns}			
Rs	0.86***				0.59*				0.79***			

Table 4.A2. Correlation coefficients between yield components, canopy traits and parameters of senescence (n = 14) of Australian wheat varieties released between 1958 and 2011 grown under conventional tillage (CT) and no-till (NT). Traits included grain yield (GY), grain number (GN), kernel weight (KW), tiller number (Tillers), head number (Heads), plant height (PHT), biomass (BM), harvest index (HI), % grain nitrogen content (%NC), leaf greenness at stem elongation ($SPAD_{SE}$), leaf greenness at flowering ($SPAD_{FL}$), leaf greenness at grain filling ($SPAD_{GF}$); minimum NDVI ($_{min}$NDVI), maximum NDVI ($_{max}$NDVI), onset of senescence (EC90), time to lose 50% of the maximum NDVI (EC50), senescence rate (SR). Coefficients above the diagonal are in CT while those below the diagonal are in NT.

Trait	GY	GN	KW	Tillers	Heads	PHT	BM	HI	%NC	$SPAD_{SE}$	$SPAD_{FL}$	$SPAD_{GF}$	$_{min}$NDVI	$_{max}$NDVI	OnS	EC50	SR
GY	-	0.82	0.16	0.20	0.36	-0.12	0.10	-0.02	0.08	0.70	0.62	0.45	0.41	-0.16	0.23	0.14	0.28
GN	0.80	-	-0.43	0.21	0.47	0.00	-0.09	0.10	-0.01	0.54	0.45	0.23	0.41	-0.17	0.51	0.33	0.50
KW	0.11	-0.50	-	-0.02	-0.19	-0.13	0.37	-0.23	0.12	0.17	0.18	0.26	-0.02	0.08	-0.42	-0.25	-0.40
Tiller	-0.12	-0.36	0.40	-	0.83	0.36	0.50	-0.09	-0.13	-0.31	-0.19	-0.19	0.09	0.73	0.07	0.12	0.01
Head	0.38	0.16	0.24	0.72	-	0.52	0.39	-0.19	-0.26	-0.18	-0.17	-0.19	0.30	0.49	0.35	0.30	0.27
PHT	-0.21	-0.30	0.24	-0.23	-0.17	-	0.71	-0.46	-0.35	-0.16	-0.21	-0.05	-0.15	0.44	0.13	0.51	-0.40
BM	0.36	0.11	0.33	-0.16	-0.02	0.04	-	-0.65	-0.17	-0.10	-0.13	0.11	-0.27	0.62	-0.12	0.38	-0.65
HI	0.62	0.62	-0.15	0.04	0.43	-0.42	0.03	-	0.41	0.32	0.52	0.24	0.42	-0.25	-0.01	-0.32	0.45
%NC	-0.18	-0.19	0.12	-0.18	-0.36	0.01	0.36	-0.29	-	0.35	0.45	0.14	0.2	-0.31	0.03	-0.09	0.24
$SPAD_{SE}$	0.69	0.46	0.20	-0.01	0.26	-0.47	0.27	0.52	-0.22	-	0.93	0.69	0.37	-0.50	0.12	0.10	0.13
$SPAD_{FL}$	0.39	0.02	0.51	0.30	0.31	-0.36	0.19	0.19	-0.13	0.81	-	0.78	0.43	-0.36	0.02	-0.02	0.13
$SPAD_{GF}$	0.41	0.13	0.34	0.15	0.12	-0.35	-0.01	0.15	-0.23	0.61	0.75	-	0.18	-0.21	-0.30	-0.22	-0.20
Nmin	0.50	0.45	-0.06	-0.10	0.18	-0.33	0.06	0.35	0.06	0.28	0.13	0.58	-	0.04	0.47	0.10	0.66
Nmax	-0.49	-0.54	0.23	0.05	-0.28	0.74	0.18	-0.72	0.27	-0.62	-0.42	-0.38	-0.40	-	-0.06	0.19	-0.34
OnS	0.47	0.58	-0.26	0.16	0.46	-0.19	-0.12	0.43	-0.40	0.30	0.28	0.10	-0.07	-0.41	-	0.79	0.66
EC50	-0.17	-0.07	-0.08	0.11	0.03	0.33	-0.08	-0.23	-0.24	-0.04	0.11	-0.24	-0.73	0.30	0.57	-	0.10
SR	0.67	0.71	-0.20	-0.03	0.33	-0.36	0.08	0.54	0.15	0.16	-0.09	0.18	0.76	-0.46	0.29	-0.52	-

🟧	$P < 0.05$	🟩	$P < 0.01$	🟨	$P < 0.001$

Table 5.A1. Analysis of variance for yield and yield components and N traits of maize crops grown under conventional tillage and no-till, three amounts of stubble and three N rates during 2015 long rains, 2015/2016 short rains and 2016 short rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station.

Treatment	Yield components							N traits				
	GY	GN	EL	ED	KW	BM	HI	NRE	GP	NNI	N uptake	NHI
Season	***	*	***	**	***	ns	***	**	ns	ns		
Tillage	***	ns	*	***	**	***	*	ns	***	ns	ns	ns
Stubble	ns	ns	ns	ns	*	ns	ns	**	ns	***	*	ns
N rate	***	***	***	***	***	***	***	***	**	***	***	**
Season × Tillage	ns	ns	ns	ns	**	*	ns	ns	*	ns		
Season × Stubble	***	*	ns	ns	ns	**	ns	ns	*	ns		
Season × N rate	***	***	ns	ns	**	***	ns	ns	ns	*		
Tillage × Stubble	**	ns	ns	ns	ns	*	*	***	ns	ns	ns	**
Tillage × N rate	***	**	ns	ns	ns	ns	ns	**	ns	ns	*	***
Stubble × N rate	ns	ns	*	ns	ns	***	ns	ns	ns	ns	***	ns
Season × Tillage × Stubble	***	ns	ns	ns	ns	ns	ns	*	**	ns		
Season × Tillage × N rate	ns	ns	ns	*	*	*	ns	ns	ns	ns		
Season × Stubble × N rate	***	***	ns	ns	***	ns	**	ns	ns	ns		
Tillage × Stubble × N rate	*	ns	ns	*	*	***	ns	***	ns	ns	***	***
Season × Tillage × Stubble × N rate	**	*	ns	ns	ns	ns	*	***	ns	ns		

GY: grain yield; GN: grain number; EL: ear length; ED: ear diameter; KW: 1000 kernel weight; BM: biomass; HI: harvest index; Crop N (kg N ha^{-1}); NRE: N remobilization efficiency; GP; grain protein; NNI: N nutrition index; NHI: N harvest index. Data for GY, GN, EL, ED and KW are for 3 seasons. Data for BM, HI, Crop N, NRE (%) and NNI are for season 1 and season 2. Data for GP is for season 2 and 3 while data for N uptake and NHI are for season 2. *P < 0.05, **P < 0.01 and ***P < 0.001; ns: not significant.

Table 5.A2. Analysis of variance for yield and yield components for maize crops grown under conventional tillage and no-tillage, three amounts of stubble and three N rates during the 2015 long rains, 2015/2016 short rains and 2016 short rains at the Kenya Agricultural and Livestock Research Organisation, Embu research station.

Treatment	2015 long rains							2015/2016 short rains							2016 long rains				
	GY	GN	EL	ED	KW	BM	HI	GY	GN	EL	ED	KW	BM	HI	GY	GN	EL	ED	KW
Tillage	ns	ns	*	*	*	*	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns
Stubble	**	ns	ns	ns	ns	ns	ns	*	ns	ns	*	**	ns	ns	**	**	ns	ns	ns
N rate	***	***	**	ns	***	***	***	***	***	*	***	***	***	***	***	**	*	**	***
Tillage × Stubble	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	**	ns	ns	ns
Tillage × N rate	ns	**	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	*	*	***	*	ns	ns	ns
Stubble × N rate	**	**	ns	ns	ns	*	**	***	*	*	*	**	***	ns	**	**	ns	ns	ns
Tillage × Stubble × N rate	ns	ns	ns	ns	ns	**	**	***	ns	ns	ns	ns	*	ns	**	**	ns	ns	ns

GY: grain yield; GN: grain number; EL: ear length; ED: ear diameter; KW: kernel weight; BM: Biomass at maturity; HI: harvest index *P < 0.05, **P < 0.01 and ***P < 0.001; ns: not significant.

Table 5.A3. Means and LSDs for effects of tillage, stubble amount and N rate on maize yield and yield components, soil water storage at sowing, evapotranspiration and water use efficiency, and traits associated with N use efficiency in maize grown during 2015 long rains, 2015/2016 short rains and 2016 long rains. Data were for yield and yield components were pooled across the three seasons while data for water storage and use components were pooled across 2015 long rains and 2015/2016 short rains. GY: grain yield (t ha^{-1}), KN: kernel number (m^{-2}), KW: kernel weight; CGR: crop growth rate (kg DM m^{-2} day^{-1}), BM: biomass (t ha^{-1}); HI: harvest index (%), SWC: soil water content at sowing (mm), ET: evapotranspiration (mm), WUE: water use efficiency (kg ha^{-1} mm^{-1}), NU: N uptake (kg ha^{-1}), NNI: nitrogen nutrition index (unitless), NRE: nitrogen remobilization efficiency (%); 0S: 0 t ha^{-1} of stubble; 3S: 3 t ha^{-1} of stubble; 5S: 5 t ha^{-1} of stubble. 0N: 0 kg N ha^{-1}; 80N: 80 kg N ha^{-1}; 120N: 120 kg N ha^{-1}.

Seasons and treatments	Yield components						Water use components			N use components		
	GY	KN	KW	CGR	BM	HI	SWC	ET	WUE	NU	NNI	NRE
2015 long rains	4.317	1297	33.09	10.44	6.873	38.57	666	768	5.36	12.42	0.83	45.43
2015/2016 short rains	3.855	1256	30.46	8.27	7.089	34.89	436	589	6.10	77.34	0.87	48.83
2016 long rains	4.139	1234	33.52							68.14		
LSD	0.100	43	0.85	0.40	1.099	1.10	19	37	0.49	2.53	0.05	2.16
Tillage												
CT	4.195	1272	32.89	9.63	7.334	36.04	550	674	5.85	52.90	0.85	47.73
NT	4.012	1253	31.82	9.08	6.628	37.42	552	683	5.61	52.37	0.84	46.52
LSD	0.081	35	0.69	0.40	1.099	1.10	19	37	0.49	2.07	0.05	2.16
Stubble amount												
0S	4.132	1263	32.64	9.79	7.136	36.83	518	657	5.24	52.29	0.89	45.65
3S	4.112	1273	31.74	9.03	6.922	36.87	561	706	6.71	50.42	0.87	49.68
5S	4.066	1251	32.69	9.25	6.884	36.49	562	676	5.48	55.19	0.78	46.05
LSD	0.100	43	0.85	0.49	1.346	1.35	23	37	0.60	2.53	0.06	2.64
Nitrogen rate												
0N	2.939	948	30.90	7.36	5.679	34.68	549	682	4.49	34.46	0.61	28.92
80N	4.622	1416	32.56	10.14	7.792	37.43	553	676	6.97	62.98	0.92	58.17
120N	4.749	1423	33.60	10.57	7.472	38.08				60.45	1.01	54.30
LSD	0.100	43	0.85	0.49	1.346	1.35	27	52	0.69	2.53	0.06	2.64

Table 5.A4. Means and LSDs for interactions between tillage, stubble amount and N rate on maize yield and yield components, soil water storage at sowing, evapotranspiration and water use efficiency, and traits associated with N use efficiency in maize grown during 2015 long rains, 2015/2016 short rains and 2016 long rains. Data were for yield and yield components were pooled across the three seasons while data for water storage and use components were pooled across 2015 long rains and 2015/2016 short rains. GY: grain yield (t ha^{-1}), KN: kernel number (m^{-2}), KW: kernel weight; CGR: crop growth rate (kg DM m^{-2} day^{-1}), BM: biomass (t ha-1); HI: harvest index (%), SWC: soil water content at sowing (mm), ET: evapotranspiration (mm), WUE: water use efficiency (kg ha^{-1} mm^{-1}), NU: N uptake (kg ha^{-1}), NNI: nitrogen nutrition index (unitless), NRE: nitrogen remobilization efficiency (%); 0S: 0 t ha^{-1} of stubble; 3S: 3 t ha^{-1} of stubble; 5S: 5 t ha^{-1} of stubble. 0N: 0 kg N ha^{-1}; 80N: 80 kg N ha^{-1}; 120N: 120 kg N ha^{-1}.

Seasons and treatments	Grain yield and yield components																	
	GY			KN			KW			CGR			BM			HI		
Season × tillage	CT	NT		CT	NT		CT	NT		CT	NT		CT	NT		CT	NT	
2015 long rains	4.425	4.208		1279	1315		34.49	31.68		10.71	10.17		7.375	6.371		37.46	39.69	
2015/2016 short rains	3.891	3.819		1275	1236		30.41	30.51		8.55	8.00		7.292	6.886		34.62	35.15	
2016 long rains	4.269	4.009		1262	1207		33.77	33.27										
LSD	0.141			61			1.20			0.56			0.340			1.56		
Season × stubble	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S
2015 long rains	4.347	4.522	4.081	1306	1337	1247	33.13	32.98	33.15	10.70	10.21	10.41	6.948	7.089	6.582	38.34	38.88	38.50
2015/2016 short rains	4.020	3.737	3.808	1289	1242	1237	31.23	29.34	30.81	8.88	7.86	8.08	7.325	6.756	7.187	35.32	34.86	34.49
2016 long rains	4.030	4.077	4.309	1195	1241	1267	33.56	32.89	34.11									
LSD	0.172			75			1.47			0.69			0.416			1.90		
Tillage × Stubble	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S
CT	4.316	4.203	4.067	1282	1292	1242	33.50	32.09	33.09	9.96	9.43	9.50	7.429	7.510	7.062	36.92	35.07	36.13
NT	3.949	4.020	4.066	1244	1255	1259	31.78	31.39	32.29	9.62	8.64	8.99	6.843	6.335	6.707	36.74	38.67	36.86
LSD	0.141			61			1.20			0.69			0.416			1.90		
Season × N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N
2015 long rains	3.380	4.751	4.818	1051	1445	1395	31.65	32.56	35.06	8.77	10.96	11.59	5.902	7.296	7.420	36.64	39.61	39.48
2015/2016 short rains	2.758	4.350	4.457	977	1385	1405	28.09	31.47	31.83	5.95	9.32	9.55	5.455	7.647	8.164	32.72	36.56	35.38
2016 long rains	2.679	4.764	4.973	817	1418	1468	32.96	33.67	33.93									
LSD	0.172			75			1.47			0.69			0.416			1.90		

Seasons and treatments	Grain yield and yield components																	
	GY			KN			KW			CGR			BM			HI		
Tillage × N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N
CT	2.948	4.816	4.822	943	1467	1407	31.17	32.90	34.60	7.39	10.51	10.99	6.088	7.888	8.024	33.47	37.87	36.78
ZT	2.930	4.428	4.677	954	1365	1439	30.63	32.22	32.61	7.33	9.77	10.15	5.269	7.056	7.561	35.89	38.30	38.08
LSD	0.141			61			1.20			0.69			0.416			1.90		
Stubble x N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N
0S	3.046	4.604	4.747	988	1393	1408	31.41	32.65	33.85	8.02	10.60	10.75	6.406	7.331	7.672	34.25	38.31	37.93
3S	2.906	4.678	4.752	954	1449	1416	29.34	32.31	33.56	6.99	9.82	10.30	5.223	7.672	7.872	35.18	37.88	37.55
5S	2.866	4.584	4.749	902	1405	1444	31.94	32.72	33.40	7.07	10.00	10.66	5.407	7.413	7.833	34.61	38.06	36.80
LSD	0.172			75			1.47			0.85			0.510			2.33		
Season x Tillage x Stubble	0N	80N	120N	0N	80N	120N	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S
2015 long rains_CT	4.665	4.465	4.146	1329	1302	1206	35.04	33.37	35.07	10.73	10.58	10.83	7.549	7.650	6.926	38.10	36.62	37.64
2015 long rains_NT	4.028	4.579	4.017	1283	1373	1289	31.22	32.59	31.22	10.67	9.84	9.99	6.346	6.528	6.238	38.58	41.15	39.36
2015/2016 long rains_CT	4.098	3.781	3.796	1296	1263	1266	31.57	29.48	30.18	9.19	8.28	8.18	7.309	7.369	7.198	35.73	33.52	34.61
2015/2016 long rains_NT	3.943	3.692	3.821	1281	1220	1208	30.89	29.20	31.44	8.57	7.44	7.98	7.340	6.142	7.176	34.91	36.20	34.36
2016 long rains_CT	4.184	4.364	4.258	1222	1310	1254	33.89	33.41	34.00									
2016 long rains_NT	3.876	3.790	4.360	1168	1171	1280	33.22	32.37	34.22									
LSD	0.244			106			2.08			0.98			0.589			2.69		
Season x Tillage x N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N
2015 long rains_CT	3.498	4.876	4.902	1053	1475	1309	32.26	33.15	38.07	8.95	11.53	11.67	6.257	7.875	7.992	35.89	38.44	38.04
2015 long rains_NT	3.263	4.627	4.735	1048	1415	1481	31.04	31.96	32.04	8.6	10.39	11.52	5.547	6.718	6.848	37.38	40.78	40.92
2015/2016 long rains_CT	2.679	4.569	4.426	956	1447	1422	28.43	31.60	31.21	5.83	9.49	10.32	5.920	7.902	8.055	31.05	37.30	35.51
2015/2016 long rains_NT	2.837	4.132	4.488	999	1322	1389	27.75	31.33	32.45	6.06	9.15	8.78	4.991	7.393	8.273	34.40	35.82	35.25
2016 long rains_CT	2.667	5.003	5.137	819	1477	1490	32.81	33.96	34.52									
2016 long rains_NT	2.691	4.526	4.809	814	1360	1446	33.11	33.37	33.33									
LSD	0.244			106			2.08			0.98			0.589			2.69		
Season x Stubble x N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N

Seasons and treatments	Grain yield and yield components																	
	GY			KN			KW			CGR			BM			HI		
2015 long rains_0S	3.428	4.723	4.888	1144	1390	1384	31.11	32.72	35.56	9.85	11.48	10.78	6.452	7.208	7.184	34.60	39.87	40.56
2015 long rains_3S	3.339	5.129	5.098	954	1575	1484	31.83	32.67	34.44	8.35	10.74	11.55	5.975	7.768	7.524	36.24	39.96	40.46
2015 long rains_5S	3.374	4.402	4.469	1054	1370	1318	32.00	32.28	35.17	8.12	10.66	12.45	5.279	6.913	7.553	39.07	39.00	37.42
2015/2016 short rains_0S	3.263	4.347	4.452	1060	1363	1443	30.85	31.96	30.88	6.19	9.72	10.73	6.360	7.454	8.160	33.89	36.75	35.31
2015/2016 short rains_3S	2.635	4.228	4.346	1059	1344	1322	23.70	31.44	32.89	5.64	8.89	9.05	4.471	7.577	8.220	34.13	35.80	34.64
2015/2016 short rains_5S	2.376	4.476	4.574	813	1447	1451	29.72	30.99	31.71	6.02	9.35	8.87	5.536	7.912	8.114	30.14	37.13	36.19
2016 long rains_0S	2.447	4.742	4.900	761	1427	1397	32.28	33.28	35.11									
2016 long rains_3S	2.742	4.677	4.811	850	1429	1443	32.50	32.83	33.33									
2016 long rains_5S	2.848	4.874	5.206	839	1399	1563	34.11	34.89	33.33									
LSD	0.299			130			2.55			1.20			0.721			3.30		
Tillage x Stubble x N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N
CT_0S	3.109	4.951	4.887	995	1455	1397	31.30	34.10	35.10	7.58	10.93	11.37	6.239	8.076	7.972	35.34	37.83	37.58
CT_3S	2.840	4.950	4.820	938	1514	1423	29.72	32.70	33.84	6.96	10.88	10.44	6.175	8.258	8.095	31.80	37.02	36.40
CT_5S	2.896	4.546	4.758	896	1431	1400	32.49	31.91	34.86	7.63	9.72	11.17	5.851	7.330	8.005	33.26	38.76	36.35
NT_0S	2.984	4.257	4.606	982	1331	1418	31.52	31.21	32.61	8.46	10.27	10.13	6.572	6.585	7.372	33.15	38.79	38.29
NT_3S	2.971	4.406	4.684	970	1385	1409	28.97	31.93	33.27	7.02	8.75	10.15	4.270	7.086	7.649	38.57	38.74	38.70
NT_5S	2.836	4.622	4.741	909	1380	1488	31.40	33.53	31.95	6.51	10.29	10.16	4.964	7.495	7.661	35.95	37.37	37.25
LSD	0.244			106			2.08			1.20			0.721			3.30		
Season x Tillage x Stubble x N rate	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N	0N	80N	120N
2015long rains_CT_0S	3.736	5.004	5.254	1185	1442	1360	31.56	34.78	38.78	9.32	11.72	11.16	6.417	8.335	7.896	36.80	37.52	40.00
2015long rains_CT_3S	3.333	5.073	4.991	941	1547	1418	32.11	32.78	35.22	8.64	11.76	11.34	6.642	8.589	7.719	33.35	37.17	39.35
2015long rains_CT_5S	3.426	4.550	4.462	1035	1436	1147	33.11	31.89	40.22	8.88	11.11	12.50	5.712	6.702	8.363	37.52	40.62	34.77
2015long rains_NT_0S	3.120	4.442	4.523	1103	1338	1407	30.67	30.67	32.33	10.38	11.23	10.39	6.486	6.080	6.473	32.40	42.22	41.12
2015long rains_NT_3S	3.346	5.185	5.206	967	1602	1549	31.56	32.56	33.67	8.05	9.72	11.75	5.308	6.948	7.329	39.12	42.75	41.56
2015long rains_NT_5S	3.322	4.255	4.475	1074	1304	1488	30.89	32.67	30.11	7.36	10.21	12.41	4.846	7.125	6.742	40.63	37.38	40.07
2015/2016 short rains_CT_0S	3.112	4.820	4.361	1007	1482	1400	31.02	32.53	31.18	5.84	10.14	11.59	6.061	7.818	8.048	33.89	38.14	35.15

Seasons and treatments	Grain yield and yield components																	
	GY			KN			KW			CGR			BM			HI		
2015/2016 short rains_CT_3S	2.476	4.621	4.245	1049	1420	1319	23.71	32.54	32.20	5.28	10.01	9.54	5.709	7.928	8.471	30.24	36.86	33.44
2015/2016 short rains_CT_5S	2.449	4.265	4.673	812	1440	1547	30.57	29.73	30.24	6.37	8.32	9.84	5.989	7.959	7.648	29.01	36.89	37.94
2015/2016 short rains_NT_0S	3.414	3.874	4.542	1114	1244	1485	30.68	31.40	30.59	6.53	9.30	9.87	6.658	7.090	8.272	33.90	35.36	35.47
2015/2016 short rains_NT_3S	2.794	3.835	4.448	1068	1268	1325	23.68	30.34	33.58	6.00	7.78	8.55	3.232	7.225	7.969	38.01	34.73	35.85
2015/2016 short rains_NT_5S	2.304	4.686	4.474	814	1453	1356	28.87	32.26	33.18	5.66	10.37	7.91	5.083	7.865	8.579	31.27	37.36	34.43
2016 long rains_CT_0S	2.478	5.028	5.047	793	1441	1430	31.33	35.00	35.33									
2016 long rains_CT_3S	2.712	5.156	5.224	825	1574	1532	33.33	32.78	34.11									
2016 long rains_CT_5S	2.812	4.823	5.139	840	1417	1506	33.78	34.11	34.11									
2016 long rains_NT_0 S	2.417	4.456	4.754	729	1413	1363	33.22	31.56	34.89									
2016 long rains_NT_3S	2.773	4.197	4.399	876	1284	1354	31.67	32.89	32.56									
2016 long rains_NT_5S	2.884	4.924	5.273	839	1382	1620	34.44	35.67	32.56									
LSD	0.422			184			3.61			1.69			1.020			4.66		

Seasons and treatments	Soil water components									N use components								
	SWC			ET			WUE			NNI			NRE			N uptake		
Season × tillage	CT	NT		CT	ZT		CT	ZT		CT	NT		CT	NT		CT	NT	
2015 long rains	668	664		761	775		5.56	5.15		0.86	0.80		45.29	45.57		76.61	78.07	
2015/2016 short rains	433	439		587	591		6.13	6.08		0.85	0.89		50.18	47.48		69.27	67.02	
2016 long rains																		
LSD	27			52			26.63			0.07			3.05			4.38		
Season × stubble	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S
2015 long rains	637	667	680	756	809	754	4.59	6.39	5.22	0.89	0.85	0.73	44.00	47.74	44.55	13.20	11.51	12.56
2015/2016 short rains	399	455	445	559	604	597	5.89	7.03	5.75	0.89	0.88	0.83	47.30	51.62	47.56	76.98	72.73	82.30
2016 long rains																66.70	67.02	70.70

Seasons and treatments	Soil water components									N use components								
	SWC			ET			WUE			NNI			NRE			N uptake		
LSD	27			63			0.84			0.08			3.74			3.58		
Tillage × Stubble	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S
CT	538	560	552	669	703	662	5.17	7.00	5.61	0.88	0.89	0.79	48.05	51.77	43.39	52.77	51.94	53.99
NT	498	563	573	646	709	689	5.31	6.42	5.36	0.91	0.85	0.77	43.26	47.59	48.71	51.82	48.90	56.39
LSD	27			63			0.97			0.08			3.74			4.38		
Season × N rate	0N	80N		0N	80N		0N	80N		0N	80N	120N	0N	80N	120N	0N	80N	120N
2015 long rains	669	663		779	757		4.59	6.13		0.59	0.86	1.03	27.17	51.35	57.77	12.25	12.72	12.30
2015/2016 short rains	428	444		584	594		4.39	7.82		0.62	0.99	0.99	30.66	57.24	58.57	51.95	88.35	91.70
2016 long rains																39.19	80.29	84.94
LSD	38			73			0.84			0.08			3.74			3.58		
Tillage × N rate	0N	80N		0N	80N		0N	80N		0N	80N	120N	0N	80N	120N	0N	80N	120N
CT	541	560		678	670		4.64	7.06		0.61	0.91	1.04	30.61	52.00	60.60	33.90	63.32	61.47
ZT	557	547		685	681		4.34	6.89		0.60	0.93	0.99	27.22	56.59	55.75	35.03	57.59	64.50
LSD	33			63			0.84			0.08			3.74			6.20		
Stubble x N rate										0N	80N	120N	0N	80N	120N	0N	80N	120N
0S										0.67	0.98	1.02	27.48	50.73	58.75	36.79	60.18	59.92
3S										0.60	0.95	1.06	31.51	57.87	59.65	28.60	59.46	63.19
5S										0.55	0.84	0.96	27.76	54.28	56.12	38.00	61.72	65.84
LSD										0.10			4.57			6.20		
Season x Tillage x Stubble	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S	0S	3S	5S
2015 long rains_CT	656	659	678	761	785	750	4.93	6.55	5.38	0.89	0.90	0.78	43.31	50.11	42.46	14.42	11.51	12.52
2015 long rains_NT	617	675	682	750	832	758	4.25	6.23	5.06	0.89	0.81	0.69	44.70	45.37	46.64	11.98	11.51	12.60
2015/2016 long rains_CT	419	460	426	576	622	575	5.41	7.44	5.84	0.86	0.88	0.81	52.78	53.43	44.33	75.39	75.53	78.89
2015/2016 long rains_NT	379	450	464	541	585	619	6.38	6.61	5.66	0.92	0.89	0.85	41.83	49.81	50.79	78.57	69.92	85.70
2016 long rains_CT																68.49	68.76	70.55
2016 long rains_NT																64.92	65.28	70.86

Seasons and treatments	Soil water components						N use components								
	SWC		ET		WUE		NNI			NRE			N uptake		
LSD	38		73		0.97		0.12			5.28			4.38		
Season x Tillage x N rate	0N	80N	0N	80N	0N	80N	0N	80N	120N	0N	80N	120N	0N	80N	120N
2015 long rains_CT	660	676	782	741	4.63	6.5	0.60	0.87	1.09	29.45	47.28	59.15	11.74	14.47	12.24
2015 long rains_NT	678	650	777	773	4.54	5.75	0.58	0.84	0.97	24.89	55.42	56.39	12.76	10.97	12.37
2015/2016 long rains_CT	421	445	575	599	4.64	7.62	0.62	0.95	0.98	31.77	56.72	62.04	50.89	91.70	87.22
2015/2016 long rains_NT	435	443	594	589	4.13	8.03	0.63	1.02	1.01	29.55	57.77	55.11	53.01	85.01	96.18
2016 long rains_CT													39.08	83.78	84.94
2016 long rains_NT													39.31	76.80	84.95
LSD	46		89		0.97		0.12			5.28			3.58		
Season x Stubble x N rate							0N	80N	120N	0N	80N	120N	0N	80N	120N
2015 long rains_0S							0.69	0.95	1.04	24.13	49.25	58.64	12.95	14.35	12.30
2015 long rains_3S							0.58	0.89	1.10	32.38	53.44	57.38	11.55	10.62	12.37
2015 long rains_5S							0.51	0.73	0.95	25.00	51.35	57.30	12.25	13.18	12.25
2015/2016 short rains_0S							0.66	1.01	1.01	30.83	52.22	58.86	60.08	85.71	85.15
2015/2016 short rains_3S							0.62	1.01	1.02	30.63	62.30	61.93	34.75	88.92	94.51
2015/2016 short rains_5S							0.59	0.94	0.96	30.52	57.21	54.94	61.02	90.43	95.44
2016 long rains_0S													37.33	80.47	82.30
2016 long rains_3S													39.51	78.85	82.70
2016 long rains_5S													40.74	81.54	89.83
LSD							0.14			6.47			10.74		
Tillage x Stubble x N rate							0N	80N	120N	0N	80N	120N	0N	80N	120N
CT_0S							0.65	0.97	1.01	26.63	53.97	63.54	36.11	65.70	56.49
CT_3S							0.61	0.94	1.11	35.79	57.02	62.48	27.14	65.07	63.60
CT_5S							0.58	0.82	0.99	29.40	45.00	55.77	38.47	59.17	64.32
NT_0S							0.70	0.99	1.04	28.33	47.50	53.96	37.47	54.65	63.34
NT_3S							0.59	0.95	1.00	27.22	58.72	56.83	30.07	53.85	62.79

Seasons and treatments	Soil water components			N use components								
	SWC	ET	WUE	NNI			NRE			N uptake		
NT_5S				0.52	0.86	0.92	26.12	63.56	56.47	37.53	64.27	67.37
LSD				0.14			6.47			6.20		
Season x Tillage x Stubble x N rate				0N	80N	120N	0N	80N	120N	0N	80N	120N
2015long rains_CT_0S				0.66	0.96	1.05	24.68	43.49	61.75	13.77	17.27	12.23
2015long rains_CT_3S				0.59	0.90	1.22	36.98	53.33	60.00	11.67	11.43	11.43
2015long rains_CT_5S				0.56	0.76	1.01	26.67	45.00	55.71	9.80	14.70	13.07
2015long rains_NT_0S				0.71	0.94	1.03	23.57	55.00	55.53	12.13	11.43	12.37
2015long rains_NT_3S				0.57	0.88	0.98	27.78	53.56	54.76	11.43	9.80	13.30
2015long rains_NT_5S				0.46	0.71	0.90	23.33	57.70	58.89	14.70	11.67	11.43
2015/2016 short rains_CT_0S				0.64	0.98	0.97	28.57	64.44	65.33	56.58	95.52	74.08
2015/2016 short rains_CT_3S				0.64	0.99	1.01	34.60	60.71	64.96	32.58	98.01	96.00
2015/2016 short rains_CT_5S				0.59	0.88	0.96	32.14	45.00	55.83	63.51	81.57	91.59
2015/2016 short rains_NT_0S				0.69	1.04	1.05	33.10	40.00	52.38	63.59	75.90	96.23
2015/2016 short rains_NT_3S				0.61	1.03	1.03	26.67	63.89	58.89	36.92	79.83	93.02
2015/2016 short rains_NT_5S				0.59	1.00	0.95	28.90	69.42	54.05	58.52	99.28	99.30
2016 long rains_CT_0S										37.97	84.32	83.17
2016 long rains_CT_3S										37.16	85.78	83.36
2016 long rains_CT_5S										42.10	81.24	88.29
2016 long rains_NT_0 S										36.69	76.62	81.43
2016 long rains_NT_3S										41.86	71.92	82.04
2016 long rains_NT_5S										39.37	81.85	91.37
LSD				0.20			9.15			7.59		

Table 6.A1. Tillage and stubble-driven traits of leaf senescence at different canopy layers of maize grown at the Kenya Agricultural and Livestock Research Organization, Embu research station during 2015 long rains, 2015/2016 short rains and 2016 long rains.

Treatment	2015 long rains				2015/2016 short rains				2016 long rains			
	SPAD_{max}	EC90	EC50	SR	SPAD_{max}	EC90	EC50	SR	SPAD_{max}	EC90	EC50	SR
Top leaves												
Tillage												
CT	47.0a	398a	597a	14a	47a	454a	610a	23a	49.9a	450a	574a	21a
NT	45.8b	398a	607a	15a	47a	454a	597a	25a	50.5a	458a	574a	23a
Stubble												
0 $t\ ha^{-1}$	47.5a	418a	607a	17a	48a	466a	597a	28a	49.3b	450a	574a	22a
3 $t\ ha^{-1}$	45.8a	408a	597a	15a	48a	466a	610a	25a	49.8b	466a	574a	27a
5 $t\ ha^{-1}$	45.9a	376a	607a	13a	46a	429a	623a	18b	51.5a	450a	584a	18a
Interactions ANOVA												
Tillage × stubble	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tillage × N rate	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns
Stubble × N rate	ns	ns	ns	ns	ns	ns	ns	ns	***	ns	ns	ns
Tillage × stubble x N rate	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Mid leaves												
Tillage												
CT	56b	482a	669a	16a	52a	492a	690a	23a	55.4a	493a	670a	16a
NT	57a	460a	659a	15a	52a	503a	663a	22a	54.8a	502a	681a	17a
Stubble												
0 $t\ ha^{-1}$	58a	460a	659a	15a	53a	503a	663a	23a	56.1a	542a	681a	20a
3 $t\ ha^{-1}$	54b	482a	669a	17a	51a	492a	677a	23a	53.8a	548b	681a	15b
5 $t\ ha^{-1}$	55b	471a	659a	15a	53a	503a	677a	21a	55.5a	496b	681a	14b
Interactions ANOVA												
Tillage × stubble	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tillage × N rate	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Stubble × N rate	**	ns	ns	ns	***	ns	ns	ns	ns	**	ns	ns
Tillage × stubble × N rate	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
Bottom leaves												
Tillage												
CT	36a	210a	567a	6a	43a	228a	597a	13a	37.5b	381a	563a	13a
NT	36a	186a	556a	5a	40b	314a	569a	13a	40.2a	350a	542a	13a
Stubble												
0 $t\ ha^{-1}$	37a	199a	556a	5a	43a	228a	584a	12a	37.7a	372a	584a	12a
3 $t\ ha^{-1}$	37a	199a	556a	5a	39b	314a	597a	14a	39.7a	361a	553a	14a
5 $t\ ha^{-1}$	34a	222a	567a	6a	42b	300a	569a	12a	39.1a	350a	522b	14a
Interactions ANOVA												
Tillage × stubble	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tillage × N rate	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Stubble × N rate	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns
Tillage × stubble × N rate	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Within a column, means followed by the same letter are not significantly different at 0.05 probability. *$P < 0.05$, **$P < 0.01$ and ***$P < 0.001$; ns: not significant.