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Title:
Impacts of changing climate variability and extremes on pasture systems in south eastern Australia

Date:
2020

Persistent Link:
https://hdl.handle.net/11343/241588

Impacts of changing climate variability and extremes on pasture systems in south eastern Australia

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A thesis submitted in total fulfilment for the degree of

Doctor of Philosophy

March 2020

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ABSTRACT

Climate variability and extreme climate events such as heat waves, droughts, extreme precipitation and frost occurrences are increasingly challenging the agricultural systems in Australia and globally. Despite this, the majority of the previous climate change studies have focused on the influence of average climate change on agricultural systems, which risks underestimating the impacts of climatic changes. In south eastern (SE) Australia, climate variability has increased in recent decades accompanying an increased frequency and severity of extreme climate events such as heat waves and droughts. The objective of this research was to investigate the impacts of changing climate variability and extreme climate events on pasture systems in SE Australia using biophysical modelling and controlled experimental approaches.

Year to year variability in pasture yields has many consequences on the key management decisions such as stocking rates and the timing of the reproductive cycle. Changes to the pasture growth patterns were investigated at five sites in SE Australia ranging from medium rainfall, warm temperate climate at Wagga Wagga in southern New South Wales to high rainfall, cool temperate climate at Elliott in Tasmania using DairyMod biophysical software over the period 1960-2015. Across the sites, winter production has increased, spring pasture growth has decreased and year to year yield variability during autumn and spring seasons has increased in the most recent period (2002-2015) compared to 1988-2001. Increased number of days with water and temperature limitation together with increased spring and summer soil moisture deficit are in line with the simulated changes in pasture growth patterns, suggesting that adaptations such as incorporating deep rooting and heat tolerant species should be prioritized to stabilize pasture production.

The year to year variability in pasture yield was better explained when extreme climate indices were used in combination with climate averages, as compared with climate average alone. Extreme climate indices together with the average climate variables explained more yield variability at the medium rainfall sites (eg. Wagga Wagga R^2=0.89) than high rainfall sites (eg. Elliott R^2=0.70)

indicating that medium rainfall sites are more sensitive to the changes in rainfall distribution and high temperatures. Increased occurrences of dry months, wet months during the winter and spring, number of hot days above 30 °C and the duration of hot days in a year decreased pasture yields highlighting the importance of considering extreme climate events in future climate change studies on agricultural systems.

El-Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) are two major rainfall drivers that influence rainfall variability in Australia and their phases reach the peak during the spring season which is the major pasture growing season in SE Australia. Each driver has a dry and hot phase (El-Niño and IOD(+)) and a cool and wet phase (La-Niña and IOD(-)). The influence of these phases individually and in combination were investigated on simulated annual pasture production from 1950-2015 in five sites in SE Australia. In dry and hot phases of both of ENSO and IOD (El-Niño and IOD(+)), lower pasture production was simulated, while the phases responsible for the wet and cool climate increased the yield. When combined ENSO-IOD phases were examined, the highest yields resulted when the La-Niña phases coincided with IOD(-) or neutral, whilst the El-Niño with IOD(+) phases led to the lowest yields. Forecast analysis revealed that the effects of climate driver phases emerge at the end of winter, but this is not a sufficient lead time for making important pasture management decisions. Therefore, further studies are warranted to increase the forecast ability of each climate driver phase to use them in agriculture decision making.

Climate models project increased frequency of extreme climate events in SE Australia in the future. A controlled environmental experiment was conducted to investigate growth and physiological responses of four summer active temperate perennial pasture species to consecutive 7-day heat and drought stresses. Exposure of perennial ryegrass, tall fescue, cocksfoot and chicory to consecutive moderate (30/20 °C, day/night) and severe (35/25 °C, day/night) heat and drought stress revealed that all the species can acclimate to moderate combined heat and drought stress by maintaining the physiological functions such as photosynthesis, maximum photochemical efficiency of photosystem II, cell membrane permeability and relative leaf water content. However, chicory was the only species that maintained the above physiological processes under consecutive severe heat and drought

stresses while all grass species decline to the minimum values. Plants that were irrigated showed cooler canopies than non-irrigated plants during high temperature treatments and this transpirational cooling mitigated the impacts of heat stress in all species.

Leaf temperature data measured using infrared images during the experiment were used to validate the leaf energy budget equation and the calculated leaf temperatures (using the energy budget) were used to model heat stress impacts on perennial ryegrass in DairyMod model. The leaf temperature calculation incorporates the interaction of air temperature and soil water through the feedback effects of transpiration through stomata. The simulations run with calculated leaf temperatures predicted the observed reduction of photosynthesis accurately while air temperature simulations overestimated the actual impacts under moderate temperature, indicating that leaf temperature more accurately represents the environment under which plants are grown under heat stress rather than air temperature. Further, the DairyMod high temperature stress recovery function (T sum) for perennial ryegrass was parameterized using measured data of the experiment. The findings demonstrated that simulations of DairyMod can be improved using leaf temperature and parameterizing heat stress recovery functions.

In conclusion, this research highlighted that the climate variability and extreme events have changed the pasture growth patterns in SE Australia in the recent period (2002-2015) therefore, climate variability and extreme climate events need to be fully considered in the future climate change studies. Chicory may be a more adapted pasture species in temperate livestock areas where extreme summer heat and moisture stresses limit summer feed supply. Leaf temperature modelling improves the heat stress simulations in the DairyMod model and this approach can also be used in other crop simulation models to improve high temperature stress modelling. Future research should aim to identify the plant traits and key metabolic processes in Chicory that confer greater heat stress tolerance and what other species would have similar traits. Future research on climate change impacts should also aim to determine critical combinations of extreme events that would result in tipping points for farming systems.

DECLARATION

This is to certify that:

(i) the thesis comprises only my original work toward the PhD and none of this work has been submitted for any other degree;

(ii) due acknowledgement has been made in the text to all other material used;

(iii) the thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies, and appendices

Thudugala Mudalige Ruchika Sandaruwan Perera

March 2020

LIST OF PUBLICATIONS

I was the lead investigator in all published chapters and original work included in this thesis.

Full Title: Changing patterns of pasture production in south-eastern Australia from 1960 to 2015
Authors: Ruchika S. Perera, Brendan R. Cullen, and Richard J. Eckard
Candidate's contribution: 75%
Journal: Crop & Pasture Science
Volume and pages: Vol. 71 pp. 70-81
Status: published online 17 January 2020
Thesis Chapter 3

Full Title: Influence of El-Niño Southern Oscillation and Indian Ocean Dipole phases on annual pasture production in south eastern Australia
Authors: Ruchika S. Perera, Brendan R. Cullen, and Richard J. Eckard
Candidate's contribution: 80%
Conference Proceedings: 2018 Australasian Dairy Science Symposium (ADSS), Palmerston North, New Zealand, 21-23 November 2018
Pages: pp. 63-70
Status: Published as a peer reviewed conference paper
Thesis Chapter 5

Full Title: Growth and Physiological Responses of Temperate Pasture Species to Consecutive Heat and Drought Stresses
Authors: Ruchika S. Perera, Brendan R. Cullen and Richard J. Eckard
Candidate's contribution: 83%
Journal: Plants MDPI
Volume and pages: Vol. 8 pp. 227
Status: Published online 16 July 2019
Thesis Chapter 6

Full Title: Using Leaf Temperature to Improve Simulation of Heat and Drought Stresses in a Biophysical Model
Authors: Ruchika S. Perera, Brendan R. Cullen and Richard J. Eckard
Candidate's contribution: 82%
Journal: Plants MDPI
Volume and pages: Vol. 9 pp. 8
Status: Published online 19 December 2019
Thesis Chapter 7

The co-authors of each of the published papers have agreed to the inclusion of these works in this thesis and signed the University of Melbourne co-author declaration form. The co-authors certify that the primary author, Ruchika S. Perera, has contributed greater than 50% to each paper published and was responsible for the planning and execution of the research, including written preparation for publication.

The inclusion of the above mentioned published papers in this thesis has been approved by the advisory committee for Ruchika S. Perera. The University of Melbourne's declaration for a thesis with publication has been certified by the candidate's principal supervisor, Dr. Brendan Richard Cullen.

ACKNOWLEDGEMENTS

First, I would like to thank my project supervisors, Dr. Brendan Cullen and Professor Richard Eckard for their great support, advice, and encouragement during this project. I greatly appreciate their patience and motivation during the hard times of my PhD particularly when I am stuck with data analysis, glass house experiment and writing the thesis. I would also like to extend my sincere thanks to Associate Professor Graham Hepworth, statistical consultant center, the University of Melbourne for the statistical advice, and Steven Elefteriadis, Glasshouse Complex Manager, Faculty of Veterinary and Agricultural Sciences for the technical assistance during the glasshouse experiment. I also express my sincere thanks to Dr. Kithsiri Dassanayake for passing my CV to Dr. Brendan Cullen and helping me to get the Melbourne Research Scholarship to carry out my PhD. Thank you all my loving school teachers and the university lecturers for helping me build up my confidence since my childhood. Finally, lots of love to my wife Dr. Himali Balasooriya for the enormous support and continuous help during my PhD and to my parents and sister for being with me and encouraging all the way to get through this challenging journey.

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CHAPTER 1. Introduction

1.1. Background

Australia has high year to year rainfall variability compared to similar other climates in the world (Love 2005). Recent observations of the Australian climate indicates that the magnitude and the frequency of extreme events such as heat waves, droughts, extreme rainfall and frost occurrences have increased as a result of climate change (CSIRO and BOM 2015). High rainfall variability has important implications in the rainfed agricultural production systems in Australia as most do not have access to irrigation, and those that do are subject to large variations in water availability and price (Chapman *et al.* 2012a). Climate change projections also indicate frequent heat and drought episodes in SE Australia which will tend to increase climate variability (CSIRO and BOM 2015; Hennessy *et al.* 2016). Despite increasing frequency and magnitude of extremes, the majority of previous climate change impact studies on agriculture have focused on changes in the average climate change (IPCC 2012b). The real impacts could be highly underestimated when only the mean climate change is considered because variability and extremes cause more damage to agricultural systems than average changes in climate (Thornton *et al.* 2014).

Australia's mean temperature has increased by 1 °C since the start of the 20th century and very high monthly day time temperatures that occurred 2% of the time (from 1951-1980) have now increased up to 12% (from 2003-2017) (BOM 2018). Heat wave frequency, duration and magnitude has also increased in Victoria since 1950 (Perkins Kirkpatrick *et al.* 2016) and in parallel to that, the fire danger days have increased in this region particularly in spring season (BOM 2018). Despite night time temperatures increasing, frost occurrences have also increased across many regions of southern Australia. This has led to an increased frost period length by 26 days during 2000-2014 compared to the period 1960-1990 (Crimp *et al.* 2016b). SE Australian rainfall has been decreasing since the 1990's, particularly during April-October (CSIRO and BOM 2015). A prolonged drought was reported from 1997-2009 known as the Millennium drought (Timbal 2009). Further, since 1999, 17 out of 20 years received below average rainfall in southern Australia during the April-October period

(BOM 2018). Despite the persistent drying trend, extreme precipitation events have also increased in Victoria since 1970 with the years 2010 and 2013 being the wettest two years on record (CSIRO and BOM 2015). These observations provide clear evidence to show that climate variability in SE Australia has increased together with increased frequency and magnitude of extreme climate events.

This increased climate variability and extremes has important implications for Australian agriculture. A recent farmer survey conducted in Australia (including 1300 farmers from every agricultural sector nationwide) revealed that climate extremes are of greater concern than climate change itself (FCA 2016). Two third of the farmers reported that they have experienced changes in rainfall patterns while 47 % and 44% of farmers have observed increased frequency of intense droughts and heat waves, respectively. With these changes, decisions on planting times, crop types and animal breeds have changed in their production systems. Farmer observations on climate extremes are consistent with the recent changes observed in the climate in southern Australian region (CSIRO and BOM 2015). Climate change projections in the major dairy regions in Australia (using 40 different climate models under high emission scenario) indicate that the existing rainfall variability will continue to increase with large rainfall declines in the major growing seasons (autumn and spring) (Hennessy *et al.* 2016).

Pasture underpins livestock production in SE Australia, because pasture is generally the cheapest source of feed for livestock (Chapman *et al.* 2014a). However, year to year pasture yield variability, greatly challenges the efficient feeding of livestock. The year to year pasture yield variability is mainly governed by rainfall variability (Chapman *et al.* 2013). Constraints of rainfall variability on pasture systems are mainly reflect in balancing feed supply and demand. Changing pasture growing patterns affects long-term strategic management decisions such as stocking rates and calving/lambing times as well as tactical and operational level decisions such as fertilizer use and supplementary feeding (Chapman *et al.* 2013; Chang-Fung-Martel *et al.* 2017). In addition to the impacts on pasture supply and decision making, climate extremes (mainly prolonged droughts and heat) also affect pasture plant survival (referred to as pasture persistence). Extensive tiller deaths of perennial ryegrass pastures have been reported in western Victoria under high temperature and

moisture deficits in summer months (Nie *et al.* 2004a). In Europe, tiller mortality in temperate perennial pasture species have been reported when the spring and summer soil moisture deficits exceeded 450 mm (Poirier *et al.* 2012). Therefore, climate variability and extreme events affect production and persistence in pasture based livestock industry.

Accurate assessment of the impacts caused by extremes is important to inform future adaptation research. Correct and timely adaptation measures such as changing species mix, changing pasture type (C3 versus C4), selection for deep rooting species and breeding cultivars for better drought and heat tolerance (Cullen *et al.* 2014b; Norton *et al.* 2016) are crucial to sustain livestock production systems in SE Australia under a warmer and drier future climate. However, care must be taken before implementing these measures through accurately assessing the impacts of changing climate variability. For example, C4 pasture species will perform better in hot and dry environment than C3 species; however, C4 pastures give lower yields and lower quality in cool winter months than C3 which may suggest that C3 pastures are still suitable for the system in terms of quality feed supply (Bell *et al.* 2013). Further, different responses of C3 and C4 pastures to increasing CO2 levels also need to consider when selecting the suitable plant types in the future.

In the absence of long term measured data from grazing trials, simulation modelling using appropriately validated tools is a useful methodology to evaluate the impacts of climate variability and extremes on pasture systems. DairyMod and the Sustainable Grazing Systems (SGS) pasture model are biophysical pasture systems models designed for simulating grazing dynamics and animal production (Johnson 2016). DairyMod has been validated for temperate regions of Australia against measured pasture growth data (Cullen *et al.* 2008) and has been used by many authors to study the nature of interannual variability of pasture growth rates (Chapman *et al.* 2009), climate change impacts on pasture production (Cullen *et al.* 2009) and impacts of extreme climate events on pasture production (Harrison *et al.* 2016). However, mechanistic modelling approaches are seldom designed to explicitly simulate extreme climate events. Therefore, simulation models could be further improved to capture the effects of climate extremes on different plant processes (such as photosynthesis, respiration, stomatal closure and transpiration) and should incorporate the

interactions between those processes (Boote *et al.* 2013; Bassu *et al.* 2014). Accurate parameterization of heat and drought stresses functions are also vital to improve the model ability to give better predictions under extreme climate.

1.2. Aims of the study

This project was carried out to assess the impacts of changing climate variability and extreme events on pasture systems in south eastern Australia using a combination of biophysical modelling and a pasture plant physiological experiment conducted under controlled environment conditions. The overall approach used in this thesis also aims to highlight the importance of designing experiments to fill the specific knowledge gaps identified in biophysical models to better simulate the impacts of extreme climate events.

1.2.1. Specific research questions

This thesis investigated five main research questions

1. Are pasture growth patterns changing under the increasing climate variability and extreme events experience in recent decades? If so, which seasons show the most year to year variability in pasture growth and what does this mean for adaptation?
2. Can year to year pasture yield variability be better explained using both average and extreme climate indices rather than using only the average climate variables? Which climate variables are more important in explaining the year to year pasture yield variability?
3. How do the large scale climate drivers of ENSO, IOD and ENSO IOD combined phases influence annual pasture production in SE Australia?
4. What are the growth and physiological responses of commonly grown temperate pasture species to consecutive heat and drought stresses?
5. Do leaf temperatures better simulate the heat stress effects of pasture plants in mechanistic biophysical plant growth models than air temperatures (Using DairyMod biophysical model as an example)?

Each research question was investigated in separate results chapter in the thesis. Chapter 3 describes how the pasture growth patterns have changed in SE Australia during the last 56 years, from 1960 to 2015, due to climate variability using simulated annual and monthly pasture growth rates using DairyMod model, which addressed the research question 1. Chapter 4 reports an approach developed to explain the observed year to year pasture yield variability, during the same period reported in Chapter 3, using a matrix of climate indices including general and extreme climate variables (Research question 2). Chapter 5 investigates the influence of large scale climate drivers (El-Niño Southern Oscillation and Indian Ocean Dipole) on annual pasture production in the region using simulated pasture growth rates from 1950-2015 which address the research question 3. Chapter 6 reported on a controlled environment experiment that investigated growth and physiological responses of four temperate pasture species to consecutive heat and drought stresses (Research question 4). Finally, in Chapter 7, the results from the controlled environment experiment are used to develop a novel simulation modelling approach in DairyMod to improve the prediction of heat and drought stress on plants by using leaf temperature to parameterize the model instead of air temperature. This chapter addressed the research question 5. Further, the high temperature stress recovery function was also parameterized using experimental data to better predict the heat stress recovery of perennial ryegrass in Chapter 7. The overall outcome of this thesis is a better understanding of the impacts of climate variability and extremes on pasture-based systems in SE Australia and improved simulation approaches to predicting heat and drought stresses in pasture plants which are the major objectives of the study. This research will make an important contribution to further research on climate change impacts and adaptation options in a changing climate.

CHAPTER 2. Literature Review

2.1. Introduction to the study region of south eastern Australia with an emphasis on pasture systems.

In south eastern (SE) Australia, the climate ranges from cool temperate in Tasmania to Mediterranean in southern New South Wales with winter-dominant annual rainfall >500 mm (CSIRO and BOM 2015) which are generally favourable for growing temperate perennial pasture species. Livestock production in the region utilising pastures as the main source of feed (Chapman *et al.* 2008) consists of dairy, sheep (meat and wool) and beef cattle production. These industries are major contributors to regional economies, with the $4.4 billion per annum is provided by the dairy sector in the region (DairyAustralia 2019a). Further 9% ($5.9 billion) of the red meat and livestock industry turnover in Australia during 2017-18 came from south Australia (MLA 2019). According to farm surveys, 96% of dairy farmers in Australia use grazed pastures in their feeding systems and, across the industry, in a favourable year, pastures fulfil 60-65% of the total herds diet (DairyAustralia 2018). In some areas of Tasmania and Gippsland where climate conditions are favourable for year-round pasture production, farmers feed their animals with grazed pastures only. This is 11% and 8% of farmers in Tasmania and Gippsland respectively, which is higher than any other dairy regions in Australia (0-4%) (DairyAustralia 2015).

Sown pastures in SE Australia mainly consist of introduced temperate perennial pasture species growing in mixtures with legumes. The main introduced perennial pasture grasses are perennial ryegrass (*Lolium perenne* L.), phalaris (*Phalaris aquatica* L.), tall fescue (*Festuca arundinacea*) and cocksfoot (*Dactylis glomerata* L.). Perennial ryegrass is the most widely grown species in temperate regions of southern Australia (nearly 6 Mha by 1994) (Reed 2014) in high rainfall areas (600-800) (Figure 1,2). Perennial ryegrass is typically established in combination with legumes, usually white clover (*Trifolium repens* L) in the higher rainfall parts of the regions or subterranean clover (*Trifolium subterraneum* L.) in the moderate rainfall zones (Fulkerson and Doyle 2001). Perennial ryegrass is popular among farmers because of its fast establishment (due to high seedling vigour),

high winter and spring yield, fast recovery after grazing, high nutritive value, high fertilizer response and well-established grazing principles (Reed 1996; Waller 2009). However, perennial ryegrass is less persistent under hot and dry summers which leads to loss of production and invasion of weeds (Nie 2011). This is because perennial ryegrass has less root density in sub soil horizons with limited capacity to uptake moisture from deep within the soil during drought. In contrast, phalaris, cocksfoot and tall fescue have better survival than perennial ryegrass under summer drought conditions so are used in areas where perennial ryegrass does not persist (Chapman *et al.* 2011; Norton *et al.* 2016). However, these species have less seedling vigour compared to perennial ryegrass hence take longer to achieve their full potential under field conditions (Culvenor and Simpson 2014; Norton *et al.* 2016).

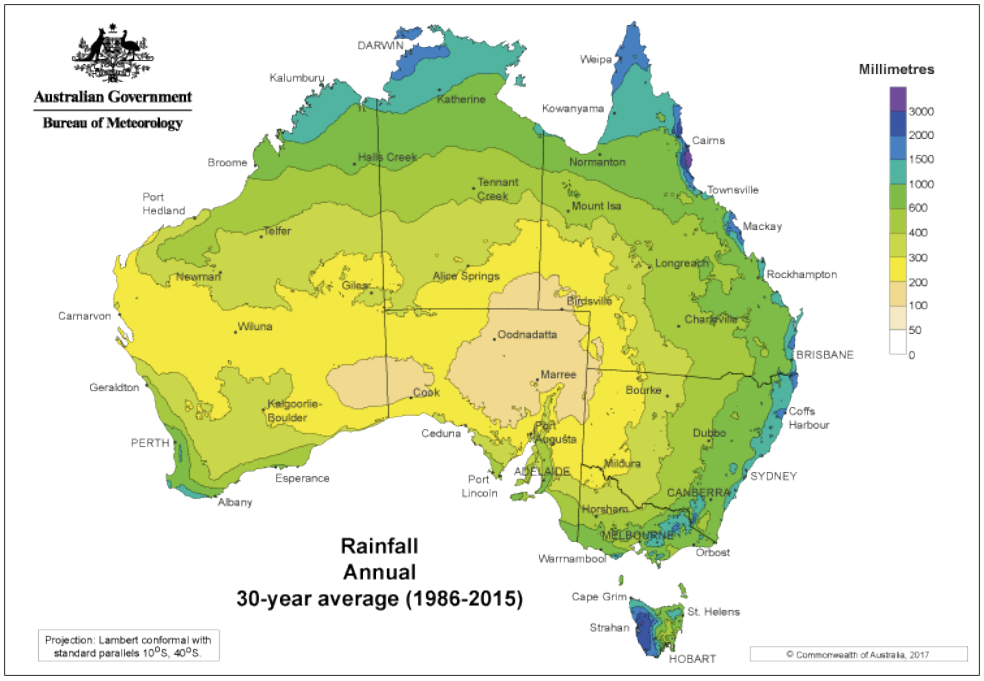

Figure 1. Average annual rainfall distribution in Australia for the last 30 years from 1986-2015. Source; (BOM 2019a) http://www.bom.gov.au/jsp/ncc/climate_averages/decadal-rainfall/index.jsp?maptype=30&period=1986-2015&product=totals#maps.

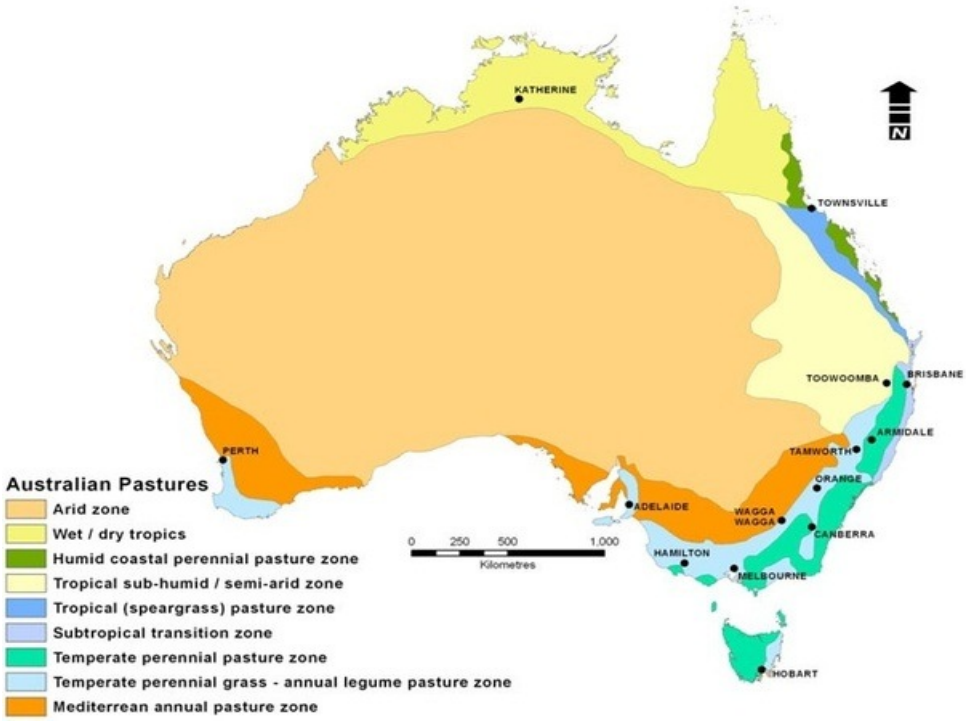

Figure 2. Pasture map of Australia (Wolfe 2020)

Phalaris is the most widely grown pasture grass after perennial ryegrass in southern Australia (covering about 2.7 Mha by 2009) which is usually mixed with subterranean clover (Reed 2014). Phalaris originated in Mediterranean region hence possesses superior drought tolerance through combination of deep rooting and summer dormancy (Lamp *et al.* 1990; Culvenor 2009). Therefore, phalaris is suitable for medium rainfall warm temperate zones and Mediterranean climates where annual rainfall range between 450 to 650 mm with characteristic hot and dry summers (Figure 2).

Other than phalaris, tall fescue is considered as another drought tolerant species due to its deep root system and efficient water uptake ability. Among the two agronomic types (summer active and summer dormant), summer active tall fescue cultivars are more responsive to summer rainfall than perennial ryegrass (Lawson *et al.* 2007; Nie *et al.* 2008) and are suitable to areas where annual rainfall is > 600 mm with some amount of summer rainfall. For the areas where summer rainfall is not very reliable, summer active types may perform well in heavy textured clay soils using the

residue moisture retained in deeper soil layers from excess water inundated in the previous winter spring seasons (Raeside *et al.* 2012). Superior salinity exchange nature of summer active tall fescue under water logging provide added advantage of using this species over perennial ryegrass (Kobayashi *et al.* 2004) and suitable in the areas of southmost regions of Victoria where these heavy clay soils are present (Newell 1962). However, tall fescue is reported to be less persistent on the light soil types and in areas with annual rainfall < 550 mm (Anderson *et al.* 1999).

Legumes also play an important role in the pasture systems in SE Australia by improving the nutritive quality of grass-based diets and fixing atmospheric nitrogen which becomes available to support the growth of grasses (DairyAustralia 2019b). Legumes in the diet of dairy cows can increase the palatability, milk yield and milk solids, nitrogen use efficiency and reduce methane emission (Harris *et al.* 1998; Woodward *et al.* 2010). Subterranean clover (*Trifolium subterraneum* L.) is the most widely grown annual legume in southern Australia covering 29 million ha across southern Australia (Revell and Sanford 2019). The most common grass legume mix in SE Australia is perennial ryegrass and white clover mix (Tharmaraj *et al.* 2008). However deep-rooted perennial legumes such as lucerne and red clover have added advantages because they have the potential to reach moisture in the deeper soil layers and provide high quality feed in summer when the grasses have stopped growth due to moisture stress. Therefore, legume component plays an important role in filling the summer feed gaps in pasture systems in SE Australia (DairyAustralia 2019b).

In rangelands and infertile soils where improved perennial grasses do not persist, the dominant species are the Australian native C4 grasses such as kangaroo grass (*Themeda triandra*), red-leg grass (*Bothriochloa macra*), and brush wiregrass (*Aristida behriana*) (Prescott 2017). Australian native grasses have evolved through millions of years and are well adapted to soil and climate conditions in Australia. Even though native grasses are less superior in nutritive quality than exotic improved grasses, natives are better able to tolerate drought and grow under less fertile soils. Therefore, native grasses are suitable in low input livestock farming systems. The superior drought resistant characteristics of native grasses have recently received recognition and are being used for selection and making new cultivars (Garden *et al.* 1996; Lodge 1996; Oram and Lodge 2003).

2.2. Influence of climate variability and extremes on pasture systems in SE Australia

Climate variability is one of the major challenges for agriculture in SE Australia including pasture production (Gentilli 1971; Clark *et al.* 2003). Climate variability can be described as the variation in the mean, standard deviation and the occurrences of extreme events on all temporal and spatial scales (IPCC 2012a) which is generally considered beyond the scale of an individual weather event. Climate variability in SE Australia can be partly described using the natural weather systems such as El- Niño Southern Oscillation (ENSO) (BOM 2016), Indian Ocean Dipole (IOD) (Cai *et al.* 2014), Southern Annular Mode (SAM) (Hendon *et al.* 2007), sub-tropical ridge (Timbal and Drosdowsky 2013), cut off lows etc. These are discussed in more detail in Section 3. However, much of the variability remained unexplained leaving seasonal weather patterns highly unpredictable (CSIRO and BOM 2015).

Year to year pasture yield variability driven by strong climate variability (rainfall and temperature) is an inherent characteristic in temperate pasture based production systems in SE Australia (Gentilli 1971; Chapman *et al.* 2013). This variability creates a certain amount of risk when making critical management decisions in livestock production systems such as setting stocking rates, determining the appropriate times to calve or lamb and supplementary feeding (Chapman *et al.* 2009; Chapman *et al.* 2013; Chang-Fung-Martel *et al.* 2017). Under such uncertainty, productivity of the livestock systems (average pasture yield, milk yield, animal body condition score and meat and wool production) mainly depend on the management skills of the farmer. In the following sections, the observed changes in the climate variability and extreme climate events over recent decades are described and the consequences for pasture-based production systems in SE Australia are discussed.

2.3. Observed climate extremes in SE Australia

2.3.1. Temperature extremes (extreme heat days, heat waves and frost occurrences)

Australia's mean temperature has increased by just over 0.9 °C since 1910 with the most warming observed since 1950 (Figure 3,a) (BOM 2018). The year 2019 was the Australia's warmest year on record with the area-averaged temperature being 1.52 °C greater than the 1961-1990 average (Figure 3,b) (BOM 2020). Along with this warming trend, both the frequency and magnitude of heat waves have increased (Alexander and Arblaster 2009; Perkins *et al.* 2012; Perkins Kirkpatrick *et al.* 2016). Very high monthly day time temperatures and very warm monthly night time temperatures (calculated using daily maximum and minimum temperatures) that occurred 2% of the time (from 1951-1980) has now increased to 12% of the time (from 2003-2017) (BOM 2018). This significant shift in the temperature distribution is consistent across all seasons with the greatest increase observed in spring (BOM 2018). Very high forest fire danger days (with Forest Fire Danger Index (FFDI) >25) have also increased in Victoria in the recent decades mainly in the spring season (BOM 2018, 2019b) indicating lengthened fire season. The dangerous bush fires that occurred in 2019 spring in NSW and Victoria (BOM 2019b) caused huge losses including over 480 million animal deaths including mammals, birds and reptiles. In Kangaroo island, more than 100,000 sheep and 25,000 other livestock were killed by the devastating bushfires in 2019 (CDP 2020).

Not only the extreme heat waves, extreme cold days are increasing in some areas of SE Australia. Even though southern Australian average minimum temperature is rising 0.17 °C per decade, since 1960, there are regions that show localised cooling and increasing frost occurrence. For example, Crimp *et al.* (2016b) reported that the average frost period length has increased in whole southern Australia by 26 days (2000-2014) compared to 1960-1990. In the 2000-2014 period, some areas of SE Australia experienced the last frost four weeks later (in mid-late October) than in 1960-1990 (late September) indicating increased climate variability and the frost damage risk for important agricultural crops.

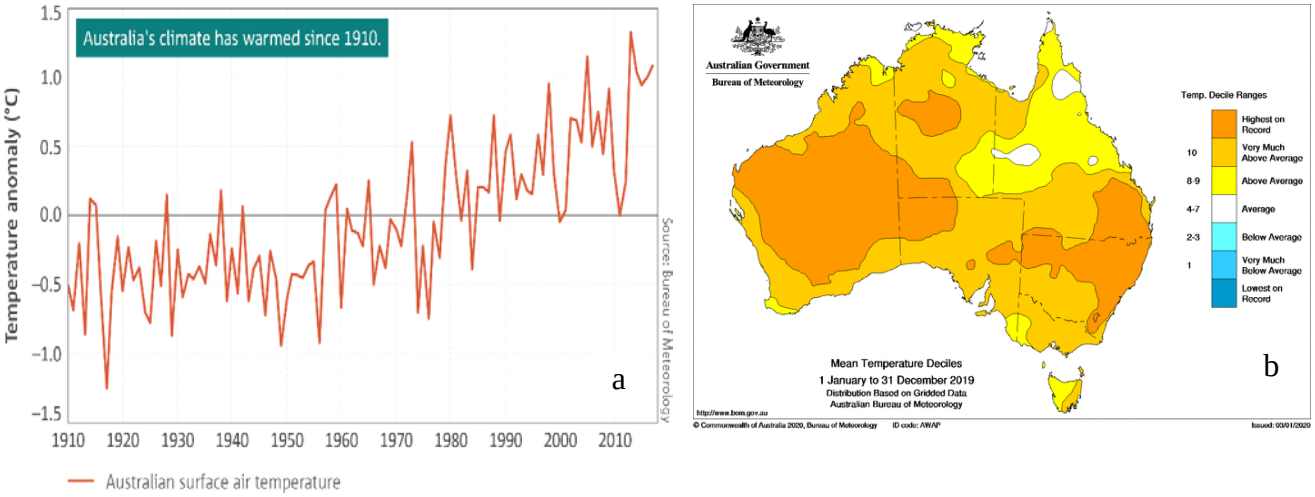

Figure 3. (a) Australia's annual temperature anomaly (deviations from the mean temperatures from 1961-1990) from 1910 to 2018 (Source: State of the climate 2018, BOM) and (b) the mean annual temperature in 2019 compared to long term temperature records (Source: Annual climate statement 2019, BOM).

2.3.2. Rainfall extremes (Droughts and extreme precipitation)

SE Australia typically receives the majority of its rainfall in the cooler months of the year (winter and spring). Recent changes to rainfall patterns indicate that the cool season rainfall has decreased in SE Australia since the 1990's (Braganza *et al.* 2011). The 1997-2009 period was the driest 13 years on record for SE Australia which is referred to as "Millennium drought" (Timbal 2009). Australia has experienced another two long term droughts in the history such as "Federation drought" (nearly a decade centered around 1902) and World war-II drought (1935-1945) (CSIRO and BOM 2015). However, the most recent Millennium drought was much worse than other two droughts with the annual rainfall during the 1997-2009 period being 11.4 % below the historical mean rainfall (Timbal 2009) compared to a reduction of 7.8 % during the period from 1933-1945 during the World war II drought (Timbal 2009). The reduction in rainfall during "Millennium drought" was pronounced in autumn (25% lower than the long term mean) in SE Australia with low rainfall variability due to absence of very wet years (Figure 4). The Millennium drought ended with severe precipitation events in 2010 due to a strong La-Nina event causing wide spread flooding including SE Australia.

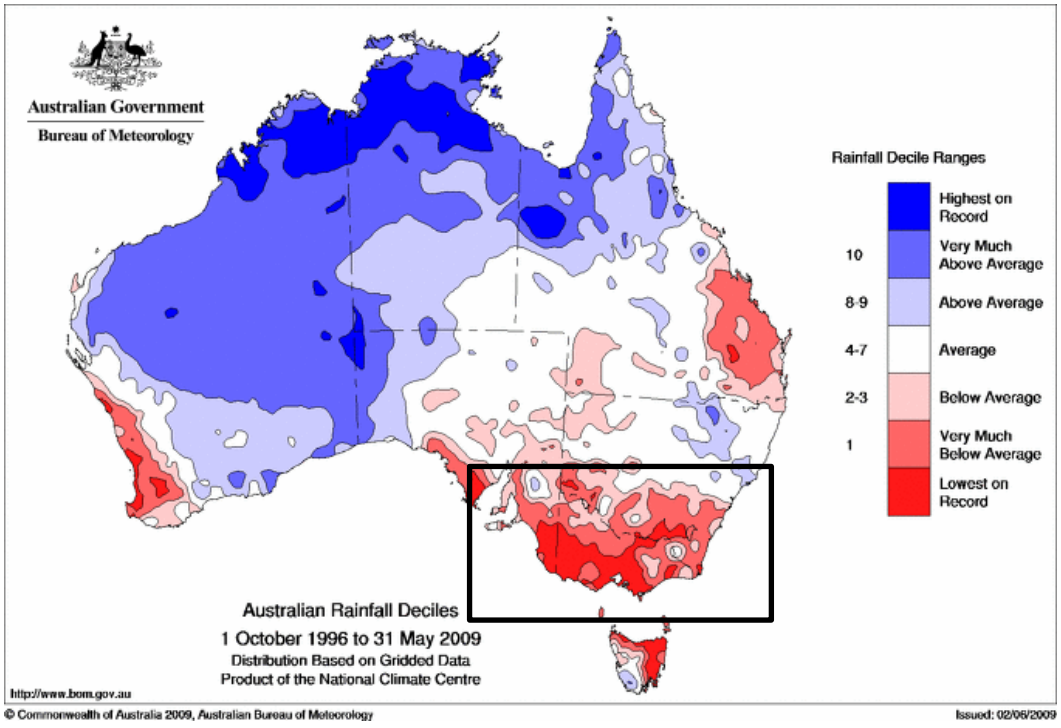

Figure 4. October to May rainfall deciles since 1996 to 2009 compared to the entire rainfall record from 1900 to 2009. (Source: BOM 2009).

2.4. Variability in pasture growth rates due to climate variability

Pasture growth rate at a location can vary from season to season (seasonal variability) and year to year (interannual variability) (Figure 5). Seasonal variability occurs due to the variation of temperature, solar radiation and soil moisture within a year. In SE Australia, radiation intensity and temperature gradually decline through autumn until winter and increase over spring and summer months. Rainfall also varies over a year with most rains fall during the winter and spring seasons. Seasonal pasture yield variability can be represented by the typical pasture growth curve at a location by plotting average pasture growth in each month of the year (Radcliffe and Baars 1990; Chapman *et al.* 2009). This curve shows the expected pasture growth rates over a considered season (summer, autumn, winter and spring) or a month. Interannual variability refers to the deviation of pasture growth from the typical pasture growth curve. This interannual variability is mainly driven by the climate variability which has a direct influence on the physiological processes of plants and subsequent pasture yield. Under extreme conditions, pasture plant survival may also be affected

(Waller *et al.* 2003). Interannual variability can be quantified using percentiles, standard deviation, variance, data range and coefficient of variation (CV%). For example, Figure 5 shows the interannual variability of monthly pasture growth rates at high rainfall site at Ellinbank over the past ~100 years and highlight the considerably large variability during late spring to summer and mid-autumn months compared to winter and early spring months (Chapman *et al.* 2009). This graph reflects the variability driven by the temperature and rainfall variation throughout the year and between years. The key climate variable responsible for the year to year pasture yield variability is the rainfall. Chapman *et al.* (2009) estimated the interannual pasture yield variability in different rainfall zones across SE Australia and NZ and showed that yield variability (estimated as coefficient of variation (CV%)) varied both spatially and temporally. Variability of pasture growth (CV%) under dryland simulations at Terang, Ellinbank, Elliott and Hamilton in SE Australia ranged from 48% (Hamilton) to 300% (Terang) in summer months during which soil moisture is limited due to low rainfall. In contrast, yield variability during winter months was much lower due to the availability of adequate soil moisture, and the variability was due to the differences in temperature. Year to year variability can be reduced to a certain extent by irrigating the paddocks, with Chapman *et al.* (2009) demonstrating that variability of the irrigated pastures was much lower compared to the rainfed conditions. The importance of rainfall variability in explaining pasture yield variability is evident in outside the Australia as well. For example, Radcliffe and Baars (1990) reported that 60% of the interannual pasture yield variability in New Zealand was due to spring and summer rainfall variability. Likewise, in Britain, 60% of the annual pasture growth rates were due to the available soil moisture contents (Morrison 1980). Therefore, seasonal and interannual yield variability are important factors in managing pasture-based systems.

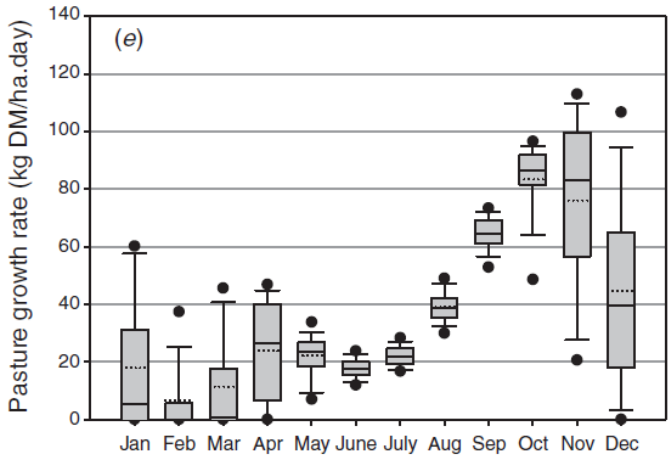

Figure 5. Interannual variability of monthly pasture growth rates (from 1907-2006) at Ellinbank under rainfed conditions. Boxes show 25th, 50th and 75th percentiles and the whiskers show 10th and 90th percentiles. Dots represent 5th and 95th percentile values while the mean is shown with a dotted line. (Source: Chapman et al., 2009).

2.5. Consequences of climate variability and extremes in managing pasture-based systems

The consequences of year to year pasture yield variability on farm decision making arise mostly when balancing feed supply and demand (Chapman *et al.* 2013). Feed demand (total amount of nutrients required by livestock, usually expressed in a dry matter or energy requirements) depends basically on the animal number per hectare (stocking rate), breed of the animal and calving or lambing time. These strategic level decisions are made by farmers depending on the average pasture supply in each month at a location. However, climate variability will cause both above and below average seasons and years which are hard to predict by seasonal forecasts with a sufficient leading time to make management decisions (Ash *et al.* 2007). In poor seasons, due to long dry periods and/or heat, feed shortages can lead to poor animal production. In such situations, farmers implement tactical level decisions such grazing the paddocks that were reserved for making hay or silage, purchasing supplementary feed (silage, hay, grain), reducing the stock numbers by selling surplus stock or agisting, reducing milking frequency and irrigate the pastures if irrigation water is available (Austen *et al.* 2002). In favourable seasons with excessive herbage mass, farmers can conserve

excess pasture by making silage or hay, slow down pasture growth by reducing nitrogen fertilizer application, increase the grazing frequency and grow crops in some of the paddocks. In addition to that, some farmers tend to increase the stocking rate if the prices are favourable (Austen *et al.* 2002). These tactical level management decisions are vital to decrease the business risk and achieve production targets (Sheath and Clark 1996; Chapman *et al.* 2013).

Several studies have highlighted the risk associated with increased climate variability and extreme events when managing livestock businesses. Stocking rates in dairy production systems are generally fixed within a year, and change only slowly from year to year. In a modelling study conducted in SE Australia, Chapman *et al.* (2009) showed that stocking rates are positively related to the total annual herbage accumulation rate but are related negatively with increasing year to year pasture yield variability. This observation reflects that farmers are concerned about the climate driven risks when taking strategic decisions on their farms. Calving time usually coincides with the peak pasture growth period which is in spring season (September to November) for the southern hemisphere including Australia (Sergeant *et al.* 2005). However, increasing milk demand throughout the year and unreliable spring pasture growth due to early finish of spring rains has led to increasing number of farmers shifting from spring calving to autumn calving (Sergeant *et al.* 2005). The consequences of climate change are likely to exacerbate the variability of pasture systems through increased frequency of exposure to extreme climate events such as heat waves and droughts (CSIRO and BOM 2015). This was demonstrated by Harrison *et al.* (2016) for pasture based systems in SE Australia using a modelling study by incorporating more heat waves, droughts and extreme precipitation events to monthly climate projections under high emission scenario (Representative Concentration Pathway 8.5) in 2080. In that study, a climate change scenario with greater frequency of climate extremes translated into decreased pasture yields, with increased year to year variability compared to average climate change scenario. Economic analysis indicated long term profitability losses due to increased dependence on purchased feed under extreme climate scenario (Harrison *et al.* 2016).

Projected climate changes in the major eight dairy regions in Australia including the sites in SE Australia for 2040 using 40 climate models and high emission scenario (Hennessy *et al.* 2016)

indicate that these regions will warm by 1-1.8 °C relative to 1995 and median rainfall will decrease by 3 % (-10 to +5%) in northern Victoria and Gippsland to 5% (-15 to +3%) in Western Victoria. This study further stressed that interannual rainfall variability in the major growing season in all the eight dairy regions will continue to increase in 2040. Increasing climate variability under intensive scale of operation is likely to affect the business profitability in future if enough pastures is not produced in the critical times of the year leading to increased supplementary feed cost and so decrease the farm profit (Harrison *et al.* 2016).

2.6. South eastern Australian climate variability and its drivers

Australian rainfall is highly variable compared to the other similar climates in the world (Nicholls *et al.* 1997) due to the influences of a range of weather systems that are both tropical and extra tropical in origin. The northern half of Australia is influenced by tropical modes of variability such as El- Niño Southern Oscillation (ENSO) (Wang and Hendon 2007), Indian Ocean Dipole (IOD) (Ashok *et al.* 2003), and Madden Julian Oscillation (MJO) (Wheeler *et al.* 2009). The influence of tropical weather systems decreases to the south and extra tropical features such as sub-tropical ridge (Timbal and Drosdowsky 2013), Southern Annular Mode (SAM) (Hendon *et al.* 2007), atmospheric blocking (Pook and Gibson 1999) and storm tracks (Frederiksen and Frederiksen 2007) become prominent in southern Australia. Even though the influence of tropical modes decreases to the south, SE Australia is affected by the tropical Pacific and Indian ocean drivers. For instance, recent rainfall deficit in south eastern Australia ("Big Dry") (Timbal 2009) has been linked to ENSO (Cai and Cowan 2008) and IOD (Cai *et al.* 2009) phases. In the following sections, tropical and extra tropical features that affect the SE Australian climate are discussed.

2.6.1. Tropical modes of climate variability in SE Australia

2.6.1.1. El- Niño Southern Oscillation (ENSO)

ENSO is one of the most important climate drivers in Australia which occurs through interactions between the tropical Pacific Ocean and atmospheric circulation (Philander 1990; BOM 2008). There are three phases of ENSO called El-Niño, La-Niña and neutral. A typical ENSO event starts in the

first half of the year, peaks in the spring season and decays over the following autumn. The spatial impacts of ENSO on Australia depend on season and the phase with ENSO having strong impact on north and east coast of Australia (Gallant *et al.* 2007; King *et al.* 2014). During an El-Niño phase, the mean maximum temperatures in Austral spring and summers are on average ~1.17 °C greater and it was ~1.36 to 2 °C cooler during a La-Niña phase (Arblaster and Alexander 2012). Austral winter and spring rainfall tend to be more variable with El-Niño phase bringing dry conditions and La-Niña years bringing wet conditions (Risbey *et al.* 2009). The magnitude of the impact during these phases on winter -spring rainfall is more related to the strength of the phase of La-Niña but not El-Niño (Wang and Hendon 2007).

In the ENSO neutral phase, trade winds in the Pacific Ocean blow from east to west direction bringing warm water to the western Pacific Ocean. Meanwhile in the eastern Pacific ocean, cold water is drawn up from the deep layers (upwelling) creating a temperature difference between eastern and western Pacific ocean. This temperature difference creates rising air (due to convection) over Australia and decending air near south America generating a cyclic air movement called Walker circulation (Figure 6,a). During neutral ENSO phases, Australia experiences usually average climate conditions (BOM 2008).

During a La-Niña phase, the Walker circulation becomes stronger. As a result, the western Pacific Ocean sea surface temperatures become warmer than average and eastern Pacific sea surface temperatures become cooler. These conditions create enhanced convection in the western Pacific, create rain clouds and bring above average rainfall to eastern Australia (Figure 6,b). Further, La-Niña years bring lower day time temperatures and more tropical cyclones. In eastern Australia, La-Niña years accounted for six wettest winter and spring seasons in the historical record (BOM 2016). In Murray Darling Basin, average rainfall during La-Niña years were estimated to be 22 % higher than historical average and severe floods were observed in 1955, 1988, 1998 and 2010-11 with the 2010-11 period being the wettest two years in Australia with widespread flooding over eastern parts of the country including Victoria (BOM 2016).

El-Niño is the opposite phase of La-Niña. During this phase, the Trade winds weaken, drifting warm water towards the east of the tropical Pacific. The Walker circulation breaks down causing more warm water to accumulate in the eastern Pacific while western Pacific ocean becomes cooler. Convection happens in the eastern warm pool which leads to droughts and warmer climate in eastern Australia (Figure 6,c). During the Millennium drought period, Cai and Cowan (2008) linked decreased autumn rainfall in SE Australia to more occurrences of El-Niño phases and less occurences of La-Niña phases.

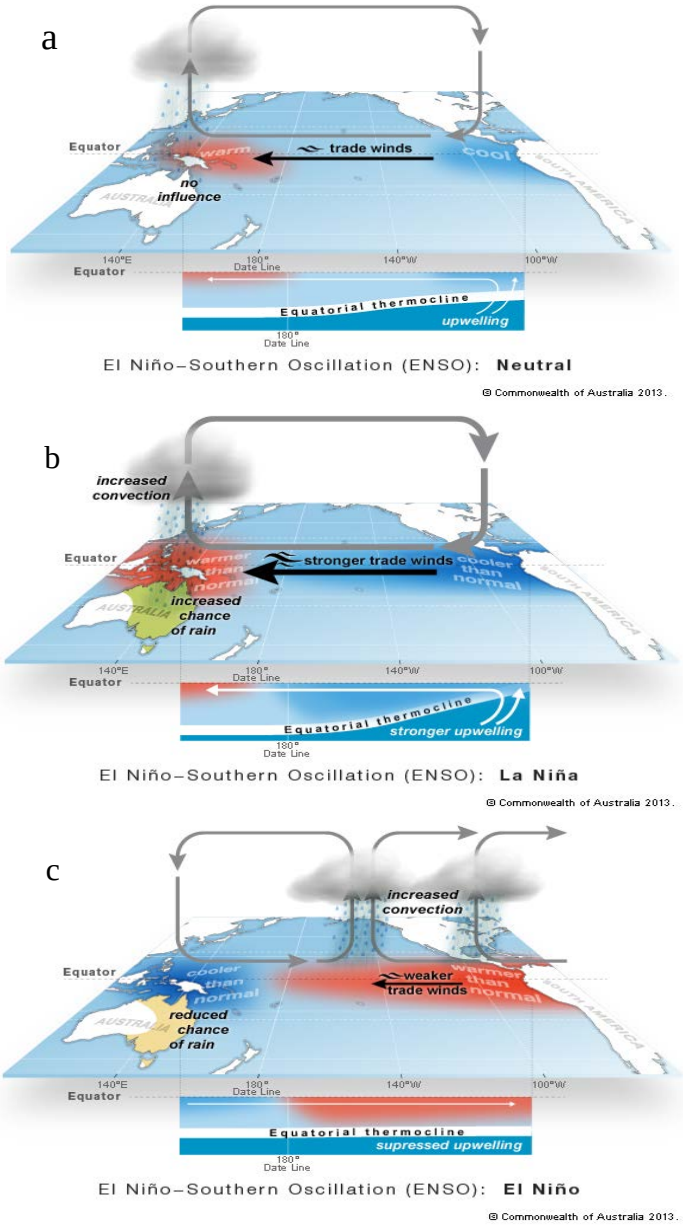

Figure 6. Walker cell circulation during ENSO neutral phase (a), La-Niña phase (b), and El-Niño phase (c). (Source: BOM, 2020)

2.6.1.2. Indian Ocean Dipole (IOD)

The IOD has similar climatology to ENSO, but occurs in the Indian Ocean basin. IOD events are defined using the sea surface temperature anomalies between western (off the eastern coast of Africa) and eastern Indian Ocean (off the coast of Indonesia) using an index called Dipole Mode Index (DMI) (Saji *et al.* 1999) (Figure 7). IOD develops during autumn or winter, peaks in August-October and decays in late spring with the start of monsoons in northern Australia (Saji 2003). The IOD swings between neutral, positive and negative phases. IOD + phases have been linked to hot and dry conditions in Australia while IOD – phases cause increased precipitation and cool temperatures (Saji 2003; Min *et al.* 2013). During the neutral phase, sea surface temperatures of north west Australia is warm. Warm air rises (convection) over islands of Indonesia and descends over western Indian ocean forming a Walker cell. This neutral phase has little influence on Australian climate.

During a negative phase of IOD, westerly winds intensify drawing warm water nearer to north west Australia. In contrast, sea surface temperatures in the western Indian ocean are cooler than average due to upwelling. Negative IOD phases bring above average rainfall to southern Australia during winter and spring seasons as this phase allows more moisture for north west cloud bands crossing the country towards SE Australia (Saji 2003; Min *et al.* 2013).

During the positive phase of IOD (Figure 7), the temperature pattern in the Indian Ocean reverses. Westerly winds break and easterly winds form causing accumulation of warm water near east Africa. In contrast, sea surface temperatures south of Indonesia get cooler due to upwelling. This temperature difference creates rising air (due to convection) near Africa and descending air near north western Australia. Decending air forms less clouds leading to less rainfall over central and SE Australia (Ashok *et al.* 2003). IOD phases are not symetric in strength. IOD + phases tend to be stronger than IOD- phases (Cai *et al.* 2009) leading to stronger droughts (Ummenhofer *et al.* 2009). Since 1950, there were more IOD+ phases than IOD- phases. This increased frequency of IOD + events have been suggested to be a major reason for the observed autumn-spring rainfall reduction since 1950 in SE Australia (Cai *et al.* 2009). The major droughts and bush fires in SE Australia are

also linked to increased occurences of IOD + phases (Cai *et al.* 2009; Ummenhofer *et al.* 2009). Climate models project increased occurences and intensity of IOD + phases due to anthropogenic climate change and therefore, more extreme wearther events can be expected in future (Cai *et al.* 2014).

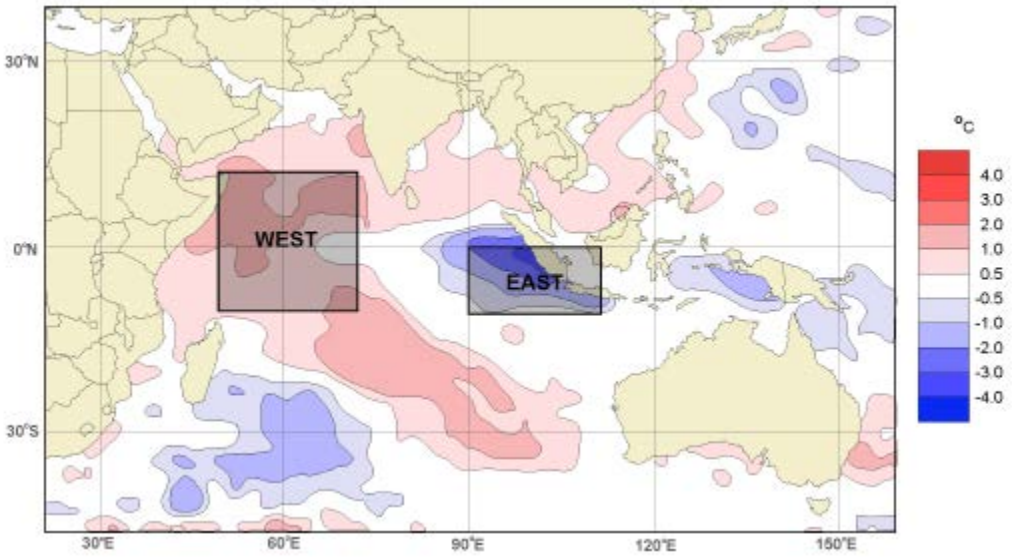

Figure 7. Locations of the Indian Ocean that are used to calculate the Dipole Mode Index. Colours indicate the sea surface temperatures with red colour representing warm waters while blue colour representing cold waters showing the conditions of IOD+ phase. (Source: BOM, 2018).

Different phases of ENSO and IOD can coincide in some years due to teleconnections that exist between ENSO and IOD (Cai *et al.* 2009; Min *et al.* 2013). In SE Australia, the driest conditions were reported to occur when El-Niño and IOD+ phase occurred together rather than when each dry phase of the drivers occurred independently (Ummenhofer *et al.* 2011). Similarly, wet phases of both these drivers can coincide (La-Niña and IOD-) bringing opposit results; higher than average rainfall to south and east of Australia and wide spread flooding in some extreme cases. For example, La-Niña and IOD- phases coincided in 1974 and 2010 creating two of the wettest years in Australia that caused devastating floods including in SE Australia (BOM 2012a).

2.6.2. Extra tropical features of climate variability in SE Austraila

2.6.2.1. Sub tropical ridge (STR)

The STR is a band of high pressure circling around the world at approximately 30° latitude in both hemispheres. The STR is closely related to rainfall variability in SE Australia (Timbal and Drosdowsky 2013). The position of the STR changes in an annual cycle and it locates north of SE Australia in winter and spring months reaching furthest north (29.1 ºS) in August and shift to the south of SE Australia in summer and autumn reaching furthest south (39.6 ºS) in February (Whan *et al.* 2014). The STR intensity is highest in June (1022.5 hPa) and lowest in December (1013.3 hPa) (Whan *et al.* 2014). When the STR positioned in the south of SE Australia, it pushes rain bearing fronts further south not allowing frontal systems to penetrate Australia. In contrast, when it positioned the north of SE Australia, frontal systems can pass over the southern part of the continent bringing rains to the region. A recent study showed that two thirds of the rainfall decline in SE Australia observed during the Millennium drought (1997-2009) period was due to the intensification of the sub-tropical ridge (Timbal and Drosdowsky 2013). Increasing intensity of the STR is associated with decreased rainfall (Ansell *et al.* 2000). It has been found that the rainfall variability in southern Australia is more closely related to the intensity than the position of the STR (Whan *et al.* 2014). Using 35 climate change models, it has been projected that STR intensity will be further increased and moved poleward under increasing global temperature (Grose *et al.* 2015). This may contribute to a further decrease in the winter-spring rainfall in SE Australia in future.

2.6.2.2. Southern Annular Mode (SAM)

SAM describes the north-south swing of the westerly wind belt in the mid and high latitudes of the southern hemisphere. SAM is responsible for rainfall variability of southern Australia by influencing the position and strength of cold fronts penetrating the southern part of the Australian continent (CSIRO and BOM 2015). Positive SAM phase reflects low pressure over polar region which leads to a contraction of the westerly wind belt towards the poles allowing fewer frontal systems to penetrate into southern Australia (Thompson and Woodworth 2007). Positive SAM phases bring

less rainfall to southern Australia during autumn and winter. Both the south eastern tip of eastern Australia and south western tip of western Australia receive less rainfall during the positive SAM phase (Hendon *et al.* 2007). However, in spring and summer, positive SAM brings more rain to southern Australia by the influence of high-pressure systems in the northern half of the continent. Easterly winds bring more moisture from the Tasman sea resulting in rainfall when these winds reach the great dividing range (Hendon *et al.* 2007). In contrast, negative SAM phase reflects low pressure over southern Australia. The westerly wind belt expands towards the continent causing more stronger storms over the region bringing rains to southern Australia (CSIRO and BOM 2015). During the Millennium drought, positive SAM phases were observed during autumn and winter period where the most reduction in rainfall was observed (BOM 2012b).

2.6.2.3. Cut-off lows

Cool air over Antarctica is surrounded by strong westerly winds (rotating clock wise) which is called polar vortex. Sometimes cool air pools break away at the edge of the polar vortex and the cool air pools move north. These air masses create low pressure systems 5-6 km high in the atmosphere which is called a cut off low (Qi *et al.* 1999). When cut-off lows move over southern Australia, they interact with the warm air masses over Australia and the surrounding oceans. This interaction often causes moderate to severe rainfall to SE Australia (CSIRO and BOM 2015).

2.6.2.4. Blocking highs

Strong high-pressure systems sometimes remain stationary over the Tasman sea for days or weeks, these are called ‘blocking highs’ because the block the low pressure systems progressing from west to east (Pook *et al.* 2013). Frontal systems progressing towards blocking highs often weaken and tend to slip to the south of the high-pressure area. Blocking high could bring stable conditions over several days or weeks while the area to the west of the high pressure could experience rains as this high-pressure system slows down the frontal systems. In some cases, cut off lows that develop to the north of blocking highs act together forming a blocking pattern which can cause sustained heavy

rainfalls to SE Australia. Both cut off lows and blocking highs are important synoptic weather systems of rainfall variability in SE Australia (CSIRO and BOM 2015).

From the above analysis, ENSO and IOD phases were identified as the major tropical drivers that contribute to the year to year climate variability in SE Australia with La-Niña and IOD- being wet and El-Niño and IOD+ being dry phases. Among the extra tropical drivers, the position and intensity of the STR largly influence the year to year rainfall variability in SE Australia affecting the rain bearing frontal systems. Among SAM phases, positive SAM brings less rainfall to SE Australia during autumn and winter but in spring and summer, positive SAM phase brings more rain to the southern Australia.

2.7. Defining extreme climate events

Extreme climate events such as heat waves, droughts, extreme rainfall and frosts are increasing in number and magnitude with the changing climate (CSIRO and BOM 2015). The drivers of climate variability, discussed in section 3, have a large bearing on extreme climate events. With increasing global temperature, these synoptic scale drivers tend to change their behaviour as a feedback response to the changes occurring in the global circulation patterns. Consequently, climate variability as well as the frequency and magnitude of extreme climate events have increased in many parts of the world including Australia (IPCC 2012b). To understand the full impacts of future climate change on agricultural systems and evaluate them, extremes need to be better characterized using appropriate definitions. This section reviews different definitions of climate extremes such as climatological, impact related and physiological thresholds.

2.7.1. Climatological definition

Climate extremes can be statistically defined as occurrences of climate or weather events (eg. minimum or maximum temperature, rainfall amount and duration, wind speed etc.) above or below a certain threshold value (eg: 99^{th}, 95^{th}, 90^{th} and 1^{st}, 5^{th},10^{th} percentile) of the range of observed values (IPCC 2012b). Extreme climate events are defined for a given period such as days, months, seasons or years relative to the historical record. Figure 8 shows the frequency distribution of a normally distributed climate variable such as maximum or minimum temperature at a location. The black line represents the frequency distribution of temperature and shaded area represents the rare extreme events which are far from the mean or median (normally defined by the 10^{th} and 90^{th} percentile etc.). A shift in the frequency distribution from base line period to warmer climate (dashed line) causes an increase in the frequency of extremely hot events and decrease extremely cold events. It is important to note that small changes to mean climate can cause large changes to the frequency of extreme events because they are non-linearly related. In Australia, changes to high temperature extremes have been more closely related to the shift in mean climate rather than changes to the shape of the distribution (Figure 8,a and 9) (Alexander *et al.* 2007; BOM 2014).

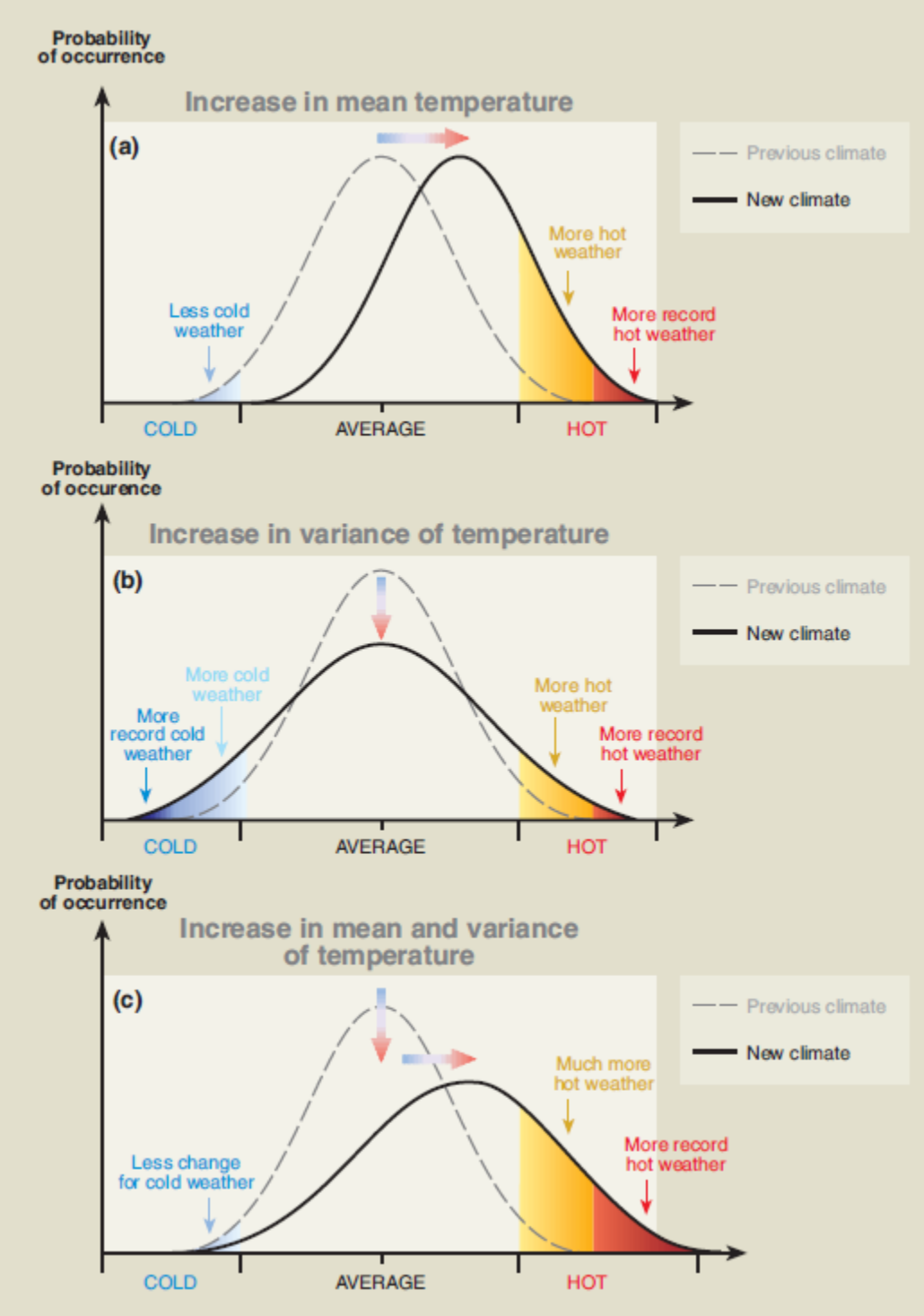

Figure 8. Schematic diagram of probability of occurrence of temperature at a location representing how increase in the mean (a), variance (b) and mean and variance together (c) affect the climate extremes events. Climate extremes are indicated by the shaded area. Source (Watson et al. 2001).

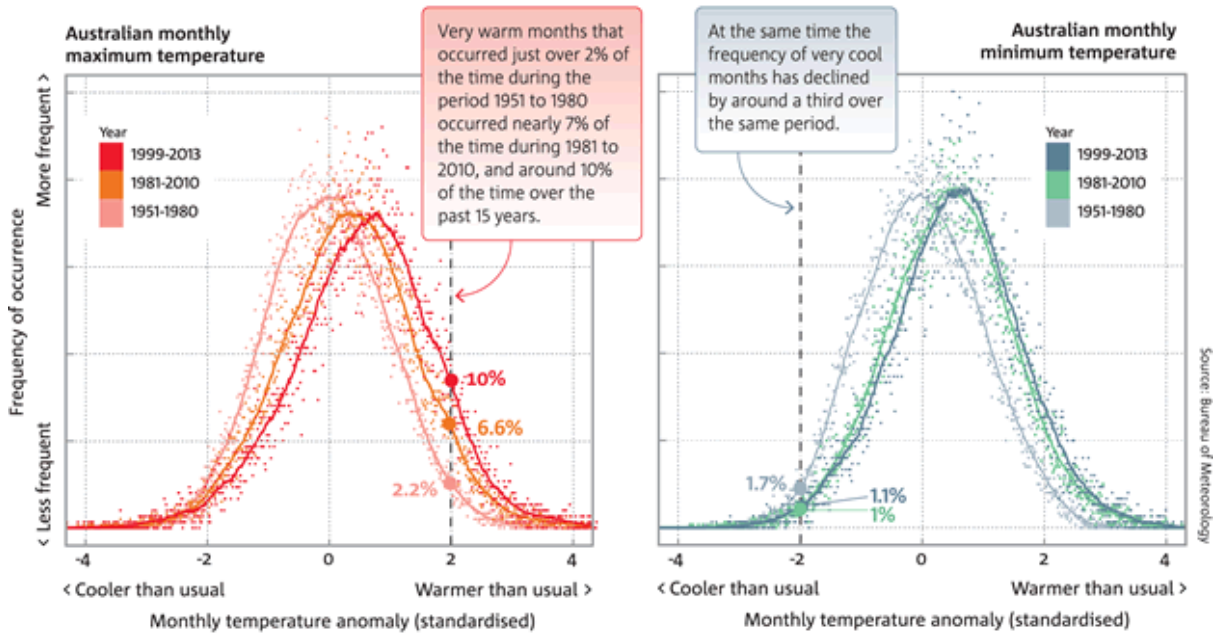

Figure 9. Monthly maximum and minimum temperature distributions for three periods (1951-1980; pink and grey, 1981-2010; orange and green, 1999-2013; red and blue). Standardised anomalies are shown compared to the baseline period of 1951-1980. Very warm or cold months are represented using 2 standard deviations from the mean. (Source: State of the climate 2014, BOM).

The variance of the distribution may also change without causing significant changes to the mean climate (Figure 8, b). If the variance (eg. standard deviation) of the distribution is increased, the distribution becomes wider. Under such cases, there will be more occurrences of extremes on both sides of the distribution. Changes to the variance of a distribution can have greater influence on extremes than changes to the mean (Katz and Brown 1992).

The symmetry of the distribution can also change (Figure 8, c). Not like the temperature, which has a normal distribution, rainfall has a gamma distribution. Therefore, change in the mean rainfall occurs together with the changes in the variance affecting extremes in different ways (Groisman *et al.* 1999). An example of a change in symmetry associated with climate changes is the warmer temperatures increasing the water holding capacity of the atmosphere and producing larger rainfall events (Wentz *et al.* 2007; Lehmann *et al.* 2015).

It is important to note that considering only the tail ends of the frequency distribution of a climate variable alone may not be adequate to assess the impacts of extreme events on natural or agricultural ecosystems. Several characteristics need to be considered such as the magnitude of the extreme event, its return frequency, duration, onset or seasonality, spatial extent and pre conditioning (Ummenhofer and Meehl 2017). Preconditioning refers to antecedent conditions that may modify the characteristics of an extreme event. For instance, accumulation of moisture deficits over several months can exacerbate the summer heat waves through the feedback effects of increased evapotranspiration (Fischer *et al.* 2007; Whan *et al.* 2015). Further, during an extreme event, several climate factors may act together. For example, during a severe drought, low precipitation often combines with high temperatures, increased radiation intensity and high vapor pressure deficits (Jentsch *et al.* 2007; De Boeck *et al.* 2010).

The definitions of extremes have been used in different ways in the literature. A heat wave is generally regarded as a period of excessive atmospheric heat (Perkins *et al.* 2012), however, there is no universal definition of a heat wave as they are measured using different methods in different areas in the world. Various definitions have been employed to explain heat wave characteristics such as intensity, duration, timing and frequency (Fischer and Schär 2010; Furrer *et al.* 2010; Russo *et al.* 2014). Commonly used definitions of a heat wave consist of thresholds based on percentiles of maximum and minimum daily temperatures at a location in a considered period. The relative thresholds used to characterise heat waves vary based on mean temperature and its variation at a location (Perkins *et al.* 2012). In Australia, most studies have defined a heat wave using the criteria that at least three or more consecutive days should be excessively hotter than the considered percentile (90^{th} or 95^{th}) temperature (Tryhorn and Risbey 2006; Alexander and Arblaster 2009; Pezza *et al.* 2012). Nairn and Fawcett (2015) developed an index to measure heat waves called the Excess Heat Factor (EHF). This approach only allows to calculate summer heatwaves as it uses the 95^{th} percentile of all maximum daily temperatures for three-day periods across a year to identify heat stress. De Boeck *et al.* (2010) devised a method that can be used to identify heat waves all year round by defining relative cut off value for each day of the year (90^{th} percentile of maximum

temperature) and a hot day is recorded if the daily maximum temperature exceeded the calculated 90th percentile value of that day. A heat wave is then defined as a consecutive seven days of such hot days. Since the relative cut off value is considered for each day of the year, heat waves can be identified during the other seasons as well. However, a 90th percentile value of a day in winter or other cooler months could not be equally considered as a hot day during the summer. For this reason, heat wave definitions based on relative threshold temperatures may not be appropriate to assess the impacts on agricultural systems. Further, different species have varying threshold temperatures beyond which the growth and physiological processes are affected. For example, heat waves/hot spells defined using relative temperature thresholds may either affect positively (during cooler months) or negatively (during warmer months) to the plant growth and development (De Boeck *et al.* 2010).

Most scientific experiments have used high atmospheric temperature levels (beyond plant optimum range) to measure heat wave impacts on plants (Jiang and Huang 2001; Cui 2006; Langworthy *et al.* 2015). However, in western Europe, it has been reported that during a heat wave plants also experience more sun light (+69%), higher VPD (+111%), lower rainfall (-78%) and high transpirational demand than normal conditions (De Boeck *et al.* 2010). This combination of climate factors is important when assessing the impacts of heat waves and must be considered when addressing the impacts of climate extremes on biological systems.

2.7.2. Impact related definitions of extremes

In climatological definitions, only the climate needs to be extreme, but in impact related definitions, the impact (biological and/or ecological) of the climate event should also be extreme. The growing importance of extreme climate events (Easterling *et al.* 2000; Jentsch and Beierkuhnlein 2008) paved the way for a number of definitions that focused on ecosystem impacts of extreme events.

By considering the ecological responses, Gutschick and BassiriRad (2003) defined climate extremes as an event which is capable of challenging the species ability to acclimate. In this definition, the impacts persist even after the climate event has finished, affecting the fitness of the species in the

ecosystem. The highest impact of this type of extreme event would be the mortality of the entire population of the considered species.

Considering both the climate driver and the response beyond the population level, Smith (2011) defined an extreme event as a statistically rare climate episode that alters the ecosystem structure and/or function well beyond the normal variability. This definition distinguishes statistically rare events which are not severe enough to cause an impact on an ecosystem if the response was not significant. In this definition "well beyond the normal variability" is a less specific term to describe the biological impact. Overcoming this limitation, Van de Pol *et al.* (2017) defined extreme climate events as "*climate events that cause the biological response to be in the 5% of most extreme values of the biological response variable*". In these impact related definitions, the biological responses are expected to be in the extreme ends, but they do not specify the nature of the biological response function. Therefore, it is suggested that the biological response function should also be non-linear to study the impacts of extreme climate events meaningfully (Van de Pol *et al.* 2017).

There is no universal definition for extreme climate events. The definitions of climate extremes in the literature were reviewed by Van de Pol *et al.* (2017) and he concluded that the use of a definition (either climatological or impact related) depends on the considered research question; what is the impact (biological) of this extreme climate event, or which climate driver caused this extreme biological impact? Secondly, most biologists would prefer to use impact related definitions as it allows to estimate the effect of these rare extremes on biological systems. Finally, the studies should clearly specify the thresholds of climatological extreme such as frequency, magnitude and duration and the response threshold (extreme 5% of the biological response).

Extremes like heat waves and droughts sometimes may not necessarily be extremes if they do not exceed the ability of species to acclimate, however, if these events persist over a long period then the cumulative effects of moderate weather events can lead to one intense event with a significant damage (eg. millennium drought in Australia, (Timbal 2009; White *et al.* 2010; IPCC 2012b).

2.7.3. Physiological Thresholds

Under field conditions, crops and pastures are often subjected to transient abiotic stresses such as heat and drought even though they cannot be always categorised as either meteorological or ecological extremes. Therefore, absolute thresholds are used in physiological and simulation modelling studies to estimate impacts of extremes. A threshold temperature can be described as a temperature level at which a noticeable decline in plant growth and development begins (Wahid *et al.* 2007). Lower and upper developmental threshold levels have been defined for different crop species using controlled experimental studies. For example, in wheat, temperatures beyond 31 °C severely affect the spikelet sterility and significantly reduce wheat yields (Porter and Gawith 1999). In rice crop, temperatures below 18 °C result sterile or poorly formed spikelets and high temperatures beyond 32 °C progressively reduce spikelet fertility of rice leading to total sterility at 41 °C (Kim *et al.* 1996; Boote *et al.* 2005). The ORYZA 2000 model can simulate yield loss of rice due to both high and low temperature extremes (Bouman *et al.* 2001; Bouman and van Laar 2006). Similarly, the optimum temperatures for shoot growth of temperate perennial grasses range between 15-23 °C and it is 10-18 °C for the root growth (Beard 1973; Turgeon 2011). The commonly grown perennial ryegrass sense heat stress beyond 30 °C and growth completely stops around 35 °C (Mitchell 1956). Therefore, species specific thresholds are useful in defining the impacts of frequent abiotic stress related yield losses in plants in simulation modelling framework. These approaches will be applicable to agricultural systems where there are individual crops or mixtures of small numbers of species, but is would be harder to apply to more diverse ecosystems.

2.8. Effects of climate extremes on growth and physiology of cool season pastures

2.8.1. Plant response to heat stress

Temperature is one of the most important factors for plant growth and development (Coakley *et al.* 1999). The optimum temperature range for the growth of cool season C3 pastures is 15-24 °C and it is 10-18 °C for the root growth (Beard 1973; Paulsen 1994). High temperatures beyond this range can impact growth and physiological processes of pasture plants leading to reduced production. Perennial ryegrass, the dominant pasture species of SE Australia, experiences heat stress at 30 °C and growth ceases at 35 °C even with irrigation (Mitchell 1956).

Heat stress on plants can be defined as a period at which temperature is beyond a threshold level which is sufficient to cause impairment of plant growth, physiology and metabolism (Hall 2000; Porter 2005; Wahid *et al.* 2007). Heat stress develops in plants in a complex manner as a function of temperature intensity, duration and the rate of temperature increase. The degree of heat damage also depends on plant characteristics including plant species and phenological stage of the crop when heat stress occurs, (Wahid *et al.* 2007). For example, tall fescue and chicory were found to tolerate high temperatures for longer periods compared to creeping bentgrass (*Agrostis palustris)* and perennial ryegrass (Langworthy *et al.* 2015; Langworthy *et al.* 2019) because the latter species have a lower threshold for impacts of high temperature (Jiang and Huang 2001; Fry and Huang 2004). In the following sections, plant physiological and metabolic responses to high temperature stresses are discussed in detail with respect to cool season pastures.

2.8.1.1. Effects on photosynthesis

Photosynthesis is highly sensitive to changes in temperature (Camejo *et al.* 2005) and a reduction of photosynthesis in cool season grasses has been widely observed beyond the optimal temperature range of 15-23 °C (Beard 1973; Paulsen 1994; Loka *et al.* 2019). It was found that photosynthesis reduction of cocksfoot started beyond 22 °C (Peri *et al.* 2003) and that of creeping bent grass start started beyond 23 °C. Further, reduction in net photosynthesis has been observed beyond 25 °C for

both perennial ryegrass (Woledge and Dennis 1982) and Kentucky bluegrass under irrigated conditions (Song *et al.* 2014).

Reduction of photosynthesis due to heat stress can occur through stomatal and non-stomatal limitations. During the early stages of heat stress, stomatal closure is the most likely reason for reduction of photosynthesis and this has been observed in tall fescue (Langjun *et al.* 2006; Yu *et al.* 2014) and perennial ryegrass (Jiang and Huang 2001). However, at the latter stages of heat stress, non-stomatal limitations become prominent. Non stomatal limitations are associated with alterations to chloroplast structure and changes to the RUBISCO enzyme which ultimately causes changes to the light energy distribution within chloroplast and changes in the carboxylation efficiency (Camejo *et al.* 2005).

2.8.1.2. Impacts on photosystem-II

PSII is a complex of proteins and pigments which is located in the thylakoid membranes in the chloroplasts. PS II captures light energy, breaks down water into hydrogen and oxygen and generates electrons to go through the electron transport chain. Hydrogen ions are added to the H^+ gradient and flow down to synthesise ATP energy (Taiz and Zeiger 2010). Photosystem II is highly thermolabile and can be damaged even under moderate temperature stress (Havaux 1993; Haldimann and Feller 2005). Damage to the PSII can be caused by several factors. At high temperatures, thylakoid membrane fluidity increases (hyperfluidity) and proteins get denatured as a direct response to heat (Havaux 1998). This results in displacement of light capturing PSII complexes which disrupts the PSII electron transport system. Secondly, PSII system can be displaced from the thylakoid membranes, if the metabolic activities related to PSII electron delivery or capture are affected by high temperatures (Havaux 1998).

Photosynthesis reduction due to heat stress can be measured by chlorophyll fluorescent measurements. Florescence readings of dark adapted leaves (maximum photochemical efficiency of PS II (Fv/Fm)) indicate how much of the incoming light is used for photochemistry (Yamada *et al.* 1996; Maxwell and Johnson 2000). In healthy leaves, Fv/Fm is approximately 0.8 for most species

(Maxwell and Johnson 2000) indicating that there is no heat stress for plants and leaves effectively utilize incoming light energy. A reduction of this ratio is an indication of damage to PS II due to extreme abiotic stress. Under high temperature stress, pasture plants (perennial ryegrass, tall fescue, cocksfoot) have shown clear reductions in photochemical efficiency (Jiang and Huang 2001; Cui 2006). This reduction was greater and occurred faster when the heat stress combined with drought stress (Jiang and Huang 2001).

High light interception during heat stress can also lead to photo damage in membrane lipids caused by active forms of oxygen during summer heat waves (Havaux 1998), causing electrons to over excite and not to follow the normal electron transport pathway (Suzuki and Mittler 2006). These electrons then connect with oxygen and produce highly reactive oxygen species such as super oxide (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl free radicals (OH^-). These reactive oxygen species (ROS) oxidise cell components like membrane lipids, proteins and DNA, leading to impairment of the cell activities (Gill and Tuteja 2010). The estimation of oxidative damage can be done by measuring the lipid peroxidation as it is easy to recognize the compounds produced after oxidative damages. Severe membrane lipid peroxidation has been reported in annual and perennial ryegrass under extreme heat stress conditions (Xu *et al.* 2006; Xu and Zhou 2006). Photo damage to cell components can be prevented into some extent by producing free radicle scavenging phenolic compounds, such as flavonoids, carotenoids and alkaloids (Havaux 1998), and have shown to be varied among species and cultivars (Huang *et al.* 2001; He 2010). Plant species with these free radicles scavenging compounds offer potential for breeding heat tolerant lines.

2.8.1.3. Impacts on dark reaction

The dark reaction of photosynthesis comprises three key steps known as fixing CO_2, carbon reduction and ribulose bisphosphate (RuBP) regeneration. Reductions of the rates of these processes have been identified under elevated temperatures in plants (Law and Crafts Brandner 1999; Salvucci and Crafts-Brandner 2004; Wise *et al.* 2004). Ribulose bisphosphate carboxylase/oxygenase (RUBISCO) is the key enzyme responsible for synthesizing carbohydrates by fixing CO_2 into long chain sugars. These sugars store energy for various plant functions and processes. RUBISCO needs

to be in an active state (free of sugar residues in its structure) to bind with CO_2. RUBISCO activase is the enzyme responsible for making RUBISCO enzymatically active for carbon assimilation. Heat stress damage the RUBP activase enzyme leads to a lack of available active forms of RUBISCO for carbon assimilation (Crafts Brandner *et al.* 2000) hence reduced photosynthesis. Liu *et al.* (2008) found that deactivation of Rubisco enzyme in Kentucky bluegrass was the primary reason for reduction in photosynthesis rates under heat stress conditions. Further, Yu *et al.* (2014) reported a reduction in maximum rate of electron transport (J_{max}) of creeping bentgrass under heat stress suggesting a possible reduction of RuBP because maximum electron transport rate is responsible for the regeneration of RuBP. Maintaining high amount of proteins related to photosynthesis can reduce heat induced damage to dark reaction. Xu *et al.* (2010) attributed the heat tolerant characteristics of creeping bent grass to the high amount of RUBISCO and RUBISCO activase enzymes in leaves.

2.8.1.4. Effect on photorespiration

The RUBISCO enzyme possesses an affinity for both CO_2 and O_2 gasses. Binding of O_2 to RUBISCO initiates the photorespiration pathway in C3 plants. Photorespiration is an energy loss to plants because energy is required to remove oxygen from RUBISCO. Heat stress can affect photosynthesis by altering the solubility of CO_2 and O_2 gasses in chloroplasts. At higher temperatures, the solubility of both gasses decreases, but the amount of decrease is less in O_2 than CO_2. This makes O_2 more available to RUBISCO enzyme to carry out photorespiration in C3 plants (Wingler *et al.* 1999).

In addition to the effects on photosynthesis, there are cascading effects of heat stress on plants related to carbon depletion. With increasing temperatures, tissue respiration rate increases (Liu 2001; Rizhsky *et al.* 2002). Carbon partitioning from shoots to roots is decreased under heat stress (Lafta and Lorenzen 1995) and increasing root respiration under high temperature further deplete the available root carbohydrate reserves (Xu and Huang 2000). It has been found that higher than optimal temperatures deplete total non-structural carbohydrate contents and fructans in tall fescue (Zhao *et al.* 2008), Kentucky bluegrass (Song *et al.* 2014), cocksfoot (Volaire *et al.* 2005) and creeping bentgrass (Liu and Huang 2000). This can be detrimental for plant survival under prolonged

severe heat waves (Gunn and Farrar 1999; Lyons *et al.* 2007). Recent studies have confirmed that cool season grasses with higher total non-structural carbohydrate contents possess high thermotolerance (Song *et al.* 2014; Sun *et al.* 2014).

The overall impact of the decreased photosynthesis, increased respiration and depletion of total non-structural carbohydrate contents under extreme temperatures is the shift of carbon balance towards low energy reserves which is not favourable for both pasture production and plant survival.

2.8.1.5. Effect on membrane stability

The plasma membrane is a structural component in plant cells that acts as a selective barrier between external and internal cell environments. Cell membranes and its structural proteins fulfil essential plant functions. Many substances are transported in and out of cells through membrane protein channels while proteins on the cell surfaces identify signals and transduce them. Proteins in the thylakoid membranes facilitate photosynthesis and those in the mitochondria synthesis ATP from sugars (Taiz and Zeiger 2010). Cell membranes are sensitive to temperature fluctuations. With higher temperature, the membrane fluidity increases as the thermal energy loosens the chemical bonds between fatty acid molecules, leading to low cell membrane function and integrity (Savchenko *et al.* 2002). Extreme heat further damages the three-dimensional structures of membrane proteins leading to electrolyte leakage from the cell membranes. The electrolyte leakage test has been widely used to identify thermostability in wide array of species such as pastures (perennial grasses, tall fescue, cocksfoot and chicory) (Jiang and Huang 2001), wheat (Blum *et al.* 2001), sorghum (Marcum 1998) and barley (Wahid and Shabbir 2005). A study conducted to test the heat and drought tolerance in perennial ryegrass and tall fescue revealed that perennial ryegrass had higher electrolyte leakage (30%) than tall fescue (23%) when exposed to 35/30°C (day/night) for 35 days under irrigation (Jiang and Huang 2001). When both heat and drought stresses were exerted, electrolyte leakage was nearly 90% in both species with perennial ryegrass losing cell membrane thermostability faster than tall fescue. This could be linked to higher net photosynthesis and photosynthetic capacity (Fv/Fm) of tall fescue (Jiang and Huang 2001). Yang *et al.* (2014) also reported that electrolyte leakage of annual ryegrass was 17% higher than perennial ryegrass at

extreme heat stress of 40/35°C (day/night) exposed for 8 days and linked this to faster decrease of turf quality. Therefore, maintaining the stability of cell membranes under heat stress is imperative for plants to maintain the biomass production and important physiological functions such as photosynthesis, signal transduction and transport molecules between cells.

2.8.1.6. Effects on chlorophyll content

At high temperatures, chlorophyll degrading enzymes accelerate their activities and chlorophyll biosynthesising enzyme activities are inhibited resulting leaf chlorosis and this may vary in young and older leaves (Todorov *et al.* 2003; Yamauchi *et al.* 2004; Jespersen *et al.* 2016). Jespersen *et al.* (2016) observed that the reduction in leaf chlorophyll content of common bentgrass under heat stress was more related to the degradation of chlorophyll than its synthesis. Reduction in leaf chlorophyll contents were reported in other pasture grasses such as tall fescue (Langjun *et al.* 2006; Yu *et al.* 2014), creeping bentgrass, perennial ryegrass and kentuky bluegrass under heat stress (Huang *et al.* 1998). Other than direct effects on leaves, Xu and Huang (2000) reported that roots of creeping bentgrass exposed to heat stress reduced total chlorophyll content even with the leaves were at the optimum temperatures.

2.8.2. Plant response to drought stress

Maintaining a continuous stream of water from the soil to the atmosphere is a fundamental requirement to maintain higher cellular water content and turgidity in plants. This link between the soil, plant and atmosphere starts to break during a drought stress. An agricultural drought can be defined as a period of suboptimal water supply coupled with high atmospheric water demand (Mishra and Cherkauer 2010) which leads to reduced water potential and turgor pressure in plants that is able to suppress the normal plant functions (Hsiao 1973; Jaleel *et al.* 2009). During a severe drought stress, plants could be irreversibly damaged (Passioura 2006). As the drought progresses, the gradual decline of soil moisture and increasing atmospheric water demand creates a physical tension in the xylem. In a severe drought stress, this tension increases until the continuous water column breaks creating a cavity inside the xylem. This causes a decrease in the hydraulic

conductivity in plants (Tyree and Sperry 1989) with effects on morphology, physiology and metabolism (Hsiao 1973). The major effects of drought stress in plants are reduction in cell division and cell expansion (leading to reduced leaf size, stem elongation and root growth), reduced stomatal conductance, reduced water use efficiency (WUE), nutrient uptake and carbon metabolism (Li *et al.* 2009). Some of the major plant responses under drought conditions are described in the following sections.

2.8.2.1. Reduction in leaf expansion rate

A reduction of the leaf expansion rate is one of the earliest responses of drought stress in plants (Taize and Zeiger 2010). Since foliage production is the primary objective in the pasture production, reduced leaf expansion rate directly impacts on pasture yield (Bittman *et al.* 1988) and potentially livestock production. In SE Australia, summer pasture production is approximately 5-10% of the total annual herbage production due to sub optimal water supply coupled with high temperature stress experienced by plants during summer months (Özkan *et al.* 2015). Reduced leaf elongation rates have been widely reported in pasture species such as perennial ryegrass, tall fescue, cocksfoot, chicory and Italian ryegrass under drought stress (Lawlor 1972a; Jones 1980; Norris 1982; Volaire and Lelièvre 2001). In some other studies, reduction in leaf elongation rates of perennial ryegrass has been reported when the soil water potential reached to -0.15 MPa (Lawlor 1972b) while leaf elongation rates of blue gramma (Bouteloua gracilis), little blue stem (Schizachyrium scoparium) and wheat grass (Agropyron smithii) completely stopped at water potential of -8 MPa, -2.4 MPa, and -3 MPa in the top 5cm of the soil respectively (Majerus 1975). It is evident from the literature that leaf elongation is more sensitive to the soil moisture content rather than changes to the leaf turgor pressure. Confirming this view, Volaire and Lelièvre (2001) reported a linear relationship between relative soil moisture content and the leaf expansion rate in cocksfoot and tall fescue plants. In maize, leaf elongation rates declined under decreasing soil moisture content while the turgor pressure of the growing points of the leaves were unaffected (Michelena and Boyer 1982; Van Volkenburgh and Boyer 1985). Since cell expansion depends not only on the cellular water content

but also the water supply to the growing points (Lockhart 1965), leaf elongation is more likely related to the soil moisture content rather than the turgor pressure of leaves.

2.8.2.2. Effects on plant water relations

Plant relative water content, water potential, osmotic potential, pressure potential and transpiration rates are sensitive to drought stress. The sensitivity depends on the ability of plants to tolerate drought based on the physiological and morphological features of the plant. Using a potted experiment, Huang and Fu (2000) reported that leaf water potentials of tall fescue and Kentucky blue grass did not significantly decrease when the drought stress was applied only to the top 20 cm of soil, but the leaves wilted when the drought applied to the whole 40 cm depth of soil profile. In another experiment, drought tolerant cultivars of Kentucky bluegrass were reported to suffer less in relation to relative water content compared to drought sensitive cultivars (Abraham *et al.* 2008). Osmotic potential also starts to fall in plants during drought stress. In perennial ryegrass, a reduction of osmotic potential from -1 MPa to -2.6 MPa and -2.8 MPa was reported in lamina and leaf base respectively after 8 weeks of drought (Thomas 1991). This was accompanied by accumulation of water-soluble carbohydrates during the drought stress.

Transpiration helps plants to reduce canopy temperature, and maintain uptake water from soil and CO_2 from air. Accumulation of heat energy and a rise in canopy temperature has been observed under drought stress in pasture plants previously (Langworthy *et al.* 2019) due to the reduced transpirational cooling. Irrigation reduces the canopy temperature by evaporative cooling which helps to maintain tissue temperatures within the optimum temperature range for photosynthesis (Michaletz *et al.* 2015). Water use efficiency (WUE) (referred to as total yield/evapotranspiration) also tends to decrease under water stress (Neal *et al.* 2009). Since irrigation water scarcity is an increasing problem in Australian dairy industry, selection of species with high WUE is required (Chapman *et al.* 2012a). A study conducted in Camden, New South Wales revealed that kikuyu has the highest WUE and birds foot trefoil has the lowest WUE under optimum irrigation. Kikuyu had the highest WUE even under water deficit stress, while white clover exhibited the lowest WUE under drought with the largest decline of 44% (Neal *et al.* 2009).

2.8.2.3. Effects on photosynthesis

The reduction of photosynthesis upon exposure to drought can either be due to stomatal or non-stomatal limitations. In the initial stages of drought, stomatal closure helps plants to reduce transpirational water loss but at the same time it decreases CO_2 influx. The decreased flow of CO_2 changes the ratio of CO_2 and O_2 in the mesophyll cells and reduces the availability of CO_2 to Rubisco enzyme, encouraging the oxygenation reaction. A significant decrease in stomatal conductance has been reported in cool season temperate grasses such as perennial ryegrass (AbdElgawad *et al.* 2015), tall fescue (Jiang and Huang 2001; Yu *et al.* 2012) and Kentucky blue grass (Xu *et al.* 2013) under sub optimal water supply. However, drought tolerant cultivars of those species showed smaller reductions in stomatal conductance and transpiration rates under drought stress compared to drought sensitive cultivars (Kosmala *et al.* 2012; Yu *et al.* 2012).

Non stomatal limitations of photosynthesis include decreased Rubisco activity (Feller 2016), reduced chlorophyll pigment contents, impairment of ATP synthesis, increased oxidative stress that leads to cell membrane damage (Bian and Jiang 2009; AbdElgawad *et al.* 2015) and decreased maximum photochemical efficiency of photosystem II (Farooq *et al.* 2009). A significant decrease in (Fv/Fm) has been observed in temperate pasture species under drought stress by many studies (Jiang and Huang 2001; Langworthy *et al.* 2018). During drought stress, marked reductions in photosynthesis rates have been observed in perennial ryegrass (Jiang and Huang 2001; AbdElgawad *et al.* 2015), tall fescue (Kosmala *et al.* 2012), Kentucky blue grass (Xu *et al.* 2013) and creeping bent grass (Fu and Dernoeden 2008) due to both stomatal and non-stomatal limitations.

2.8.2.4. Drought resistance mechanisms of pasture species

Summer drought is characteristic of the winter-dominant rainfall regions of SE Australia, and with the reduced rainfall and warmer temperatures experienced in SE Australia during recent decades (CSIRO and BOM 2015), exploring drought resistance is an increasingly important objective for pasture plant breeding (Cullen *et al.* 2014b). Drought resistance mechanisms include drought escape, drought avoidance and drought tolerance (Turner 1986). Plants that possess drought escape

properties are mostly annual species. They can grow rapidly when water is available and complete their life cycle before severe soil moisture deficits develop. The plants then exist as seeds during the drought period until the next growing season begins (Kooyers 2015). Perennial grasses also show some drought avoidance characters. Mediterranean cocksfoot cultivars show early flowering and seed formation before they experience severe drought (Volaire and Leliévre 2004). Kentucky bluegrass which survive through rhizomes during severe water stress also considered as a drought escape strategy (Fry and Huang 2004).

While drought escaping plants grow only when there is enough moisture in soil, a species ability to grow longer into drought is determined by other mechanisms of drought avoidance or tolerance. Drought avoidance is the maintenance of high tissue water potential during periods of water deficits either by reducing transpirational water loss from leaves or/and increasing water uptake from roots (Levitt 1987). Plants with drought avoidance mechanisms exhibit specific traits such as development of an extensive deep system to extract more water from deep soil layers, high stomatal sensitivity, decreased leaf growth/area, leaf senescence, osmotic adjustment and leaf modifications (including leaf rolling, leaf folding, pubescence, and waxiness) to reduce incoming radiation load and transpirational water losses (Turner 1986). These traits exist in some native and introduced pasture species in SE Australia (Bolger *et al.* 2005). For example, in phalaris, senescence of foliage during dry summer is shown to reduce transpiration water losses (McWilliam 1968) while in tall fescue and phalaris, deep extensive root systems extract water from deep soil layers during dry months (Garwood and Sinclair 1979; Wilman *et al.* 1998). Other than phalaris and tall fescue, buffalo grass (*Buchloe dactyloides*), Bermuda grass (*Cynodon dactylon*) and zoysia grass (*Zoysia japonica*) have also shown drought avoidance characteristics (Burton *et al.* 1954; Marcum *et al.* 1995; Qian *et al.* 1997).

Plants are considered to be drought tolerant if they can maintain cell turgor and metabolic processes with lower tissue water potential compared to other plants (Turner 1986; Volaire *et al.* 2005; Norton *et al.* 2014). Drought tolerance can be measured by using the lethal moisture content of plants. Drought tolerance is higher if plants can tolerate lower tissue water potential (Flower and Ludlow

1987). Norton *et al.* (2014) reported that cocksfoot can tolerate lower dehydration of meristems up to 0.54 gH_2O /g dry weight while tall fescue and phalaris died much earlier when meristems' water content declined to 0.72 and 0.7 gH_2O /g dry weight respectively, indicating that cocksfoot is more drought tolerant. Strategies for drought tolerance include turgor maintenance through osmotic adjustment (accumulating of sugars, amino acids, and mineral ions) and increase of structural stabilization under low water potential (Levitt 1987).

Desiccation tolerance is a superior state of drought tolerance where plants maintain live tissues and recover when rehydration occurs even after leaves become air dry. However, this type of adaptation response has not been reported in cultivated C3 cool season pasture species (Norton *et al.* 2016).

Summer dormancy is another mechanism that help plants survival during long dry summers in areas of Mediterranean and semi-arid climates where dry period lasts for about four months (Norton 2011). In general, plants require water to continue their growth. All plants show decreased plant growth during drought due to inadequate moisture supply which is referred to as drought-imposed dormancy (facultative dormancy). By contrast, summer dormancy is the reduction or cessation of pasture growth in summer under non-limiting moisture conditions (Volaire and Norton 2006; Norton 2011). The summer dormancy trait has evolved naturally to enhance the ability of grasses to survive droughts. This trait is thought to be controlled endogenously through coupling of a series of processes however, the exact mechanisms have not been identified (Norton *et al.* 2012). Summer dormancy exists in several important pasture species used in SE Australia, in particular those that originated in the Mediterranean Basin such as tall fescue, cocksfoot and phalaris, which allows improved survival under summer drought conditions characteristic of the region (Culvenor 2009; Norton *et al.* 2016). There are summer active and summer dormant cultivars of these species and the appearance of both types under drought may be very similar. The only difference is that when rewatering, non-summer dormant species will response quickly and commence growth, but summer dormant species will not. Studies have shown that cool temperatures and short photoperiods in winter are required to induce summer dormancy in Mediterranean tall fescue and phalaris (Norton *et al.* 2006a; Norton *et al.* 2006b). In cocksfoot, 'Kashba' is a summer dormant cultivar and 'Medley'

is a non-dormant but drought tolerant cultivar. Both these cultivars were reported to survive moderate drought spells (cumulative evapotranspiration) of 650 mm and 790 mm, but exposure to 870 mm drought declined the sward cover of non-summer dormant Medley while summer dormant Kashba survived that severe drought (Norton *et al.* 2006a). Compared to both these cultivars, the ground cover of a temperate cultivar 'Lutetia' declined to 39% of its pre-drought level indicating that summer dormancy of Kashba enhanced the survival of cocksfoot under severe drought. Similar responses of these cultivars have been observed under drought experiments by Poirier *et al.* (2012). In Australia, a recent study also confirmed the enhanced drought survival of cv. Kashba where it maintained 51% of the basal cover under an 880 mm drought while the basal cover of the less dormant cv. Hispanica declined to 24% after drought (Culvenor *et al.* 2016). Similar to cocksfoot cv. Kashba, tall fescue cv. 'Flecha' also show summer dormant characteristics. Norton *et al.* (2006b) reported that tall fescue cv. Flecha exposed to drought spells of 650 mm, 790 mm, 870 mm maintained the pre-drought sward density whereas non-summer dormant cv. Demeter could maintain only 75% of its pre-drought sward density under 650 mm and 870 mm drought treatments. Phalaris survived summer droughts through a combination of a deep root system and partial summer dormancy. However, the relative contribution of summer dormancy and deep rooting to summer survival of phalaris is not well understood (Norton *et al.* 2012). While summer dormancy is an effective drought survival mechanism, it also has some disadvantages. Summer dormant plants do not use the occasional summer rainfall events effectively and therefore miss the opportunity to produce some feed in the summer and may lead to other problems such as water logging or weed infestations might arise (Norton 2011).

2.9. How temperate grasses respond to high temperature and drought stress alone and in combination

The responses of temperate pastures to drought and heat stress alone and in combination have been studied by many authors (Table 1) (Jiang and Huang 2001; Milbau *et al.* 2005; Langworthy *et al.* 2015; Langworthy *et al.* 2018). Observed eco-physiological and morphological changes of pasture species to heat and drought stress show clear differences in terms of their tolerance and ability to

recover. In general, pasture species have shown reduced biomass production (Baker and Jung 1968), leaf and canopy photosynthesis rate (Jiang and Huang 2001; Cui 2006), photochemical efficiency of PS II (Jiang and Huang 2001; Langworthy *et al.* 2018), membrane thermostability (Yang *et al.* 2014), water use efficiency and leaf water potential (Yang *et al.* 2014) and at severe stage; plant survival (Milbau *et al.* 2005; Langworthy *et al.* 2015; Langworthy *et al.* 2018), under both heat and/or drought stresses. The impacts were greater and occurred faster when the heat and drought stresses occurred together compared to single stress (Jiang and Huang 2001; Langworthy *et al.* 2019). However, varying responses of different pasture species and types (C3 and C4 photosynthetic pathways) have been reported under heat and drought stresses.

Plants ability to tolerate heat stress is higher when there is water available in the soil. This is mainly because increasing atmospheric water demand during heat stress is met by non-limiting water supply from the soil and this water flow provides evaporative cooling. Therefore, canopy temperatures tend to be several degrees lower than air temperature under irrigated conditions (Jiang and Huang 2001; Langworthy *et al.* 2019). Langworthy *et al.* (2019) reported that the crown temperatures of tall fescue and chicory pastures were lower than perennial ryegrass when the pastures were cut at lower stubble heights (35 and 55 mm) and the authors suggested that the high survival and growth of tall fescue and chicory under hot and dry conditions was due to their effective cooling ability. Further, Yang *et al.* (2014) reported that turf quality (measured using visual ratings from 1 to 9) of annual and perennial ryegrass did not decline at the end of 8-day moderate heat stress of 30 °C when the water was supplied, but when high temperatures overlap with summer dry periods the quality cannot be maintained especially under extended water stress periods. In such situations, canopy temperatures tend to increase several degrees higher than air temperature causing additive effects on plants (Jiang and Huang 2001; Feller and Vaseva 2014). Even with well-watered conditions, extremely high temperatures suppress the normal plant functions due to structural damage (cell membrane) and impairment of essential metabolic functions. Yang *et al.* (2014) observed this phenomena with annual and perennial ryegrass that turf quality declined sharply under severe heat stress of 40°C

even with moisture supply. Mitchell (1956) also reported that perennial ryegrass stopped growth above 35 °C under well-watered conditions.

Plant survival of heat and drought stresses and recovery after the events have been studied by several authors (Milbau *et al.* 2005; Langworthy *et al.* 2018). A simulated extreme heat and drought experiment with maximum canopy temperature of 36.5±3.6 °C demonstrated differences between species in their recovery after rewatering (Milbau *et al.* 2005). Among tall fescue, cocksfoot and perennial ryegrass, only 50% of the perennial ryegrass plants recovered after 12 days of stress, but more than 90% of tall fescue and cocksfoot survived. Langworthy *et al.* (2015) also reported that the perennial ryegrass population did not survive when exposed to a combined heat wave treatment (38˚C day/26˚C night) and drought treatment after 12 days. Generally, the species ability to survive has been found to be highly related to two physiological attributes related to photosynthesis capacity. Those are the ability to maintain substantial photochemical capacity (Fv/Fm) and low internal CO_2 concentration (C*i*). Relatively heat tolerant species such as chicory, cocksfoot and tall fescue have exhibited high photosystem II functionality and lower C*i* (Milbau *et al.* 2005; Langworthy *et al.* 2015). These measures indicate that the capacity of the electron transport has not been reduced under high stress while stomatal closure prevented transpirational water loss (Flexas 2002). However, perennial ryegrass began to reduce photosynthesis rates earlier than tall fescue under heat stress of 35 ˚C day and 30 °C night with well-watered conditions and this can be attributed to low Fv/Fm, high electrolyte leakage and a shallower root system of perennial ryegrass compared to tall fescue and cocksfoot (Volaire, 2008; Pecetti *et al.*, 2011). It has also observed that the longer-lived species of cocksfoot and tall fescue were less responsive in terms of stomatal conductance and photosynthetic rate to daily fluctuations in temperature, radiation and vapour pressure deficits compared to perennial ryegrass (Milbau *et al.* 2005).

The impact of high temperature and water stress on the below ground environment is equally important when considering whole plant response. Heat stress alone, and heat and drought stress together, can have a substantial impact on root biomass and root viability of pastures (Jiang and Huang 2001). However, deep rooted tall fescue has shown higher root viability than shallow rooted

perennial ryegrass because heat stress reduced the root viability of plants in the upper layers of soil (Jiang and Huang 2001). Therefore, deeper roots can have advantage over shallow rooted species. Viable roots are very important in to absorb soil moisture from deep soil layers. This characteristic is especially important under severe drought and heat in order to prevent internal injuries and to reduce stomatal resistance and maintain canopy temperature far below the plants with shallow roots (Bonos and Murphy 1999).

It is also important to note that plants are usually much slower to show impacts of heat and drought treatments in field experimental where the stress symptoms progress slowly compared to controlled experiments with simulated stress conditions (De Boeck *et al.* 2010). This is mainly due to restricted root growth and low soil volume compared to field grown plants. Therefore, extending the results of controlled environment studies to the field conditions must be done with caution.

Different plant functional types have varying capabilities to cope with temperature and moisture stresses in their environments. Chapman *et al.* (2014b) reviewed the strategies of perennial grasses to flourish in different environments according to their plant functional types. The C4 photosynthesis pathway favours higher temperature environments than the C3 pathway. This is partly due to the photorespiration process in C3 plants that accelerates with increasing temperatures. This process utilises ATP energy that would otherwise be used for plant growth. C4 plants do not have the photorespiration mechanism and not reach to a light saturation like in C3 photosynthesis pathway. A study conducted to compare water deficit stress on photosynthesis in paspalum (C4) and white clover (C3) clearly displayed that paspalum could maintain substantially high photosynthetic rate even under a higher water deficit (70 mm) than white clover (25 mm) (Blaikie *et al.* 1988). The ability of C4 plants to continue to photosynthesise even with nearly closed stomata make them more water use efficient than C3 plants under water stressed and high temperature conditions.

The physiological advantages of C4 grasses compared to C3 grass raise a question about incorporating C4 species into the SE Australia region. In summer conditions, the contribution of C4 grasses for forage production is high (Johnston 1996). However, C3 grasses are still a key component in grassland productivity, because of their high growth rates achieved at lower optimum

temperatures and they perform well during the cool season (Pan et al., 2013; Still et al., 2003). Further, C3 grasses are well adapted to the lower radiation levels received in cooler seasons than C4 in temperate environments like southern Australia. Most importantly when considering nutritive quality, C3 grasses are always better than C4 (Minson 2012). The frost sensitivity is also higher in C4 grasses than C3 species. Nevertheless, in areas with mild winters like Northern Inland New South Wales (NSW), pasture development with C4 species is being already undertaken. These species are expected to be well adapted to future climates in these regions (Johnston 1996). However, in the Tableland District where frost incidences are high and prominent cool temperatures present, C3 grasses are more suitable to grow. Even though farmers are likely to have C3 perennial grasses in terms of having quality feed supply, the environment resilience with suitable species under future increasing climate variability with extreme heat and drought events need to be considered equally.

Table 1: Effect of drought and heat stress alone and in combination on pasture species.

Category	Stress treatment	Pasture species	Observed changes in visual quality, plant growth and physiological processes	Reference
Heat stress	Moderate heat 30/25°C (8 days)	Annual ryegrass, perennial ryegrass	Turf quality did not decline significantly during the stress	(Yang *et al.* 2014)
	Extreme heat40/35°C (8 days)	Annual ryegrass, perennial ryegrass	Turf quality of annual ryegrass declined faster than perennial ryegrass, Leaf relative water content declined by 6% in annual ryegrass and by 4.5% in perennial ryegrass, Cell membrane thermostability declined by 20% in annual ryegrass and 9% in perennial ryegrass	(Yang *et al.* 2014)
	34.8°C	Kentuky blue grass	Top growth reduced by 50% of the growth at optimum temperature at 21.6°C	(Baker and Jung 1968)
	35/30°C (35 days)	Perennial ryegrass, tall fescue	Slight reduction in photochemical efficiency in tall fescue and perennial ryegrass net canopy photosynthesis rate declined to zero in perennial ryegrass earlier (21st day) than tall fescue (on 35th day) Electrolyte leakage was higher in perennial ryegrass 30% than tall fescue 23%	(Jiang and Huang 2001)
	35/30°C (20 days)	Tall fescue	Net photosynthesis rate decreased from 10µmolm-2s-1 to 7.3µmolm-2s-1 Stomatal conductance decreased from 0.21µmolm-2s-1 to 0.11µmolm-2s-1 water use efficiency decreased from 2.5µmol µmol^{-1}kPa to 1.8 µmol µmol^{-1}kPa Slight reduction of photochemical efficiency from 0.8 to 0.65 after 20 days	(Cui 2006)
Drought stress	6-day drought	Perennial ryegrass	Mid-day leaf water potential and osmotic potential declined from -1 to -2MPa Leaf expansion rate maintained until day 3, then declined by 70% Canopy photosynthesis maintained until day 3, then declined by 80% Mid-day leaf resistance increased from 1.8scm^{-1} to 20.4scm^{-1} Leaf wilting occurred at leaf water potential of -2MPa	(Holloway Phillips and Brodribb 2011)
	Drought treatment until 90% tiller death	Perennial ryegrass	Complete stomatal closure and 90% reduction of leaf hydraulic conductivity at leaf water potential of -2.35MPa Decline in photosynthetic rate at leaf hydraulic conductivity below 5mmolm^{-2}s^{-1}MPa^{-1}	(Milbau *et al.* 2005)
Heat and drought stress	35/30°C and drought (35 days)	Perennial ryegrass, tall fescue	Photochemical efficiency decreased to 0.2 on day 12 Canopy photosynthesis rates of both species fell below zero in the 9th day Electrolyte leakage was higher in perennial ryegrass than tall fescue and reached to 80% in day 21 Soil water content reduced faster in tall fescue than perennial ryegrass Evapotranspiration rate was higher in tall fescue compared to perennial ryegrass	(Jiang and Huang 2001)
	38/26°C (18 days) and drought	Perennial ryegrass, chicory	Chicory maintained live tissues during stress period and recovered upon rewatering Perennial ryegrass dried out in 12 days of stress and did not recover upon rewatering	(Langworthy *et al.* 2015)
	36±3°C and drought	Perennial ryegrass, tall fescue, cocksfoot	Photochemical efficiency of Tall fescue and cocksfoot were higher than perennial ryegrass Recovery ability was related to higher total leaf area in tall fescue and cocksfoot.	(Milbau *et al.* 2005)

2.10. Plant acclimation to stress

Plants develop strategies to deal with abiotic stresses, such as drought and heat stress, using the memory of previous exposure to the stress referred to as acclimation or priming effect (Bäurle 2016). When a plant is exposed to a moderate heat stress, the stress memory primes the plant to withstand severe heat stresses which could be lethal to a non-primed plant (Mittler *et al.* 2012). In this process, the memory phase is maintained in plants over several days after the stress ceased which is called acquired thermotolerance. Acquired thermotolerance is achieved by activating the heat shock transcription factors in plants and synthesizing heat shock proteins (Finka *et al.* 2015; Haslbeck and Vierling 2015). It has been reported that acquired thermotolerance can increase plant performance as well as protect plants from the recurring stresses (Kissoudis *et al.* 2014; Rejeb *et al.* 2014). Xu *et al.* (2006) reported that perennial ryegrass and tall fescue species exposed to moderate heat stress of 30 °C for three days reduced the water loss, membrane lipid peroxidation and cell membrane damage from plants when exposed to a subsequent severe level of heat stress at 38 °C. Plants exposed to the heat acclimation pre-treatment had higher levels of the antioxidant compounds; ascorbate and glutathione, compared to non-heat acclimated plants (Xu *et al.* 2006). Similarly when heat acclimation pre-treatment (25°C) was applied to wheat plants, there was less reduction of maximum photochemical efficiency of PSII in wheat cultivars at 40 °C heat stress compared to non-heat acclimated plants (Haque *et al.* 2014). Ability of plants to acclimate is increasingly important and have the potential to incorporate to the future pasture plant improvement programmes by selecting the cultivars with high acclimation ability because the recurring stresses are predicted to be more common in the future (CSIRO and BOM 2015; Hennessy *et al.* 2016).

2.11. Modelling heat stress impacts on plants

Crop simulation models are mathematical representations of plant ecophysiological processes. These models are used to predict plant growth and development under different climates, soil types and management systems (Hodson and White 2010; Asseng *et al.* 2015). Crop models are used primarily as decision making tools for managing the agricultural systems but together with

physiology and molecular biology, these models can also be used for crop improvement (Slafer 2003; Boote *et al.* 2013; Cullen *et al.* 2014b). Simulation modelling is the only way to evaluate long term yield trends in the historical climate (Chapman *et al.* 2013; Hochman *et al.* 2017) as long term quality data sets are unavailable particularly for pasture production systems. Further, modelling is a tool that can be used to assess the potential impacts of future climate change on crop and pastures yields (Bassu *et al.* 2014; Harrison *et al.* 2016).

Current crop simulation and ecosystem models were originally optimized to operate under average conditions using long term climate data (Reichstein *et al.* 2013) however, their abiotic stress algorithms have not been parameterised well to account for extreme climate events such as heat waves and droughts (Asseng *et al.* 2015). This is either because of slow phase of model parameterization or lack of quality experimental and field data sets available to parameterise heat and drought stress algorithms in crop models (Rezaei *et al.* 2015). To date, a limited number of simulation modelling studies have considered such heat and drought stress effects on crop yields and most of these studies are on cereal crops (Teixeira *et al.* 2013; Deryng *et al.* 2014; Jin *et al.* 2016; Webber *et al.* 2017). The following sections describe the common modelling approaches used to represent heat stress on crops with a particular focus on the heat stress function in the DairyMod pasture model (Johnson 2016).

One of the simplest approaches used in crop models to incorporate high temperature stress impacts on cereal crops is based on reduction functions associated with final grain yields. Daily accumulation of stress thermal time (STT, the accumulated temperature sums during which yield formation of a crop is sensitive to heat stress) was related to grain yield loss of wheat by Blumenthal *et al.* (1991). Using a similar approach, Teixeira *et al.* (2013) developed a method to simulate heat stress impacts on rice, maize, wheat and soybean yields in Global Agro-Ecological Zones (GAEZ) model (Fischer *et al.* 2002) using a factor called damage intensity factor. Damage intensity factors (ranging from 0 (no stress) to 1 (full stress)) for crops were calculated using threshold temperature values for each crop on each day for 30-days (15 days before and after anthesis - thermal sensitive period) and averaged over the thermal sensitive period to scale the potential yield loss due to heat stress (Teixeira

et al. 2013). A slightly modified approach to GAEZ model (using daily maximum temperature instead of daytime temperature) was employed by Rezaei *et al.* (2013) to simulate high temperature stress effects on final wheat yields using the SIMPLACE (Scientific Impact assessment and Modeling PLatform for Advanced Crop and Ecosystem management) modelling framework. Even though this method is simple and attractive, it does not account for heat stress impacts on growth and developmental processes on crops (i.e. photosynthesis, assimilate partitioning, flowering or grain filling).

Process based modelling is the key to simulate abiotic stresses on different growth and developmental processes. For example, using two photosynthesis modelling approaches, Seidel *et al.* (2016) demonstrated that under heat and drought stress conditions, biochemical photosynthesis modelling approach (the Farquhar-Ball-Collatz model) performed better than the simple empirical photosynthesis modelling approach (the Goudriaan and van Laar or GvL model) in simulating final yields of common bean measured in experimental conditions. This was due to better prediction of soil water dynamics, stomatal conductance and plant growth modelled in the biochemical photosynthesis modelling approach compared to the empirical approach.

The relative importance of the response of photosynthesis, crop developmental rate and the reproductive processes to final yields of cereal crops were reviewed extensively by Rezaei *et al.* (2015). According to the experimental evidence, flowering and grain filling have been identified as the most heat sensitive phenological stages of cereal crops (wheat, maize and rice). Process-based crop simulation models have included some of the effects of heat stress on those reproductive processes. For example, the APSIM maize model starts to decrease grain number linearly between the mean daily temperatures 30 °C and 38 °C (Carberry *et al.* 1989). In the CERES-4.0 model, grain filling of maize starts to decrease when mean temperature exceeds 38 °C and completely stops at 48.5 °C (Jones *et al.* 2003). Likewise in CropSyst model, flowering of maize start to decrease when hourly temperatures exceed 31 °C and reaches its minimum at 44 °C (Stöckle *et al.* 2014). Similarly in wheat crop, the STICS model stops grain filling when the maximum temperature exceeds 38 °C (Brisson *et al.* 2003).

Other modelling approaches simulate the high temperature effects on leaf senescence. For example, in APSIM Nwheat model, leaf senescence accelerates between the daily maximum temperatures 32 °C and 34 °C by 50% (Porter and Gawith 1999; Asseng *et al.* 2011). Leaf senescence rate further accelerates (three-fold) when daily maximum temperature reaches 40 °C. Similarly in FASSET model, leaf senescence rate of wheat is accelerated by 9.5% when the maximum temperature increased beyond 30 °C (Olesen *et al.* 2002; Doltra *et al.* 2015) and in SiriusQuality model each 1 °C increase in maximum temperature beyond 34 °C accelerates leaf senescence by 45% (Martre *et al.* 2006).

Running an ensemble of simulation models with different heat stress algorithms is one option to identify the most appropriate approaches to represent heat stress functions in crop models. Evaluating heat stress algorithms of 16 maize models, Jin *et al.* (2016) found that heat stress impacts can be best described by the models that includes event based descriptions of heat and drought stress. With ensemble simulations, Wang *et al.* (2017) reported that modifying temperature response functions of process-based models can reduce the uncertainty of simulated yields by about 42%. Further, use of leaf temperature instead of air temperature have shown to improve simulation of the heat stress effects and reduce the uncertainty of yields in crop models (Webber *et al.* 2017).

In DairyMod and SGS pasture models, growth limitation due to temperature is calculated based on the temperature response curve for photosynthesis using a factor called growth limiting factor_temperature (GLF_T) (Johnson 2008). GLF_T range from 0 (full stress) to 1 (no stress) where growth limitations occur (GLF_T<1) when the daily maximum temperature fluctuates above or below the optimum temperature for photosynthesis for a considered species (20 °C for perennial ryegrass). In addition to that, growth limitation due to high temperature stress of pasture species is calculated using high temperature stress coefficient in the model (Johnson *et al.* 2008). When the maximum daily temperature exceeds the high temperature-onset threshold, the model starts to implement heat stress and completely shuts down canopy photosynthesis and growth when the maximum daily temperature reaches the high temperature-full threshold. Recovery from heat stress is defined in the DairyMod using an empirical function called Tsum recovery. This is

simulated by 25-mean temperature after the heat stress. When the summation of 25-mean daily temperature after heat stress reached the Tsum recovery, The GLF_T is gradually increased until full recovery is achieved. For example, if the Tsum for perennial ryegrass is 100 and the average temperature of the following day is 20, 5 heat units accumulate in that day. Perennial ryegrass will fully recover after 20 such days upon reaching the Tsum of 100. Tsum recovery is used for two purposes in DairyMod. For pasture species that exhibit summer dormancy, Tsum recovery is normally set to higher values (eg. 200) to prevent reaching full recovery until the summer period finished thereby simulate ceased growth during dormancy period. In contrast, for summer active species like perennial ryegrass, Tsum recovery is set to lower values to allow them to recover quickly and grow when the temperature resume to normal. However, these heat stress and recovery functions were not parameterized well and not validated with measured data for different pasture species. The model users have to depend on the model defaults or arbitrary values when simulating pasture production using the model. This has been a concern when evaluating the climate change impacts on pasture systems in SE Australia under future warming and drying climates particularly with increased frequency and magnitudes of extreme events (CSIRO and BOM 2015). Further, DairyMod model does not simulate tiller death under extreme heat and drought stress hence, does not account for the pasture persistence.

2.12. Knowledge gaps

The literature review critically evaluated the scientific literature on the historical and future predicted climate variability and extreme climate events and their possible implications on plant growth and physiology with special emphasis on pasture based systems in SE Australia. The importance of changing climate variability and extremes in the context of managing pasture based livestock systems was discussed in detail using the literature from experiments, surveys and simulation modelling studies. The tropical and extratropical modes of climate variability that affect SE Australian climate were evaluated with respect to their influence on the regional rainfall, temperature and extremes. Key ENSO and IOD phases seem to be increasingly important for pasture production as the phases coincide with the key pasture growing seasons in SE Australia. The recent changes to

the frequency and the intensity of these phases that contribute to the drying and warming trend observed in the region from 1990's were discussed. Possible impacts of climate variability and extreme events were discussed in relation to the plant growth and physiology and found that these abiotic stresses in turn can lead to low energy reserves and lower pasture persistence when the stresses are extreme. The importance of simulation modelling in studying climate change impacts were reviewed emphasizing the importance of parameterizing and validating the heat and drought stress algorithms using the experimental evidences collected from both glasshouse and field studies. The following research gaps were identified from the literature review and addressed in this thesis.

Majority of previous climate change modelling studies on pasture-based systems in SE Australia have investigated the effects of average changes of rainfall and temperature on yields, and very few studies have focused on methodologies that account for climate variability and extreme events. Therefore, it is an important and urgent need to study about the impacts of climate variability and extremes on pasture systems in SE Australia because both variability and extremes are projected to increase in the coming decades (Hennessy *et al.* 2016). This was identified as a key research gap from the literature review.

It has been well known that large scale climate drivers such as ENSO and IOD have a greater bearing on the interannual rainfall variability in SE Australia. The impacts of different climate driver phases on other major food crops in the world such as wheat maize and grapes wines have been studied extensively, but their influence on pasture-based systems have not been studied in detail. This was another area with limited information.

Impacts of extreme heat and drought stresses individually or in combination on commonly grown pasture species in SE Australia have been studied previously. However, it is expected that, their frequency and severity will be increased in future. While prolonged drought and heat stress will impact negatively on both production and persistence, consecutive stresses with short recurring time may have altered responses such as acclimation to previous stresses through stress memory or priming. Such responses may be useful to breed new varieties with better heat and drought tolerant characters. However, there is limited amount of research in this area for cool season pastures.

Even though simulation modelling is the only way to explore yield variability under changing climate, most of these models are not well parameterised to capture the effects of extreme events; particularly high temperature stress on pasture plants. Under field conditions perennial pasture species may experience heat and drought stress frequently but being perennials, they recover when the stress is over. Therefore, it is important to accurately parameterise both the impacts and the recovery functions in the model in order to predict the pasture yields under future climate change. Currently the DairyMod biophysical model uses the default values to simulate heat stress and recovery of pasture species but they are not supported by the experimental evidence. This is a constraint in predicting climate change impacts accurately in the future. Further, recent studies have showed that leaf temperature can differ from air temperature by several degrees. However, current crop simulation models use air temperature to parameterise the heat stress functions and this may cause considerable uncertainty around predicted yields. Research into new approaches should investigate the benefits of using leaf temperature to improve the representation of impacts high temperature stress functions in crop models.

Adaptation to climate variability and extreme events is the key to sustain livestock production in future. This was identified as a key limitation in the climate change literature for pastures. The result chapter 3 and 6 discuss some of the possible adaptation options in relation to the simulated changes in pasture growing patterns in SE Australia and experimental evidences.

Simulation modelling is the only possible way to assess the impacts of climate change on agricultural systems across a range of climates, soil types, different crop and pasture species and management. However, accurate calibration and validation of these models is important when estimating the impacts of climate variability and extremes. Therefore, there is a need to use simulation modelling in combination with field and controlled environment experiments to address these research questions.

CHAPTER 3. Changing patterns of pasture production in south-eastern Australia from 1960 to 2015 (Journal article)

Perera, R, Cullen, B, Eckard, R (2020) Changing patterns of pasture production in south-eastern Australia from 1960 to 2015. *Crop and Pasture Science* **71**, 70-81. https://doi.org/10.1071/CP19112

CSIRO PUBLISHING
Crop & Pasture Science, 2020, **71**, 70–81
https://doi.org/10.1071/CP19112

Changing patterns of pasture production in south-eastern Australia from 1960 to 2015

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Abstract. The seasonal pattern of pasture production and its variability from year to year are important for pasture-based livestock production systems in south-eastern Australia because they influence key strategic decisions such as stocking rate and timing of the reproductive cycle. In this study, the effects of observed climate variations over the period 1960–2015 on pasture growth patterns were investigated by using a biophysical modelling approach. Pasture growth rates were simulated using DairyMod biophysical software at five sites ranging from high-rainfall, cool temperate at Elliott in Tasmania to medium-rainfall, warm temperate at Wagga Wagga in southern New South Wales. Annual pasture yields showed a small increasing rate of 50 kg DM/ha.year at Elliott and 40 kg DM/ha.year at Ellinbank ($P < 0.05$), whereas other sites showed no significant trend over time. A cross-site analysis of seasonal average pasture growth rates predicted under four different discrete periods of 14 years each showed that winter growth has increased steadily through time ($P = 0.001$), and spring pasture growth rate has decreased ($P < 0.001$) in 2002–15 compared with the earlier periods. Year-to-year pasture yield variability (coefficient of variation) during autumn and spring seasons has also increased ($P < 0.05$) across sites in the period 2002–15 compared with 1998–2001. At each site, the number of spring days with water stress (growth limiting factor_water <0.7) was ~10 times greater than the number of days with temperature stress (growth limiting factor_temperature <0.7). There was an increase in the number of days with water stress at Wagga Wagga, and increased heat stress at Wagga Wagga and Hamilton ($P < 0.05$) in the most recent period. These results highlight the importance of incorporating more heat-tolerant and deep-rooting cultivars into pasture-based production system. Although previous studies of climate-change impact have predicted increasing winter growth rates and a contraction of the spring growing season in the future (2030), this study provides clear evidence that these changes are already occurring under the observed climate in south-eastern Australia.

Additional keywords: climate variability, simulation modelling.

Received 19 March 2019, accepted 30 October 2019, published online 17 January 2020

Introduction

Grazed pasture is usually the cheapest feed source for livestock. In the dairy industry of south-eastern (SE) Australia, grazed pasture comprises 60–65% of total cow diet in a year under normal seasonal conditions (DairyAustralia 2018). However, efficient feeding of cattle and sheep is hindered by uneven pasture growth within a year (seasonal variation) and between years (inter-annual variation). Both seasonal and inter-annual variation of pasture production are largely governed by climate variability, which ultimately influences soil moisture, atmospheric temperature and solar radiation, affecting plant physiology and growth processes (Radcliffe and Baars 1990; Chapman *et al*. 2009). The major source of year-to-year variability in pasture growth in SE Australia is rainfall, particularly during spring, when the majority of pasture is grown by temperate pasture species (Chapman *et al*. 2009). This is similar to findings in other regions with temperate climates. For example, in Britain, 60% of variation in pasture growth rates was related to variation in soil moisture (Morrison 1980), and in New Zealand, 60% of pasture growth variation was due to variation in total spring and summer rainfall (Radcliffe and Baars 1990).

This year-to-year variation in rainfall largely influences pasture growth and quality, impacting on both longer term, strategic management decisions (such as stocking rates and lambing or calving times) and shorter term tactical decisions such as management of feed supply and demand by supplementary feeding and use of fertiliser (Chapman *et al*. 2013). In dairy systems, Chapman *et al*. (2009) found that total annual pasture growth was closely positively related to mean stocking rate in SE Australia, whereas increasing inter-annual variation was associated with lower stocking rates. On a more tactical level, lower rainfall and pasture production are associated with increased feed gaps (Rawnsley *et al*. (2013) or greater supplementary feed requirements (Clark *et al*. 2003).

In addition to the effects on pasture growth and management decisions, climate variability has a significant effect at the level of individual plants or the plant population that might limit

pasture plant survival (termed 'pasture persistence') (Chapman *et al*. 2011). Culvenor and Simpson (2014) reviewed the elements of pasture persistence in SE Australia and found that whereas the loss of sown plant species from the pasture is usually caused by multiple, interacting factors, climate, and in particular drought, played a key role. Although perennial ryegrass produces greater biomass at the end of winter and spring, its survival ability is poor under dry summers (Nie *et al*. 2004*a*). Those authors reported a significant decline in tiller density of perennial ryegrass pastures in south-western Victoria (annual average rainfall 600–800 mm) under very low rainfall during summer months (average 20 mm/month). In the same region, several other authors also state that perennial ryegrass show poor persistence in the drought years (Reed 1974; Anderson *et al*. 1999; Waller and Sale 2001). Poirier *et al*. (2012) identified threshold soil-moisture deficit levels for tiller mortality in temperate and Mediterranean pasture species (*Festuca arundinacea* Schreb. and *Dactylis glomerata* L.), using an indicator termed 'cumulative spring and summer soil moisture deficit' (CSSSMD), calculated as rainfall minus potential evapotranspiration (PET). In that study, a significant increase in tiller mortality was observed at CSSSMD of 450 mm for temperature populations and 550 mm for Mediterranean populations. In the absence of data more relevant to SE Australia, the CSSSMD was adopted in this study as an indicator of drought stress that may impact on persistence of temperate pastures. This addresses an acknowledged gap in previous climate-change-impact analyses (Cullen *et al*. 2009; Moore and Ghahramani 2013), which is likely to be increasingly important in drier and hotter climates with more intense spring and summer droughts (CSIRO and BOM 2015; Harrison *et al*. 2016).

Recent changes observed in SE Australian climates provide clear evidence of increased climate variability, particularly with rainfall changes since the 1990s (CSIRO and BOM 2015). SE Australia typically receives rainfall during the cooler months of the year, and the region has experienced an overall drying trend during these months since the 1990s (Timbal 2009; Braganza *et al*. 2011), including a 20% decrease in rainfall in Victoria (Hennessy *et al*. 2016). Further, SE Australia experienced a prolonged drought during 1997–2009 (Millennium Drought) with the greatest decline in rainfall occurring in autumn and winter (Timbal 2009). This has been attributed to the intensification of the subtropical ridge (STR) associated with expansion of the Hadley cell with global warming (Timbal and Drosdowsky 2013). Despite the drying trend, the percentage area of Victoria receiving heavy rainfall has also increased since 1970s, with 2010–13 being considerably wetter than average in the south-eastern region (CSIRO and BOM 2015). In addition, a considerable increase in heat records has been observed in the recent past compared with the long-term temperature trend (Trewin and Smalley 2013). For example, from 1968 to 2007, the percentage of exceptionally hot years in Victoria and Tasmania has doubled (10–12%) compared with the long-term average of 5% (Hennessy *et al*. 2008). Atmospheric heat waves have also increased in their intensity, frequency and duration since the 1950s in Australia and are projected to keep increasing throughout the rest of the 21st Century (Perkins *et al*. 2012). Although minimum temperatures are rising by 0.17°C per decade across the region, localised cooling has also been observed, with the frost season lengthening by 26 days across the whole southern part of Australia (Crimp *et al*. 2016). These climate records clearly show that the variability (yearly fluctuations of climate above or below a long-term average value) has increased with increased frequency of periods of high moisture stress, intense rainfall events, high temperature stresses and frost occurrences.

Several studies focusing on effects of increased variability and change in climate on agricultural yields have been conducted nationally and globally (Wheeler *et al*. 2000; Chapman *et al*. 2009; Craufurd and Wheeler 2009; Mohammed and Tarpley 2009; Lobell *et al*. 2011). These approaches help to understand the effects of future anticipated changes on crop yields. For instance Lobell *et al*. (2011) linked decline in wheat (–5.5%) and maize (–3.8%) yields in the world's key grain-growing areas to increasing temperature trends during 1980–2008. In Europe, despite genetic progress in wheat, climate change has led to stagnating yields, particularly after the 1990s (Brisson *et al*. 2010). In Australia, Hochman *et al*. (2017) found a similar trend in which wheat yields stalled after the 1990s because of a decline in rainfall and an increase in temperature coinciding with flowering and grain-filling stages. However, no such historical analysis has been conducted for pastures in Australia to assess recent changes to climate variability. Therefore, the aims of this study were to: (*i*) analyse how annual and monthly pasture production and its variability have changed over a historical period; and (*ii*) investigate climate factors that may influence the persistence of temperate pasture species, such as growth-limiting factors (GLF) for water and temperature, and CSSSMD.

Methodology

Site selection, pasture species and simulation modelling

Pasture growth patterns were simulated at five sites representing some of the livestock-production zones in SE Australia by using the DairyMod (version 5.6.5) biophysical model. The period of simulation was from 1960 to 2015, this being when climate records in the region are more reliable (especially for temperature) (Cai *et al*. 2009; CSIRO and BOM 2015). DairyMod has been shown to simulate annual pasture yields and seasonal patterns realistically across a range of climatic zones, soil types, pasture species and management options used in SE Australia and New Zealand (Cullen *et al*. 2008; White *et al*. 2008). In the absence of long-term measured pasture growth data, simulation modelling is the only way to investigate the effects of climate (rainfall, temperature, CO_2) and its variability on agricultural yields over the historical period.

The location, soil type and pasture species simulated at each site in this study are described in Table 1; monthly climate patterns are presented in Fig. 1. The sites ranged from Wagga Wagga in southern New South Wales, which has a medium annual rainfall with even distribution through the year, to Elliott in Tasmania, which has high annual rainfall with a winter-dominant pattern. Pasture mixtures used at each site ranged from perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) at Elliott and Ellinbank, to phalaris (*Phalaris aquatica* L.) and subterranean clover (*Trifolium subterraneum* L.) as major species at Dookie and Wagga

Table 1. Description of site locations, soil type, average annual rainfall, average annual maximum and minimum temperatures, potential evapotranspiration (PET) between 1960 and 2015 and species composition used for simulations

Soil type according to Australian Soil Classification (Isbell 2002)

Site	Lat., long.	Soil type	Climate	Rainfall (mm)	Temperature (°C) Max.	Min.	PET (mm)	Species composition
Wagga Wagga	–35.16, 147.46	Red Chromosol/ Leptic Tenosol	Medium rainfall warm temperate	575	22.3	9.0	1295	Phalaris, subterranean clover, annual ryegrass, with native C_4 grasses and without native C_4 grasses
Dookie	–36.37, 145.70	Vertic Calic Red Chromosol	Medium rainfall warm temperate	559	20.4	8.0	1164	Phalaris, subterranean clover
Hamilton	–37.83, 142.06	Brown Chromosol	Medium rainfall temperate	675	18.6	7.5	946	Perennial ryegrass, subterranean clover
Ellinbank	–38.25, 145.93	Red Mesotrophic Haplic Ferrosol	High rainfall temperate	1046	18.7	8.8	942	Perennial ryegrass, white clover
Elliott	–41.08, 145.77	Red Mesotrophic Haplic Ferrosol	High rainfall cool temperate	1187	15.7	7.4	786	Perennial ryegrass, white clover

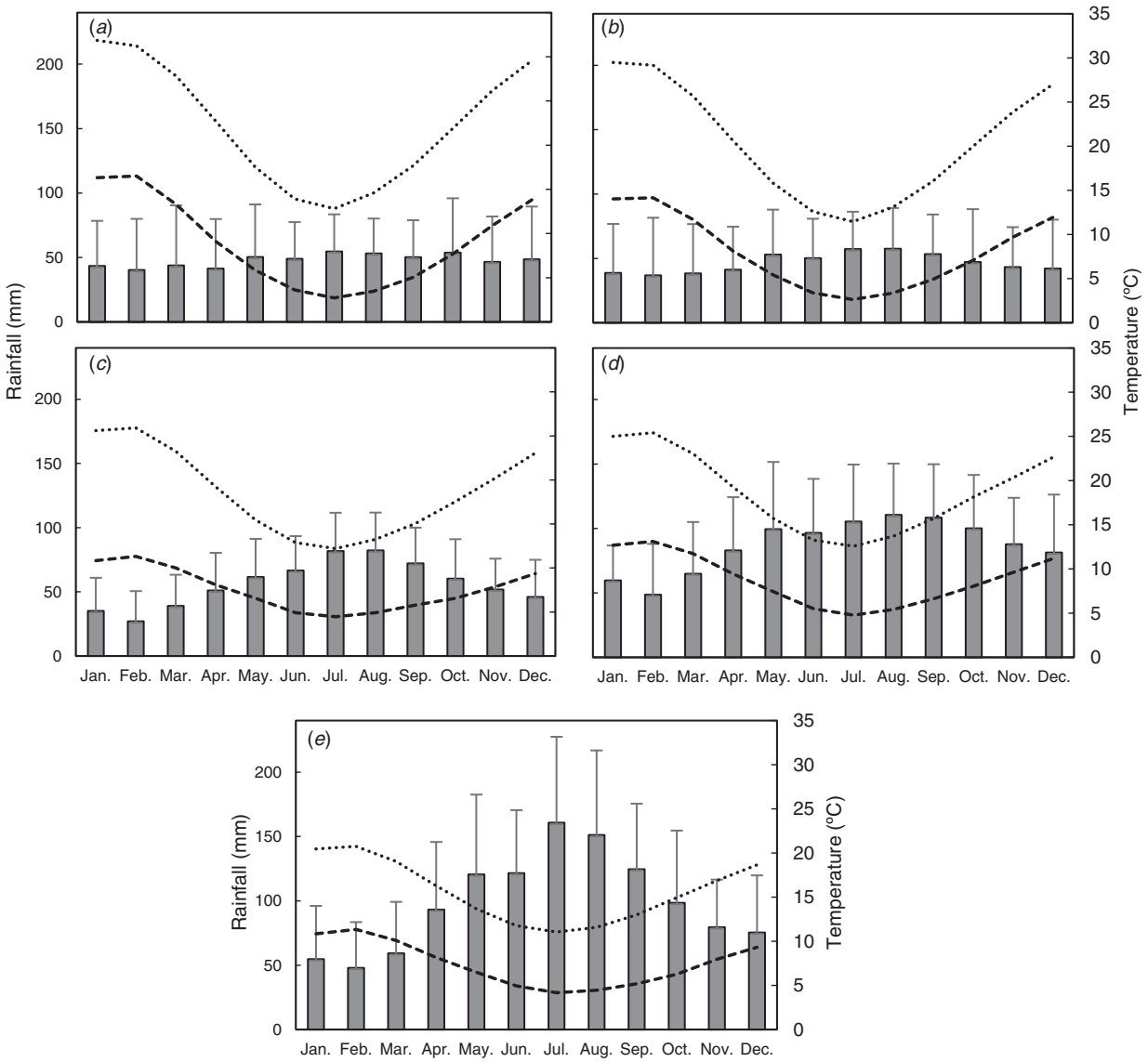

Fig. 1. Climate summary with average rainfall (grey bars) on the primary *y*-axis, and average maximum (dotted line) and minimum (dashed line) temperatures on the secondary *y*-axis in each month at (*a*) Wagga Wagga, (*b*) Dookie, (*c*) Hamilton, (*d*) Ellinbank and (*e*) Elliott during 1960–2015. Capped lines show the variation in rainfall as one-sided standard deviation.

Wagga. The Wagga Wagga site also used annual ryegrass (*Lolium rigidum* Gaud.), and involved the presence or absence of native C_4 grasses.

Daily weather data including daily rainfall (mm), minimum and maximum temperature (°C), solar radiation (MJ/m^2) and evaporation (mm) for each site was obtained from the SILO database service (Jeffrey *et al*. 2001). Atmospheric CO_2 data, measured at Cape Grim, Tasmania, baseline air pollution station (from 300 ppm in 1960 to 398 ppm in 2015) were used in the climate file to account for gradual increase in atmospheric CO_2 in the historical period. Simulations in DairyMod were conducted as a cut-trial where the pasture in the paddock (1 ha) was harvested on the last day of each month to a residual mass of 1.4 t DM/ha. The pasture was not irrigated, and growth was simulated under non-limiting soil-nutrient conditions so that variation in pasture growth due to climate variability could be characterised. Annual pasture yield (t DM/ha.year) was computed for each year by using simulated daily net herbage accumulation rates (kg DM/ha.day).

Pasture production and variability

Annual pasture yield was simulated at each site for the period 1960–2015 and analysed by using a linear regression model to detect any significant yield trends. Ten-year rolling-average annual pasture yields and the 10-year rolling-average coefficients of variation (CV%) were plotted to identify long-term yield trends and associated variability. Mean seasonal pasture growth rates (summer, autumn, winter and spring) (kg DM/ha.day) were calculated by dividing the seasonal net positive growth rate by the number of days in each season.

In order to investigate whether seasonal pasture yields have changed over time, the simulation period was divided into four equal 14-year periods (1960–73, 1974–87, 1988–2001 and 2002–15), and seasonal yields of each 14-year period were analysed at each site by using one-way analysis of variance (ANOVA), taking seasonal yields as the response variable and four time periods as the factor. The variability of seasonal growth rates at each site was assessed by using the median and differences of interquartile range (75th percentile–25th percentile).

In addition to the analysis of individual sites, simulated yields and variability (CV%) across the sites were analysed to determine whether they have changed over time at the regional scale. One-way ANOVA was performed (for the SE Australian region) taking annual or seasonal yields or CV% across sites as the response variable and time (four 14-year periods) as the factor.

Climate anomalies and growth-limiting factors

Anomalies of average rainfall and average maximum temperatures from the historical mean (1960–2015) were calculated for each month at 14-year periods separately to account for seasonal pasture production patterns (Fig. 2).

Growth-limiting factors for temperature (GLF_T) and water (GLF_W) obtained from DairyMod were analysed consisting of the same 14-year periods to identify the variations in abiotic stresses over time. GLFs are empirical functions used in DairyMod to account for the growth limitation due to moisture stress and temperatures above and below the optimum levels (Johnson 2008). GLF_W on each day was extracted from the DairyMod export file. GLF_T was calculated manually by using the following equations:

$$\text{GLF\_T} = \frac{fp(T)}{fp(Topt)}$$

where fp is the temperature response function in the leaf photosynthesis response, and can be calculated as:

$$fp = \begin{cases} \dfrac{(T - Tmn)^q (Tmx - T)}{(20 - Tmn)^q (Tmx - 20)}, & Tmn \le T \le Tmx; \\ 0, \text{otherwise} \end{cases}$$

$$Tmx = Topt + \frac{(Topt - Tmn)}{q}$$

where T is the mean temperature of any given day; Tmn, $Topt$ and Tmx are the minimum, optimum and maximum temperatures for photosynthesis, respectively; and q is the curvature coefficient, which is 2 by default for both perennial ryegrass and phalaris.

High-temperature stress coefficient (ξT, *high*) was also calculated for situations when the daily maximum temperature exceeds the critical temperature above which high temperature stress will occur (*Tmx, low*) or is less than the critical temperature

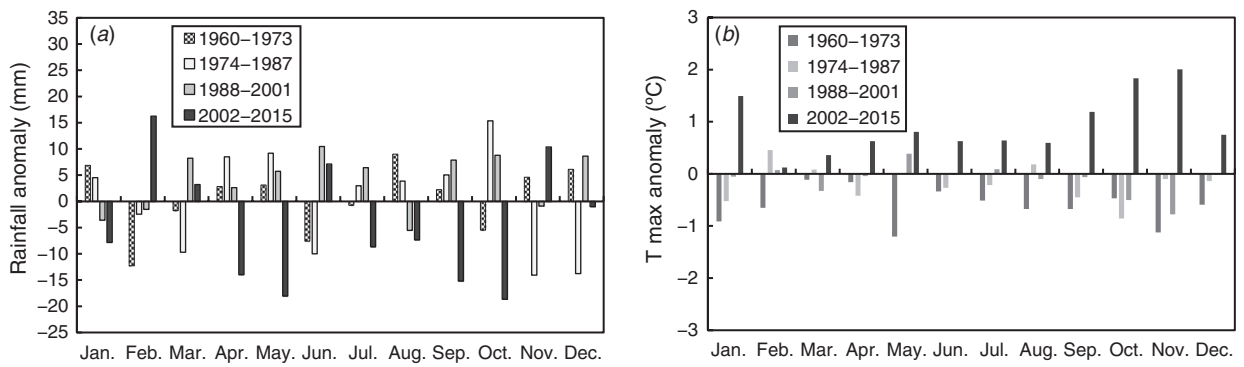

Fig. 2. Average anomaly of (*a*) monthly rainfall and (*b*) monthly maximum temperature during four periods (1960–73, 1974–87, 1988–2001, 2002–15) at Wagga Wagga compared with the long-term (1960–2015) mean rainfall and maximum temperature.

at which high-temperature stress is maximum (*Tmx, high*) (see Table 2):

$$\xi T, high, i = \begin{cases} \dfrac{Tmx, high - Tmx}{Tmx, high - Tmx, low}, & Tmx < Tmx, high \\ 0, & Tmx \geq Tmx, high \end{cases}$$

When the high-temperature stress function is implemented, the model employs the lowest value from GLF_temperature and high-temperature stress coefficient to calculate the daily gross photosynthesis rate. Therefore, the lowest value from these two factors was used as GLF_T in each day for the analysis. GLF_T values on days with mean temperature above optimum temperature (20°C for perennial-ryegrass-based pasture and 23°C for phalaris-based pasture) were used only to account for heat stress. All of the biophysical parameters used for calculations and model simulations for each pasture species are given in Table 2.

Both GLF_water and GLF_temperature are scaler factors ranging from 0 to 1, where 0 denotes full stress and 1 denotes no stress. Number of days with GLF_W <0.7 and GLF_T <0.7 during the autumn and spring seasons were analysed consisting of the same 14-year periods at each site, using one-way ANOVA, to investigate whether number of drought-stress and heat-stress days have increased over time.

Cumulative spring and summer soil moisture deficit

The CSSSMD was computed by subtracting PET (Allen *et al.* 1998) during spring and summer from the accumulated rainfall during the same period (Poirier *et al.* 2012). Box plot distributions of CSSSMD over 1960–2015 were compiled at each location, consisting of the same four periods used for previous analyses (1960–73, 1974–87, 1988–2001, 2002–15). One-way ANOVA was performed at each site to investigate any mean differences between the four periods. All statistical analyses were performed using Minitab statistical software version 17 (Minitab, State College, PA, USA).

Results

Trends in climate anomalies

Rainfall anomalies indicated a major decline in both autumn (April–May) and spring (September–October), with 18 mm less rainfall received in both May and October in the 2002–15 period at Wagga Wagga (Fig. 2). A similar trend in spring rainfall anomalies was seen at other sites, and an autumn rainfall reduction was prominent at the Dookie and Ellinbank sites (data not shown). Temperature changes also showed an increasing trend during the same period, with the greatest warming observed during October–November; at Wagga Wagga, this was nearly 2°C.

Individual site analysis

Annual and seasonal pasture production and variability

Time-series plots for annual pasture production and its 10-year rolling averages and associated variability (CV%) are presented for each site in Fig. 3. Mean annual pasture yields over 1960–2015 ranged from the highest at Elliott (13 t DM/ha.year) to the lowest at Wagga Wagga with native C_4 grasses (9 t DM/ha.year). Annual pasture yields, although highly variable, displayed a slight increasing trend ($P < 0.05$) at Elliott (50 kg DM/ha.year) and at Ellinbank (40 kg DM/ha.year), but no significant trend was observed at other sites. Ten-year rolling average CV% values showed an increasing trend at Wagga Wagga both with and without C_4 grasses, and at Dookie and Elliott ($P < 0.05$).

High-rainfall sites such as Ellinbank and Elliott exhibited a longer growing season than medium-rainfall sites, with considerable summer pasture production (10–20 kg DM/ha.day). At medium-rainfall sites such as Wagga Wagga and Dookie, summer is generally less productive, with production closer to zero in some years (Fig. 4). However, when C_4 grasses were included, increased summer production was predicted at Wagga Wagga (5–10 kg DM/ha.day), whereas the subsequent winter production was again low.

Analysis of seasonal pasture production by 14-year periods showed that mean pasture growth rates in winter have increased steadily from 1960 to 2015 ($P < 0.05$) at the high-rainfall sites, Ellinbank and Elliott (Fig. 4*e*, *f*). Spring pasture growth rates decreased by ~50% ($P < 0.05$) at Wagga Wagga (both with and without C_4 grasses) in the 2002–15 period compared with the periods before. Although not significant ($P > 0.05$), Dookie and Hamilton sites also showed a reduction in mean pasture growth

Table 2. Key model parameters used in DairyMod model to simulate perennial ryegrass, phalaris, subterranean clover, white clover, annual ryegrass and native C_4 grass

Recovery function of pasture species following a high or low temperature stress is calculated by DairyMod as T-sum. For perennial ryegrass, T-sum for high-temperature stress recovery is 50; this means that when the daily values of 25-Tmean (daily accumulation of heat units) following heat stress reach 50, perennial ryegrass will fully recover from heat stress. For example, if the mean daily temperature of the day following the heat stress is 20°C, the number of heat units accumulated on that day is 5; perennial ryegrass will completely recover from heat stress after 10 days with mean temperature of 20°C

Biophysical parameter	Perennial ryegrass	Phalaris	Subterranean clover	White clover	Annual ryegrass	Native C_4 grass
Minimum temperature for photosynthesis (°C)	2	3	3	3	3	12
Optimum temperature for photosynthesis (°C)	20	23	23	23	23	35
High-temperature stress: onset (°C)	30	31	30	30	–	–
High-temperature stress: full (°C)	35	36	35	35	–	—
High-temperature stress recovery (T-sum)	50	200	50	50	–	–
Low-temperature stress: onset (°C)	–	–	–	–	–	7
Low-temperature stress: full (°C)	–	–	–	–	–	3
Low-temperature stress recovery (T-sum)	–	–	–	–	–	100
Maximum root depth (cm)	40	80	50	40	40	100
Depth of 50% root distribution (cm)	15	20	15	15	15	20

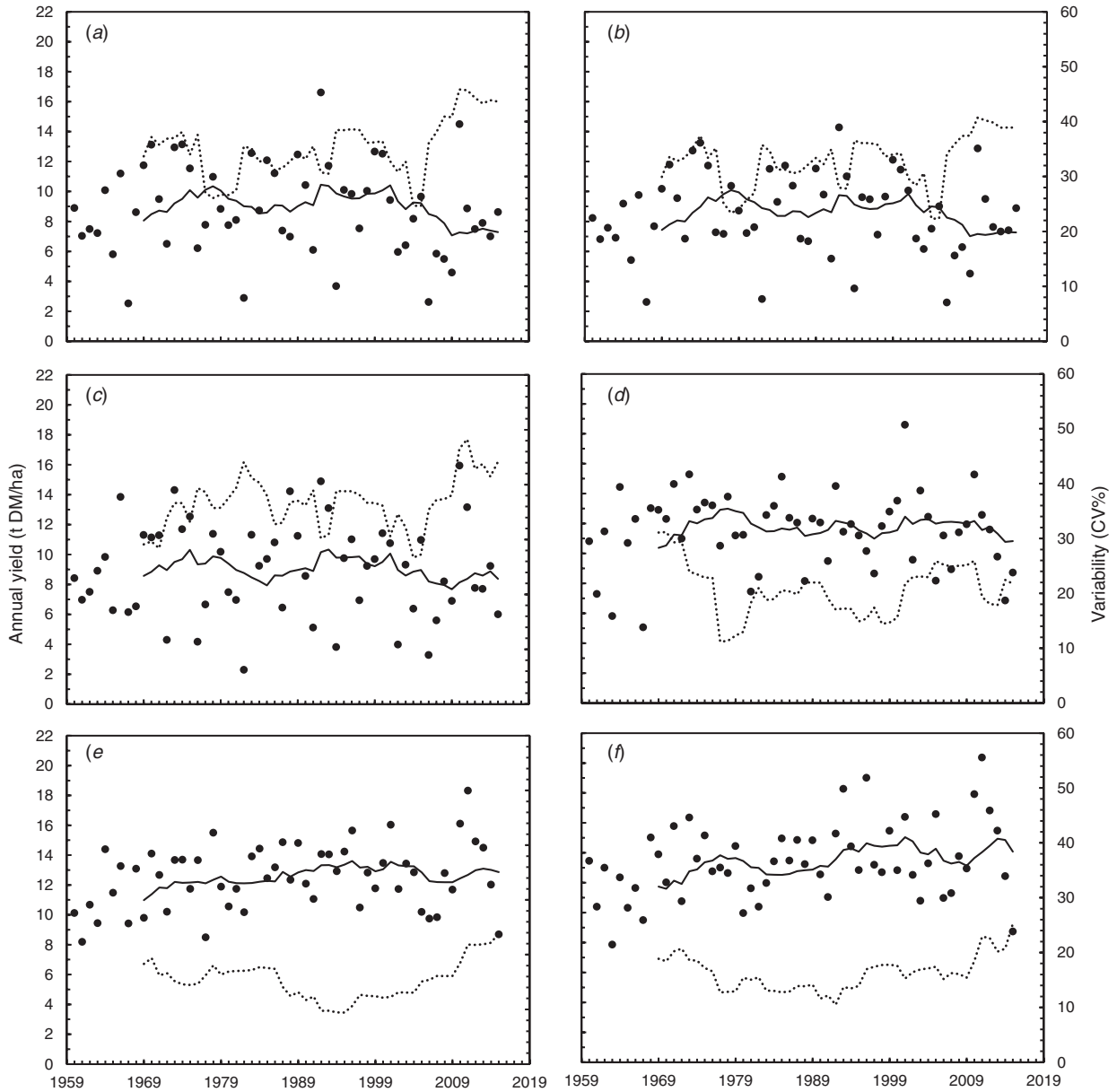

Fig. 3. Annual pasture production (t DM/ha, •), and its 10-year rolling average (solid line) and associated variability expressed as 10-year rolling-average coefficient of variation (CV%) (dotted line on secondary *y*-axis) from 1960 to 2015 at (*a*) Wagga Wagga without C_4 grasses, (*b*) Wagga Wagga with C_4 grasses, (*c*) Dookie, (*d*) Hamilton, (*e*) Ellinbank, and (*f*) Elliott.

rates in spring season, by 32% and 27%, respectively, during 2002–15 compared with 1988–2001.

Growth-limiting factors

Growth limitation due to water and temperature in the DairyMod model, shown in Fig. 5, followed a pattern similar to the observed climate anomalies across sites. At each site, the number of water-stress days (GLF_W <0.7) in spring was ~10 times higher than the number of heat-stress days (GLF_T <0.7). For example, at Wagga Wagga, there were ~60 water-stress days in spring in the 2002–15 period compared with 6 heat-stress days. There was a significant increase in the number of water-stress days at Wagga Wagga (by ~20 days) and heat-stress days at Wagga Wagga and Hamilton (by ~3 days) in the most recent 14-year period compared with periods before (Fig. 5).

Cumulative spring and summer soil moisture deficit

In general, soil moisture deficit was higher at the lower rainfall sites (~600 mm at Wagga Wagga and Dookie) and lower in the high-rainfall sites (~100 mm at Elliott and ~200 mm at Ellinbank) (Fig. 6). Although not significant ($P > 0.05$), there was an increase

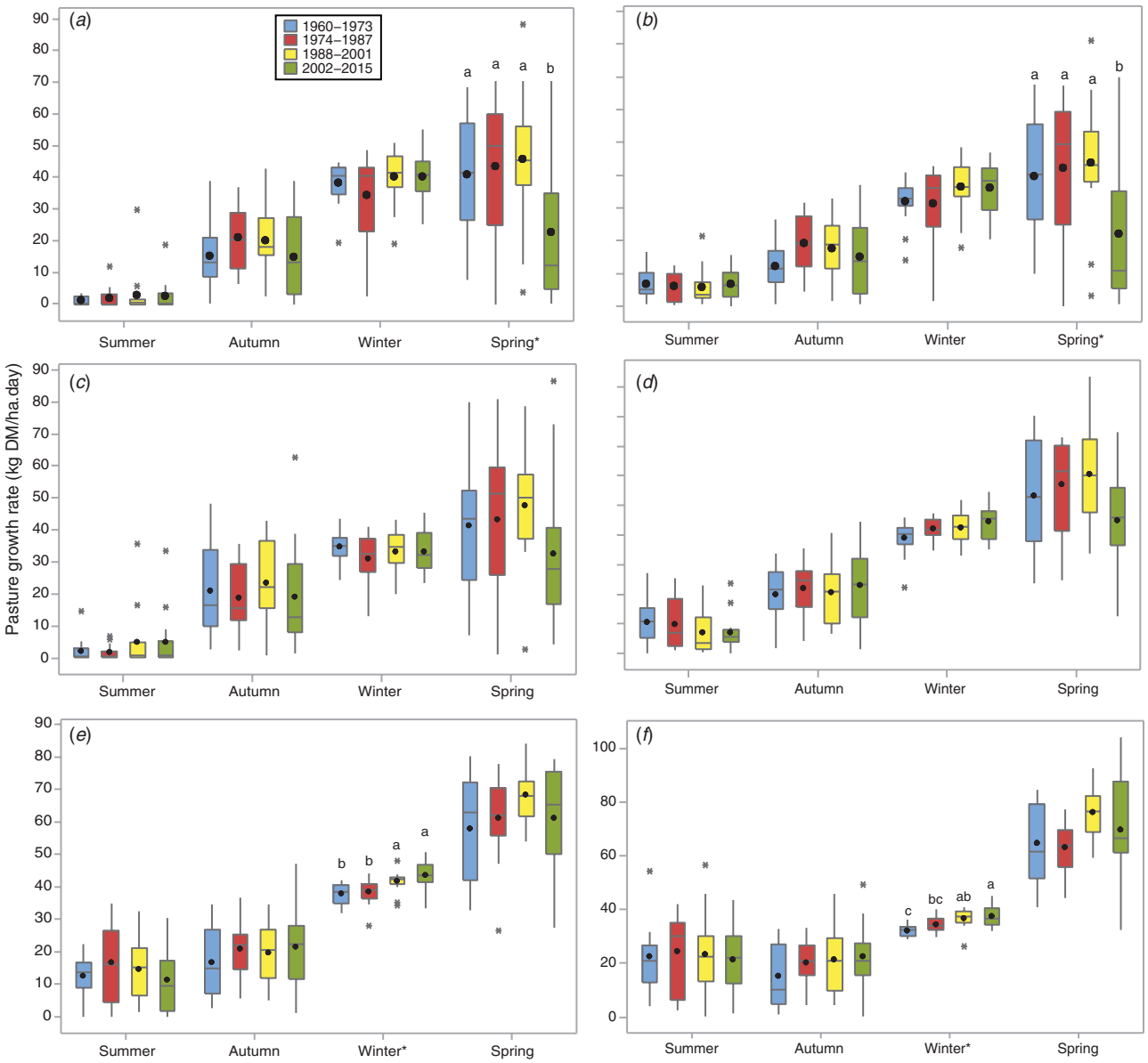

Fig. 4. Seasonal average pasture production (kg DM/ha.day) from 1960 to 2015 in 14-year time intervals at (*a*) Wagga Wagga without C_4 grasses, (*b*) Wagga Wagga with C_4 grasses, (*c*) Dookie, (*d*) Hamilton, (*e*) Ellinbank and (*f*) Elliott. Box plots for each season represent 25th, 50th (median) and 75th percentiles. The symbol (•) in the middle of the box is the mean pasture growth rate, with outlying symbols (*) representing values outside the 10th and 90th percentile. Seasons with significant results from ANOVA are followed by an asterisk (*) on the *x*-axis, and in these cases, time-period means with the same letter are not significantly different at $P = 0.05$.

in CSSSMD in the 2002–15 period at all sites compared with the periods before. For example, at Hamilton where perennial ryegrass is the major pasture species, mean CSSSMD increased from 350 mm in 1960–2001 to ~450 mm in 2002–15. Median CSSSMD at Hamilton was also closer to 450 mm, indicating that 50% of the years between 2002 and 2015 had soil moisture deficits >450 mm.

Regional analysis

Analysis of seasonal yields and their variability (CV%) across all five sites simulated are shown in Fig. 7. There was a significant reduction (26%) ($P < 0.001$) in the spring pasture growth rates across the SE Australian region in the most recent period simulated (2002–15), compared with 1988–2001 (Fig. 7*a*). By contrast, winter pasture growth rates steadily increased ($P = 0.001$) by ~10% compared with the start of the simulation period.

Analysis of seasonal variability using the CV% showed an increase ($P < 0.05$) in both autumn and spring variability across sites in the most recent 14-year period (Fig. 7*b*). For instance, the CV% in spring during 2002–15 had more than doubled (to 62%) compared with 1988–2001 (27%) across sites. This result is confirmed by increased interquartile ranges at some sites during

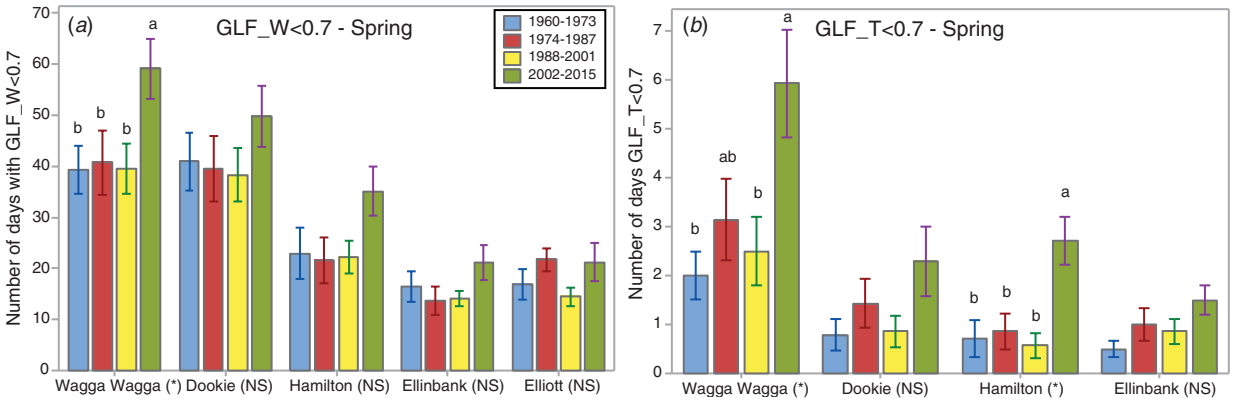

Fig. 5. Number of days with (*a*) GLF_W <0.7 and (*b*) GLF_T <0.7 during spring at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott sites during 1960–73, 1974–87, 1988–2001 and 2002–15. Means (n = 14) are provided with capped lines representing ± 1 standard error. Sites with significant differences of means between time periods are followed by an asterisk (*) on the x-axis (n.s., not significant); time-period means with the same letter are not significantly different at P = 0.05.

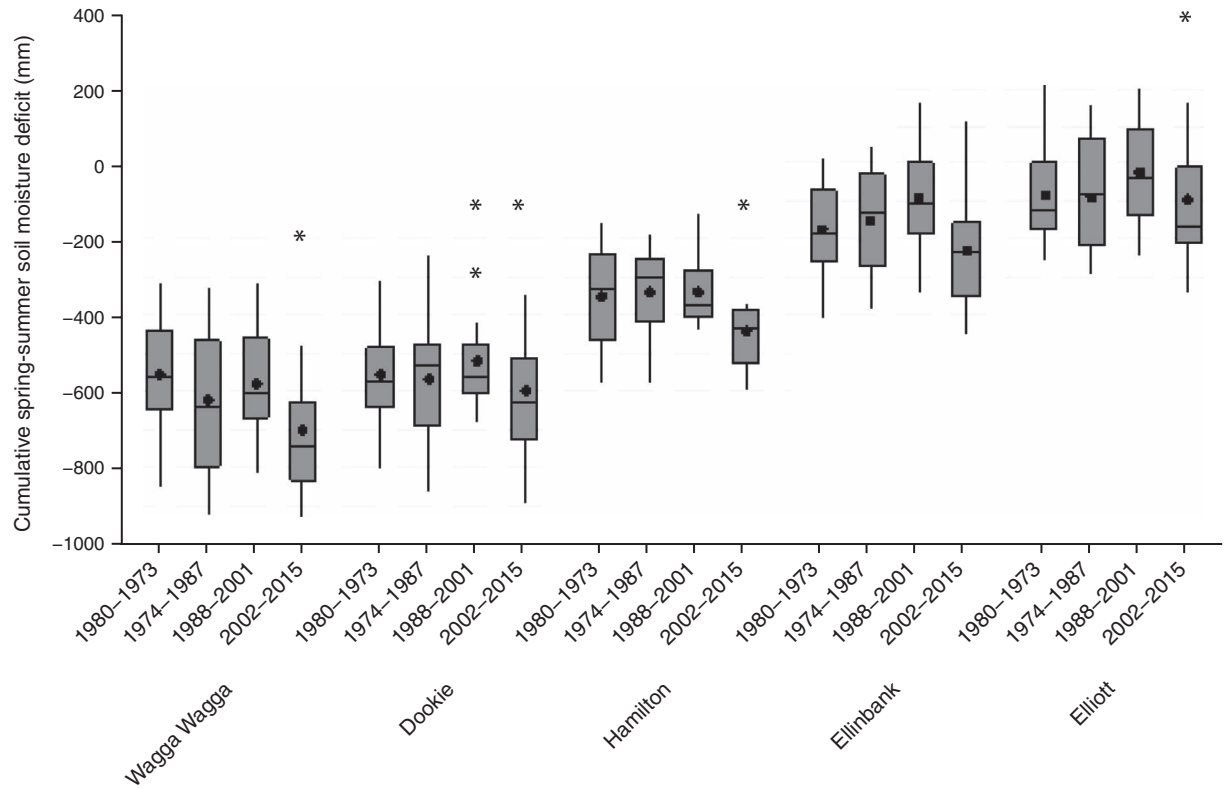

Fig. 6. Boxplots of cumulative spring and summer soil moisture deficit (CSSSMD) at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott from 1960 to 2015, displaying the change in variability for four time periods. The boxplots represent the 25th, 50th (median) and 75th percentiles; the filled symbol (•) represents the mean CSSSMD value; and outlying symbols (*) represent values outside the 10th and 90th percentile.

spring in the most recent 14-year period simulated (Fig. 4). At Ellinbank, the interquartile range in spring has increased from 10 kg DM/ha.day in 1988–2001 to 25 kg DM/ha.day in 2002–15. Similarly at Wagga Wagga, the interquartile range in spring has increased from 18 kg DM/ha.day in 1988–2001 to 31 kg DM/ha. day in 2002–15. In autumn, the interquartile range at Wagga Wagga has increased from 11 kg DM/ha.day in 1988–2001 to 25 kg DM/ha.day in 2002–15. The results indicate that increased variability and reduction in the mean and median pasture growth rates has occurred simultaneously in these seasons.

Discussion

Time-series plots of annual yields and the monthly pasture-growth boxplots showed that pasture growth patterns have changed during the past 56 years in SE Australia, with

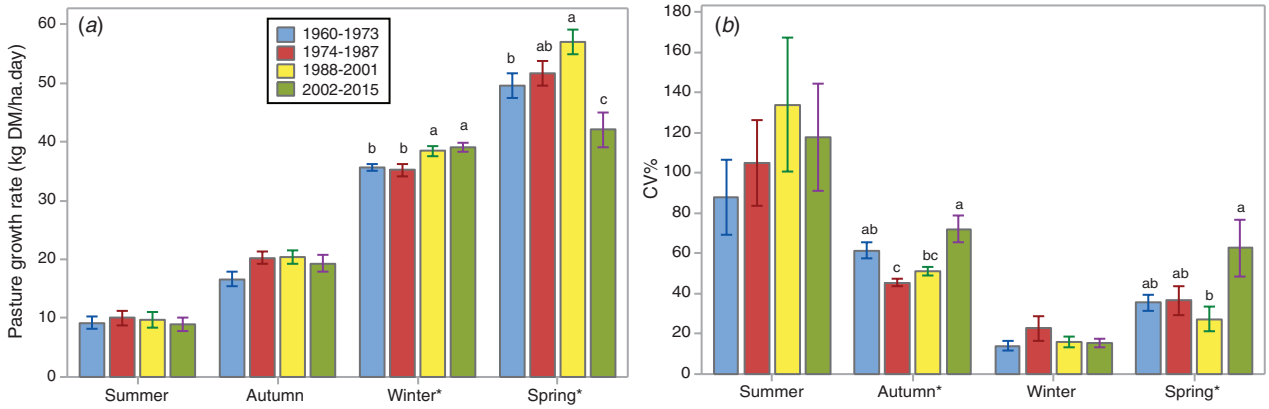

Fig. 7. Seasonal (*a*) pasture production and (*b*) pasture yield variability (CV%) from 1960 to 2015 in 14-year time intervals across all sites (Wagga Wagga without C_4 grasses, Wagga Wagga with C_4 grasses, Dookie, Hamilton, Ellinbank and Elliott). Means ($n = 6$) are presented with capped lines representing standard errors. Seasons with significant results from ANOVA are followed by an asterisk (*) on the *x*-axis, and in these cases, time-period means with the same letter are not significantly different at $P = 0.05$.

increased winter production at high-rainfall sites and decreased spring production at the medium-rainfall sites. Regional analysis conducted across all the sites simulated revealed that spring pasture yields have decreased significantly and year-to-year variability has increased in the autumn and spring seasons across SE Australia during the most recent period (2002–15). Increased frequency of days with heat and moisture stresses, along with increased CSSSMD, in the most recent period (2002–15) as a result of declining rainfall and increasing PET suggested an increase in abiotic stresses on pasture species. Although changes to the pasture growth patterns similar to those reported in this study have been suggested to occur as a result of warmer and drier future climate projections for 2030 (Cullen *et al*. 2009; Alcock *et al*. 2010; Moore and Ghahramani 2013), this analysis provides evidence that these changes are already occurring.

Contraction in the growing-season length in the 2002–15 period, most notably in spring (Fig. 7*a*), was a key finding in this study. This was mainly due to the reduction in growing-season rainfall across SE Australia. At Wagga Wagga, the rainfall reduction was ~31% in April and 36% in May during 2002–15, and this was greater than the rainfall reduction in those months during the Millennium Drought of 1996–2009, which was nearly 25% (Timbal 2009). Further, a 34% reduction in September rainfall at Wagga Wagga during 2002–15 may have accounted for the significant increase in the number of days with GLF_W <0.7 in spring during 2002–15 compared with the periods before (an increase of 20 days), and consequently a 50% reduction in mean pasture growth rates simulated in spring. Maximum temperatures also showed a positive anomaly during the late spring–early summer months across sites, with the largest temperature increase observed at Wagga Wagga (2°C in October–November during 2002–15). This was again evident in the model, with a significant increase in the number of heat-stress (GLF_T <0.7) days at Wagga Wagga and at Hamilton during the 2002–15 period.

One of the key extratropical modes of climate variability in southern Australia that contributes to this observed rainfall reduction is the STR associated with the Hadley circulation (Risbey *et al*. 2013). SE Australia is situated under the descending part of the Hadley cell, and the changes to Hadley circulation affect frontal rains, which are a main source of rainfall to SE Australia. High intensity of the STR and its more southerly position push the rain-bearing fronts further south, leading to decreased rainfall in SE Australia; however, the intensity has a more pronounced effect on rainfall than STR position (Risbey *et al*. 2013; Whan *et al*. 2014; Grose *et al*. 2015). The intensity of STR has increased significantly during the 20th Century and the early 21st Century (Timbal and Drosdowsky 2013) and this was found to be related to nearly two-thirds of the rainfall decline in SE Australia during the Millennium Drought (1997–2009) (Risbey *et al*. 2013; Timbal and Drosdowsky 2013; Chowdhury *et al*. 2015). Further, Coupled Model Intercomparison Project phase 5 (CMIP5) models have projected that the intensity of STR will strengthen further and move poleward under global warming (Grose *et al*. 2015). This may suggest that growing-season dryness could intensify further with the future warming trend.

Other processes may have affected the recent drying trend and variability. Negative Indian Ocean Dipole (IOD) events bring above-average rainfall to SE Australia during the winter–spring months (Gallant 2012; Westra *et al*. 2016). However, analysis of DMI (dipole mode index) data (periodically updated data, source: https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Data/dmi.long.data) (Saji 2003) during winter–spring months using the method of Jarvis *et al*. (2018) showed no negative IOD years from 2002 to 2015 (Perera *et al*. 2018). Further, seven positive IOD phases occurred during the same period (Perera *et al*. 2018), which is consistent with the increased number of water-stress days reported. Moreover, from 2006 to 2008, spring contribution to the total rainfall decline across the whole of SE Australia was reported as 43% (Timbal 2009). Eventually, consecutive 2010–11 and 2011–12 La Niña events brought heavy rainfall to the south-eastern region, contributing to increased rainfall variability in the region (CSIRO and BOM 2015). These rainfall declines in the recent period are very similar to future climate projections based on the

IPCC-AR4 model and other available emission scenarios by 2030 (Timbal 2009).

Analysis of average seasonal pasture growth rates during different time periods revealed increased winter growth rates at the high-rainfall sites (Ellinbank and Elliott; Figs 4 and 7*a*). The growth of temperate pastures is usually limited by low winter temperatures (McKenzie *et al*. 1999). Analysis of temperature anomalies in the historical climate showed that winter temperature has increased by ~0.6°C at Wagga Wagga, by 0.35°C at Hamilton and by 0.45°C at Ellinbank during June–August in the recent time window (2002–15) compared with the long-term average (1960–2015) (Fig. 2, only Wagga Wagga is provided). Although rainfall in winter months has declined at these sites, there would still be adequate soil moisture to support the increasing pasture growth trend at the high-rainfall sites.

Failed spring seasons with an early finish of rainfall not only affect pasture growth but may also affect pasture survival. Extreme summer droughts in combination with high summer temperatures increase evaporative demand while there is no soil-water supply. This may cause death of laminae and stem tissues (Salisbury and Ross 1978; Volaire and Lelièvre 2001), affecting subsequent pasture regrowth and the re-establishment of pasture mixtures in highly variable climates (Silcock 1993). Spring–summer droughts have been identified as a main factor associated with persistence of perennial pasture species (Nie *et al*. 2004*b*; Poirier *et al*. 2012), and research in the northern hemisphere showed increased tiller mortality with higher CSSSMD (Poirier *et al*. 2012). In the present study, the increased number of days with heat and drought stress (GLF_W and GLF_T <0.7) in spring in the most recent period (2002–15) might have challenged the persistence of temperate perennial pasture species in SE Australia. A previous modelling study has identified that deep-rooting and heat-tolerant traits would be suitable adaptation strategies for perennial ryegrass under warmer and drier future climate scenarios in SE Australia (Cullen *et al*. 2014). The warming and drying trends observed in the recent period in this study suggest that those adaptation strategies should be prioritised in the future adaptation research in order to sustain pasture production in the future.

Taken together, the changing pasture growth patterns and increased risk of reduced pasture persistence highlights the need for livestock-production systems in SE Australia to adapt to a changing climate. These adaptation strategies may involve long-term decisions such as adopting a more conservative stocking rate, animal breeding for heat tolerance, and changing calving and lambing times to cope with the contraction of growing-season length (Ash *et al*. 2007; Chapman *et al*. 2013). In a simulation study conducted with future climate projections, Ghahramani and Moore (2013) found that increasing soil fertility and adding summer-active species such as lucerne to the pasture base would be the best adaptation options to the anticipated drying trends and seasonal shifts in SE Australia. However, to manage high year-to-year pasture yield variability, tactical and operational level decisions are important with respect to balancing the feed supply and demand in the short term (Chapman *et al*. 2013). They are relatively easy to implement but need frequent monitoring. Such adaptations include early destocking before animals decline in condition, application of fertiliser to maximise benefit from the available soil moisture, fodder conservation or purchasing of supplementary feed (Austen *et al*. 2002). Seasonal climate forecast can be highly beneficial in managing a variable climate (Ash *et al*. 2007), but lack of accuracy and insufficient lead-time prevent their widespread use (Hayman *et al*. 2010).

The simulated changes in the pasture growth patterns in this study reflect the changes in recent climate and are consistent with the results of other crop responses in the region and in many other areas of the world. For instance, Hochman *et al*. (2017) showed that water-limited yield reduction in Australian wheat was 27% from 1990 to 2015 and came to a plateau even with the genetic improvement. Brisson *et al*. (2010) attributed the declining grain yields in France partially to climate change. In the world's major growing regions, temperature has increased by over one standard deviation of the historical year-to-year variation from 1980 to 2008, and that has accounted for a 5.5% wheat yield decline (Lobell *et al*. 2011). These studies suggest that the climate-related impacts have become a major challenge in the recent past, not only in Australia but the major agricultural regions of the world.

Conclusion

The modelled outcomes of pasture growth rates show clear evidence of changing seasonal patterns with increased winter growth rates, shorter spring seasons and increased year-to-year variability in autumn and spring seasons across SE Australia in the most recent period (2002–15). Increased CSSSMD and number of days with heat stress (GLF_T <0.7) and drought stress (GLF_W <0.7) observed during the last two decades across SE Australia highlight that the present grazing systems would not be sustainable in the near future if climate variability persists at the current magnitude. Adaptation options would include incorporation of deep-rooted pasture species to the system so that they can reach the moisture in the deeper soil layers. Because the observed seasonal rainfall changes and subsequent pasture growth response during the recent period reported in this study align with future climate-change projections, suitable adaptation practices will be needed urgently to sustain a profitable grazing industry in SE Australia.

Conflicts of interest

The authors declare no conflicts of interest.

Funding

This research did not receive any specific funding.

Acknowledgements

The authors acknowledge the kind support of the Associate Professor Graham Hepworth, Statistical Consultant Centre, The University of Melbourne, for providing statistical advice.

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Handling Editor: Andrew Fletcher

CHAPTER 4. Changing annual and seasonal patterns of pasture production in south eastern Australia; Influence of climate variability and extreme events

Abstract

Previous studies have shown that extreme climate events such as heat waves, droughts, frost and intense precipitation have increased in the recent decades in combination with warming and reduced rainfall in south eastern (SE) Australia. Although these changes are known to impact on pasture production, their relative influence on seasonal and inter annual variation in pasture production is not well understood. The Chapter 3 results highlighted the changes to the seasonal patterns of pasture growth with increased variability in late spring and early summer during the recent decades. In this study, an approach was developed to identify the climate factors that influence this variability using a matrix of climate indices with general and extreme climate variables. General climate indices were, annual and seasonal rainfall, annual and seasonal averages of daily maximum (Tmax) and minimum (Tmin) temperatures and atmospheric CO_2 concentration. Extreme climate indices were, the number of 'wet' and 'dry' months based on the standardised precipitation index (SPI), number of hot days (days with Tmax ≥ 30 °C), length of hot period and number of frost days (days with Tmin < 2 °C) during winter and spring. Simulated annual and seasonal pasture yields at five sites (Wagga Wagga in southern NSW, Dookie in northern Victoria, Hamilton in south western Victoria, Ellinbank in Gippsland and Elliott in Tasmania) using DairyMod biophysical software from 1960-2015, were related to the climate indices using partial least squares (PLS) regression model fitting procedure. Both general and extreme climate indices explained more annual yield variability in medium rainfall sites (Wagga Wagga R^2-89%) than in high rainfall sites (Elliott R^2-70%). Spring rainfall and CO_2 concentrations were strong positive factors at all the sites but increasing maximum spring temperatures decreased pasture production except in the coolest site at Elliott. Among extreme indices, dry month categories translated into lower pasture yields when they occurred in the winter-spring months. However, wet month categories had both positive and negative impacts dependent

on the time of the year that they occurred. Number of frost days in spring and number of hot days in autumn and summer months both suppressed the pasture production across the sites. However, Wagga Wagga produced high summer pasture yields when the C4 grass was incorporated and responded more to the summer rains and moderately wet months compared to a pasture with only C3 species. This analysis demonstrates the importance of including extreme climate events in any analysis of climate change impacts on agricultural production systems and highlight the importance of including projections for changes in climate extremes in the future climate projections to improve the yield predictions.

Key words: general climate, extreme indices, predictive models, simulation modelling, DairyMod

4.1. Introduction

In recent decades, the seasonal patterns of pasture production in SE Australia have changed with increased pasture production in winter, decreased production in spring and increased year to year variability (CV%) in the autumn and spring periods (Perera *et al.* 2020). These predicted changes in pasture growth rates reflect observed climatic changes in the region including rising temperatures, declining rainfall (particularly in late spring season but also in autumn), and increasing carbon dioxide concentration (CSIRO and BOM 2015). These climate changes have also been accompanied by changes in the frequency and intensity of extreme climate events, such as heatwaves, frost and intense rainfall (CSIRO and BOM 2015; Crimp *et al.* 2016a). It is almost certain that climate variability and extremes will increase with increasing global temperature (IPCC 2012b). Despite this, the particular importance of climate extremes in agricultural systems has not been studied in detail.

In a statistical sense, extreme climate events are the values that are far from the mean of the typical probability distribution (generally outside the 10% to 90% percentiles) of a climate variable such as daily maximum temperature (IPCC 2012b). These are very rare events that occur may be once in 10 or 100 years. However, if the temperature distribution at a location shifts towards a warmer climate, it will certainly lead the initially rare hot extremes to occur more frequently (Mearns *et al.* 1984;

Smith 2011). Extremes can also be explained using the changes in the variance or the symmetry of a distribution, but in Australia, observed extremes were more linked to the changes in the mean rather than to the changes in the variation or symmetry (Alexander *et al.* 2007). In ecological studies, extreme climate events are defined with respect to both driver and the response of the system as any statistically rare climate episode that alters ecosystem structure and/or function which is way outside the effects of natural variability (Smith 2011). Extremes of such magnitude may result in rapid decline of a particular species or population of a system (Dix and Weaver 1968; Breshears *et al.* 2005; Bigler *et al.* 2006), produce long lasting changes in structure and/or functions in a community (MacGillivray and Grime 1995; White *et al.* 2000; Mueller *et al.* 2005), or shift the ecosystem boundaries of species (Allen and Breshears 1998). These extremes often can lead into significant and much harmful damage than the average climate change to the agricultural and natural landscapes worldwide.

Analysis of the past climatic records of Australia have shown that extreme climate events have increased in number and magnitude during the recent decades (CSIRO and BOM 2015). Heat wave frequency and duration has increased in Australia since 1950 (Alexander and Arblaster 2009) with several high impact heat waves reported from the start of this century (Perkins Kirkpatrick *et al.* 2016). In 2009, Victoria experienced an extreme heat wave followed by a devastating bush fire called "Black Saturday" (NCC 2009). In summer 2013, a large area of Australian continent experienced another unprecedented heat wave, with new spatially and temporally higher maximum temperature records (BOM 2013). Despite the high temperature changes over SE Australia, Crimp *et al.* (2016a) reported increasing frost occurrences in some months and increased frost period by 26 days across SE Australia. Drought severity and duration have also increased particularly since 1990's with the experiencing drying trend (Murphy and Timbal 2008; Timbal 2009; Gallant and Karoly 2010). The prolonged dry period from 1996 to 2010 (Millennium drought) was the driest period for Victoria surpassing the previous protracted droughts in the climate records (Timbal 2009). This caused significant economic losses in agriculture (CSIRO 2010) due to well below average rainfall received during this period (NCC 2008) and restricted water allocations in the Murray Darling Basin

(Chapman *et al.* 2012a). Temperature and evaporation rates during droughts were also increasing in SE Australia suggesting that droughts have become hotter than the previous droughts in historical records (Cai *et al.* 2014). Heavy rainfall events were also prominent over Australia since 1970s (CSIRO and BOM 2015) with 2010 and 2011 being the wettest two years for the whole of Australia and 2011 recording as the wettest January for Victoria (NCC 2012).

The impacts of changes in climate extremes on agricultural production have been suggested to be over and above the changes to average climate variables alone (Thornton *et al.* 2014). For example, Katz and Brown (1992) found that relative sensitivity of flowering (Tasselling) stage of corn crop increased exponentially to the changes of standard deviation of temperature, while it was increased linearly with the increasing mean temperature. In Tanzania, Rowhani *et al.* (2011) reported that the yield reductions of maize, sorghum and rice were underestimated by 3.6%, 7.2% and 28.6%, respectively, when only the projected mean climate change was considered, and variability was ignored. Similarly, greater downside impacts on pasture growth rates, pasture utilization, milk production and farm profitability were simulated in three SE Australian dairy sites, when frequent heat waves, extreme precipitation and severe droughts were incorporated into the projected future climate (Harrison *et al.* 2016). These findings suggest that including climate variability and extreme events into climate scenarios is important to realistically estimate impacts of future climates on agricultural systems.

A variety of drought and heat stress indices exist (Keyantash *et al.* 2002; Pereira *et al.* 2009; De Boeck *et al.* 2010; Mishra and Singh 2010; Nairn and Fawcett 2015), but most of them are used to characterise the climate in terms of drought and heat stress, but relatively few studies have related these indices to agricultural production. (Popova *et al.* 2014). Despite this, SPI has been a useful index to study vulnerability of agricultural systems to drought (Potop *et al.* 2010; Popova *et al.* 2014) and climate risk assessments (Holz *et al.* 2010; Fraser *et al.* 2013; Hennessy *et al.* 2016) because of its calculation based on standardised rainfall data and probabilistic interpretation (Guttman 1998). SPI is defined as the number of standard deviations above or below the mean rainfall when computed based on the normalised cumulative rainfall distribution (McKee *et al.* 1993). SPI can be calculated

at different time steps but shorter time steps (1or 2 monthly time steps) are usually used to identify short term agricultural droughts that may impact crop water use. Hennessy *et al.* (2016) used SPI to analyse future climate scenarios for Australian dairy regions and projected that almost all the main dairy regions will experience more percentage of time in a year in drought (SPI<-1) during 2030-2049 period compared to 1986-2005. This suggests possible implications of feed management, stocking rate decisions and heat and drought stress on pasture systems (Holz *et al.* 2010).

Even though climate variability and extremes are important, their explicit use in climate change studies is lagging behind. While several studies have discussed about the non-linear threshold responses of pasture species to the simulated heat waves and droughts under controlled environmental conditions (Jiang and Huang 2001; Milbau *et al.* 2005; Poirier *et al.* 2012; Langworthy *et al.* 2015; Langworthy *et al.* 2018), few studies have been conducted so far to reveal the impacts of these events on long term pasture production analysis in SE Australia (Harrison *et al.* 2016). Therefore, the objective of this research is to study the effects of both average climate variables and extreme events on historical pasture growth patterns in SE Australia.

4.2. Material and methods

4.2.1. Site selection and modelling pasture growth

Site details including location coordinates, average climatic conditions, soil types, pasture composition and the model parameters used in this analysis were provided in Perera *et al.* (2020) and so only a brief description of simulation modelling approach is provided here. Pasture growth rates were simulated from 1960-2015 using DairyMod biophysical software version 5.6.5 (Johnson 2016) at five livestock production sites in SE Australia. The sites ranged from medium rainfall from Wagga Wagga in southern NSW and Dookie in Northern Victoria to high rainfall in Hamilton in south western Victoria, Ellinbank in Gippsland and Elliott in Tasmania. Perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) pasture mix was simulated at Ellinbank and Elliott while perennial ryegrass and subterranean clover (*Trifolium subterraneum* L.) pastures were used at Hamilton. In the medium rainfall sites at Dookie, phalaris (*Phalaris aquatica* L.) and subterranean

clover was the main pasture mix and in addition to that, annual ryegrass (*Lolium rigidum* L.) was simulated at Wagga Wagga with and without C4 native grasses. Pasture growth rates were simulated as a cut trial, harvesting to a residual level of 1.4 t/ha at the end of each month. Simulations were managed without irrigation and non-limiting nutrients to identify the pasture yield variation due to climate variability. The measured CO_2 levels (at Cape Grim, Tasmania) were also used with daily weather data (from SILO database) (Jeffrey *et al.* 2001). The range of pasture yields (annual and seasonal) simulated at each location over the historical period are shown in Figure 1.

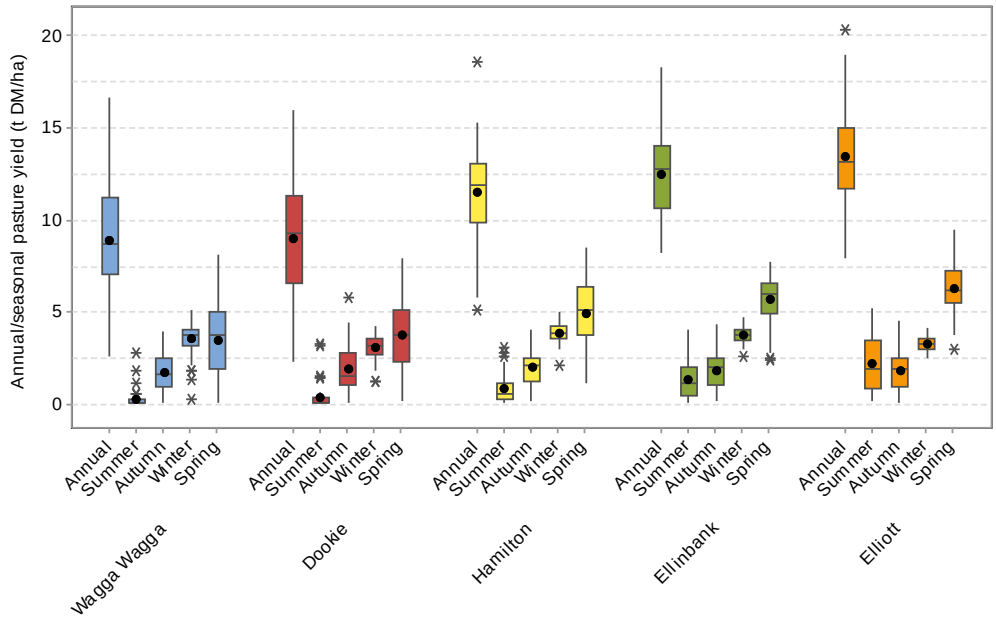

Figure 1. Range of annual and seasonal pasture yields (t DM/ha) at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott from 1960-2015. Box plots display 10th, 25th 50th, 75th, and 90th percentile values with mean (solid symbol) and median (horizontal line) values represented inside the interquartile range box.

4.2.2. Development of climate indices

To explain year to year pasture yield variability caused by the climate, two groups of climate indices (termed “general” and “extreme”) were developed for each site and each year using the historical climate data from 1960-2015. General climate indices are the annual and seasonal averages of climate in each site while the extreme indices were designed to reflect extreme wet and dry and hot and cold

spells. General climate indices were the total annual and seasonal rainfalls, annual average of daily maximum and minimum temperatures, seasonal average of daily maximum and minimum temperatures and atmospheric CO2 concentrations. Extreme climate indices were the number of total wet/dry months, number of hot days, hot period length and number of winter and spring frost days. Number of total wet and dry months were calculated using the standardised precipitation index, one month time scale (SPI-1) and categorised into either dry or wet severity classes based on the method used by McKee et al. (1993) and given in Table 1. High temperature extremes such as number of hot days per year or season and the hot period length were calculated using a threshold value of 30 °C since the growth of perennial ryegrass began to decline at 30 °C (Mitchell 1956). The definitions of the extreme climate indices used in this study are provided in Table 1 and a summary of general and extreme climate indices calculated for each site is shown in Table 2. Climate indices like rainfall, temperature, hot days, hot period length and frost occurrences contrast across sites from north to south (Table 2).

Table 1. Definitions of extreme climate indices related to rainfall (using SPI drought/wet severity classes) and temperature

Extreme climate index	Unit	Definition
Moderately wet/dry months	Number of months	Number of months in a year or season with SPI values between 1 to 1.49 / -1 to -1.49 respectively
Severely wet/dry months	Number of months	Number of months in a year or season with SPI values between 1.5 to 1.99 / -1.5 and -1.99 respectively
Extremely wet/dry months	Number of months	Number of months in a year or season with SPI values 2 and above / -2 and below respectively
Hot days	Days	Number of days in a year or a season with daily maximum temperature equal to or above 30 °C
Hot period length	Days	Length of the period between the first and the last hot day. Computed starting from January 1st to the last hot day until winter and added the rest of the hot period from the mid spring to the December 31st in the same year.
Frost days	Days	Number of days in a year or a season with daily minimum temperatures equal to or below 2 °C

Table 2. General and extreme climate indices at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott calculated from 1960-2015. Rows contain mean annual and seasonal (summer, autumn winter and spring) Figures with the range given in the parenthesis. N/A-not applicable

		General climate indices			Extreme climate indices								
	Site	**Total rainfall (mm)**	**Average maximum temperature (°C)**	**Average minimum temperature (°C)**	**Moderately dry months**	**Severely dry months**	**Extremely dry months**	**Moderately wet months**	**Severely wet months**	**Extremely wet months**	**Number of frost days***	**Number of hot days**	**Hot period (days)**
Annual	Wagga Wagga	575(245-1019)	22.3(21-24)	9.0(8-10)	1(0-4)	0.4(0-3)	0.3(0-2)	1.4(0-7)	0.4(0-3)	0.3(0-3)	45(23-80)	71(34-109)	150(112-203)
	Dookie	559(200-1022)	20.4(19-22)	8.0(7-10)	1(0-3)	0.6(0-2)	0.2(0-2)	1.2(0-4)	0.5(0-3)	0.3(0-2)	45(9-83)	48(25-74)	132(92-186)
	Hamilton	675(376-968)	18.6(17-20)	7.5(6-9)	1(0-4)	0.6(0-3)	0.4(0-2)	1.2(0-4)	0.5(0-3)	0.1(0-2)	25(4-54)	27(13-42)	127(71-186)
	Ellinbank	1046(671-1377)	18.7(17-20)	8.8(8-10)	1(0-3)	0.6(0-3)	0.3(0-3)	1(0-3)	0.4(0-3)	0.2(0-1)	15(1-29)	22(5-33)	119(61-186)
	Elliott	1187(649-1797)	15.7(14-17)	7.4(6-9)	1(0-3)	0.6(0-4)	0.3(0-2)	1.1(0-5)	0.5(0-3)	0.1(0-2)	26(4-54)	0(0-2)	2(0-54)
Summer	Wagga Wagga	132(41-367)	30.9(28-34)	15.5(13-18)	0.3(0-2)	0.1(0-2)	0(0-1)	0.4(0-2)	0.1(0-1)	0.1(0-2)	0	52(27-72)	N/A
	Dookie	118(12-363)	28.5(26-31)	13.4(11-17)	0.4(0-2)	0.1(0-1)	0	0.3(0-2)	0.2(0-2)	0.1(0-1)	0	37(14-61)	N/A
	Hamilton	109(30-270)	24.8(22-28)	10.5(8-13)	0.3(0-2)	0.1(0-1)	0.1(0-2)	0.2(0-1)	0.2(0-1)	0.1(0-1)	1(0-5)	20(6-37)	N/A
	Ellinbank	190(86-363)	24.3(21-26)	12.3(11-14)	0.1(0-1)	0.2(0-2)	0.1(0-1)	0.3(0-2)	0.1(0-1)	0.1(0-1)	0	16(3-29)	N/A
	Elliott	180(43-523)	19.9(18-22)	10.5(9-12)	0.2(0-1)	0.1(0-2)	0.1(0-2)	0.2(0-2)	0.1(0-1)	0.1(0-1)	0(0-1)	0(0-2)	N/A
Autumn	Wagga Wagga	136(26-337)	22.7(21-25)	9.4(7-12)	0.3(0-2)	0.1(0-1)	0	0.2(0-2)	0.2(0-2)	0.1(0-1)	7(0-21)	10(0-22)	N/A
	Dookie	132(23-391)	20.7(19-22)	8.4(6-12)	0.2(0-2)	0.1(0-1)	0	0.2(0-1)	0.1(0-1)	0.1(0-1)	7(0-16)	6(0-15)	N/A
	Hamilton	152(44-308)	19.3(17-21)	8.2(6-10)	0.3(0-1)	0.1(0-2)	0.1(0-1)	0.2(0-2)	0.1(0-2)	0(0-1)	5(0-14)	5(0-12)	N/A
	Ellinbank	247(94-516)	19.3(17-21)	9.5(8-11)	0.3(0-2)	0.2(0-1)	0(0-1)	0.2(0-1)	0.1(0-1)	0.1(0-1)	1(0-6)	4(0-11)	N/A
	Elliott	273(91-560)	16.3(15-18)	8.3(6-11)	0.1(0-2)	0.2(0-2)	0.1(0-1)	0.3(0-2)	0.1(0-1)	0(0-1)	3(0-10)	0	N/A
Winter	Wagga Wagga	157(26-264)	13.7(12-15)	3.2(0-5)	0.1(0-1)	0.1(0-3)	0.2(0-2)	0.4(0-2)	0(0-1)	0(0-1)	36(18-63)	0	N/A
	Dookie	165(45-398)	12.3(11-14)	3.1(0-5)	0.3(0-1)	0.2(0-1)	0.1(0-2)	0.3(0-1)	0.1(0-1)	0.1(0-2)	36(8-64)	0	N/A
	Hamilton	231(116-371)	12.7(11-14)	4.7(3-7)	0.2(0-1)	0.1(0-1)	0.1(0-1)	0.4(0-2)	0.1(0-1)	0(0-1)	17(2-36)	0	N/A
	Ellinbank	312(117-540)	13.1(12-14)	5.2(4-6)	0.3(0-2)	0.2(0-2)	0.1(0-1)	0.2(0-2)	0.2(0-2)	0.02(0-1)	13(0-28)	0	N/A
	Elliott	433(208-679)	11.5(10-12)	4.5(3-6)	0.2(0-1)	0.1(0-2)	0.1(1-1)	0.3(0-3)	0.1(0-2)	0.1(0-1)	19(3-42)	0	N/A
	Wagga Wagga	151(43-309)	21.9(19-26)	7.9(6-10)	0.3(0-2)	0.1(0-1)	0.1(0-1)	0.3(0-3)	0.1(0-1)	0.1(0-1)	10(2-20)	9(0-27)	N/A

	Dookie	144(24-342)	20.0(17-23)	7.2(6-10)	0.3(0-2)	0.1(0-2)	0.1(0-1)	0.3(0-2)	0.1(0-1)	0.1(0-1)	10(0-26)	5(0-17)	N/A
Spring	Hamilton	184(69-298)	17.6(16-20)	6.7(5-8)	0.3(0-2)	0.3(0-2)	0.1(0-1)	0.4(0-2)	0.1(0-2)	0(0-1)	8(0-18)	2(0-13)	N/A
	Ellinbank	296(121-442)	18.1(16-20)	8.1(7-9)	0.3(0-2)	0.1(0-1)	0.1(0-1)	0.3(0-2)	0.1(0-1)	0(0-1)	2(0-7)	2(0-8)	N/A
	Elliott	303(103-536)	14.9(14-16)	6.5(5-7)	0.2(0-1)	0.2(0-2)	0.1(0-1)	0.3(0-2)	0.1(0-2)	0	7(1-19)	0	N/A

*Number of frost days - annual column contains number of frost days in the winter and spring period

4.2.3. Statistical analysis

Annual and seasonal pasture yields were related to climate indices using partial least-squares (PLS) regression model fitting procedure (Wold 1985), taking the simulated annual and/or seasonal pasture yield as the dependent variable and both general and extreme climate indices as the independent variables. PLS regression was used in this analysis because it avoids the issue of multicollinearity (correlations between climate variables) by reducing the predictors (climate variables) to smaller sets of components not correlated with each other (Dijkstra and Henseler 2011). The magnitude of standardized PLS coefficients (SC) corresponding to each climate index indicates the relative importance of each climate variable in determining pasture yield variation. The sign of each SC indicates whether the effect is positive or negative on yield. In this study, the positive or negative influences were determined if the SC were above +0.1 or below -0.1. Climate indices with the SC between these values were considered to contribute very little in explaining the yield variability. Normal regression coefficients are the multiplicative factors of predictors (climate indices) when calculating the actual yields using the fitted models. However, since all the climate variables are not in the same unit, it is difficult to easily judge the more important climate indices contributing to the yield variability using normal regression coefficients. Therefore, SC were used in this analysis to interpret the relative importance of climate indices in the fitted PLS models. PLS models were fitted using the Minitab statistical software (version 17).

4.2.4. Climate trend analysis

Total dry and wet months were analysed using Mann Kendall trend test (Mann 1945; Kendall 1975; Gilbert 1987) using XLSTST 2020 (A statistical add-in for Microsoft Excel) to detect any significant trend over time. Mann Kendall test was used because of the total dry and wet months data set was not normally distributed. Temperature trends for the average maximum spring season temperatures were analysed using linear regression procedure.

4.3. Results

4.3.1. Effect of general and extreme climate indices on annual pasture growth

Details of the fitted PLS models with the statistical parameters for the prediction of annual pasture yields at five sites are given in Table 3. In general, annual yield models explained more year to year pasture yield variability (high coefficient of determination-R^2) with more predictive power (R^2 predicted) at medium rainfall sites (R^2 - Wagga Wagga - 89% and Dookie - 85%) than at high rainfall sites (R^2 – Ellinbank - 65% and Elliott – 70%).

Among general climate indices, annual rainfall, spring rainfall and autumn rainfall components had positive relationships with annual pasture yields at all the sites with spring season rainfall showing the greatest positive influence. The relative importance (SCs) of positive rainfall components in determining annual pasture yields were generally larger in the medium rainfall sites than in high rainfall sites (Table 3). However, increasing winter rainfall was slightly negative at the high rainfall site at Ellinbank. Average maximum winter temperature was a favourable factor for the annual yields particularly at cooler sites (Elliott and Ellinbank) but, increasing average maximum spring temperature had a negative impact at all sites except Elliott. Additionally, atmospheric CO_2 concentration enhanced annual pasture yields at all sites with Elliott and Ellinbank showing the greatest response.

Among the extreme climate indices, dry month categories translated into lower annual pasture yields at all the sites with varying magnitude of impacts. At Dookie and Wagga Wagga, almost all the drought severity classes (moderate, severe and extreme dry months) appeared as negative factors in the fitted annual yield models, while only one or two severity classes at each site (Moderately dry months at Elliott, severely dry months at Hamilton, Extremely dry months at Ellinbank and Elliott) appeared as negative factors at high rainfall sites. However, the largest negative impact of the dry months severity classes was observed from the severely dry months at Hamilton and Dookie with the SC of -0.35 and -0.21, respectively. Unlike the drought severity classes, wet months showed both positive and negative impacts on annual pasture yields across all the sites. For instance, moderately wet months increased annual pasture growth at Wagga Wagga with and without native C4 grasses and Elliott sites while

displaying negative impacts at Hamilton. In contrast, severely wet months increased the pasture growth rate at Hamilton, but the response was negative at Ellinbank. Hot period length also displayed a negative impact on annual pasture production particularly at high rainfall sites at Elliott, Ellinbank and Hamilton, among which Ellinbank had the highest negative impact (SC = - 0.22).

Table 3. Summary of the PLS regression models fitted for annual pasture yields at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott. The relative influence of each climate index on annual pasture yield is indicated by the size of the standardized coefficient and the colour intensity indicates a positive (blue) or negative (red) impact. Coefficient values are the multiplicative factors that describe the size of effect each climate variable has on the yield.

	Climate indices	Wagga Wagga		Wagga Wagga with C4		Dookie		Hamilton		Ellinbank		Elliott	
		Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.
General climate indices	Annual rainfall	4	0.22	4	0.21	3	0.19	4	0.18	2	0.14	1	0.13
	Rainfall - summer	-5	-0.09	0	0.00	5	0.10	6	0.09	4	0.12	14	0.37
	Rainfall - autumn	8	0.20	5	0.15	5	0.10	7	0.14	4	0.15	0	0.01
	Rainfall - winter	10	0.16	5	0.09	-3	-0.05	-4	-0.07	-4	-0.15	-2	-0.09
	Rainfall - spring	11	0.25	10	0.25	13	0.30	11	0.26	6	0.21	4	0.15
	Avg. annual Tmax	-123	-0.04	-129	-0.04	-262	-0.06	-157	-0.04	-167	-0.05	-14	0.00
	Avg. annual Tmin	-269	-0.05	-73	-0.02	140	0.04	-171	-0.04	-106	-0.02	-20	0.00
	Avg. T max summer	182	0.08	58	0.03	-58	-0.02	45	0.02	-94	-0.05	-236	-0.07
	Avg. T max autumn	62	0.02	-46	-0.02	-70	-0.02	-114	-0.04	-7	0.00	5	0.00
	Avg. Tmax winter	16	0.00	109	0.03	-42	-0.01	182	0.04	452	0.12	737	0.15
	Avg. Tmax spring	-291	-0.16	-204	-0.12	-197	-0.08	-222	-0.10	-282	-0.12	-182	-0.05
	Avg. T min summer	-230	-0.09	-111	-0.05	-18	-0.01	-1	0.00	-221	-0.07	-63	-0.02
	Avg. T min autumn	81	0.03	122	0.06	101	0.04	-278	-0.10	114	0.04	20	0.01
	Avg. Tmin winter	-163	-0.05	-236	-0.08	1	0.00	-152	-0.05	-132	-0.03	152	0.04
	Avg. Tmin spring	5	0.00	164	0.05	389	0.10	75	0.02	58	0.02	-173	-0.05
	CO_2	16	0.14	15	0.15	21	0.18	19	0.21	28	0.36	30	0.32
Extreme climate indices	Moderately dry months	-351	-0.12	-267	-0.10	-282	-0.10	-150	-0.06	-160	-0.06	-569	-0.16
	Severely dry months	-417	-0.11	-297	-0.09	-891	-0.21	-1049	-0.35	-72	-0.03	-28	-0.01
	Extremely dry months	-618	-0.11	-487	-0.10	-696	-0.10	-150	-0.04	-591	-0.17	-425	-0.10
	Moderately wet months	547	0.22	421	0.19	146	0.05	-269	-0.12	-91	-0.04	357	0.15
	Severely wet months	-16	0.00	42	0.01	212	0.05	373	0.11	-349	-0.12	134	0.04
	Extremely wet months	-359	-0.08	-56	-0.01	-321	-0.06	-694	-0.11	272	0.05	235	0.04
	Winter spring frost number	13	0.05	11	0.05	5	0.02	8	0.04	-19	-0.05	-2	-0.01
	Hot days/yr (>30 °C)	7	0.04	2	0.01	-13	-0.05	1	0.00	-33	-0.10	-91	-0.03
	Hot period length	-7	-0.05	-8	-0.07	-6	-0.04	-15	-0.16	-17	-0.22	-39	-0.13
	R^2		0.89		0.83		0.85		0.76		0.65		0.70
	R^2 predicted		0.78		0.70		0.73		0.48		0.33		0.42
	Number of components		4		3		3		3		3		3
	X variance		0.57		0.51		0.48		0.51		0.46		0.49

4.3.2. Effect of general and extreme climate indices on seasonal pasture growth

The SCs and the statistical parameters of the PLS models fitted for spring, autumn and summer periods are shown in Tables 4-6. The highest seasonal yield variability was explained by the models fitted for the spring season (87% in Wagga Wagga to 61% in Elliott (Table 4)) followed by the autumn (70% in Wagga Wagga with C4 grasses to 37% in Hamilton (Tables 5)). Simulated summer pasture growth rates were normally very low or closer to zero in medium rainfall sites at Wagga Wagga and Dookie hence had very low model R^2 and predicted R^2 (Table 6). However, when C4 native grasses were included, pasture growth at the Wagga Wagga site explained substantially higher yield variation with higher model R^2 (56%) compared to the regression model without C4 grasses (26%). Also in high rainfall sites at Elliott, Ellinbank and Hamilton, where growth season extends into summer months showed model R^2 closer to 50% (Table 6). In the winter, pasture growth rates were nearly similar between years. Therefore, the variability of winter season was not sufficiently signifiant to include in the models.

The effects of the general climate indices on spring, autumn and summer pasture yield models generally followed a similar pattern to that of annual yield models but with varying relative importance (Table 4-6). However, atmospheric CO_2 concentration had a very weak realtionship with summer pasture production at all the sites.

The effect of extreme climate indices on spring pasture yields varied by site. Spring rainfall was a positive factor in the model but the distribution of rainfall can have negative effects. For example, spring production in high rainfall sites was negatively affected by dry month severity classes and the medium rainfall sites were negatively affected by wet month severity classes. Hamilton and Elliott showed strong negative responses to severely dry months while Ellinbank and Elliott sites had strong negative impacts from extremely dry months. In comparison, both Dookie and Wagga Wagga sites were negatively impacted by the extremely wet months. Additionally, frost occurrence at Dookie, Wagga Wagga and Elliott was negatively related with spring production while hot days appeared only at Ellinbank as a negative factor.

In Autumn and summer, the effects of extreme climate indices were similar across the sites. All the dry month severity classes in autumn and summer translated into decreased pasture yields whereas wet month severity class translated into higher pasture yields during these seasons. However, both autumn and summer pasture production has been limited by the increasing number of hot days above 30 °C in all the sites except at the coolest site at Elliott.

Table 4. Summary of the PLS regression models fitted for spring pasture yields at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott. The relative influence of each climate index on spring pasture yield is indicated by the size of the standardized coefficient and the colour intensity indicates a positive (blue) or negative (red) impact. Coefficient values are the multiplicative factors that describe the size of effect each climate variable has on the yield.

		Wagga Wagga		Wagga Wagga with C4		Dookie		Hamilton		Ellinbank		Elliott	
		Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.
General climate indices	Rain fall	21.1	0.72	19.2	0.69	27	1.00	7.4	0.28	11.76	0.71	5.64	0.43
	T max	-494	-0.39	-443	-0.37	-435	-0.29	-249	-0.19	-277	-0.19	-464	-0.24
	T min	-153	-0.06	-130	-0.05	77.7	0.03	54.69	0.03	-50.4	-0.02	102.9	0.05
	CO_2	0.7	0.01	-1.2	-0.02	11.4	0.16	3.75	0.07	16.91	0.36	17.39	0.37
Extreme climate indices	Moderately dry months	423	0.11	419	0.12	70.9	0.02	-346	-0.11	9.5	0.00	-404	-0.13
	Severely dry months	218.8	0.03	72.2	0.01	231	0.05	-859	-0.28	-94.6	-0.02	-749	-0.24
	Extremely dry months	159.9	0.02	-2.9	0.00	659	0.09	-557	-0.10	-958	-0.21	-1357	-0.30
	Moderately wet months	-204	-0.06	-88.8	-0.03	-477	-0.14	354.5	0.14	-327	-0.12	-173	-0.07
	Severely wet months	-614	-0.09	-641	-0.09	-921	-0.16	675.7	0.15	-1821	-0.46	-244	-0.07
	Extremely wet months	-1686	-0.27	-1561	-0.27	-2212	-0.29	-1260	-0.15	-317	-0.05	N/A	N/A
	Frost days	-85	-0.18	-85.4	-0.19	-88.2	-0.25	-26.6	-0.08	-45.4	-0.06	-37.4	-0.12
	Hot days (>30 °C)	-17.8	-0.06	-15.7	-0.05	2.34	0.00	-25.1	-0.04	-114	-0.16	N/A	N/A
	R^2		0.87		0.86		0.87		0.79		0.74		0.61
	R^2 predicted		0.77		0.77		0.79		0.71		0.52		0.40
	Components		10		10		9		2		10		4
	X variance		0.95		0.94		0.90		0.45		0.89		0.62

Table 5. Summary of the PLS regression models fitted for autumn pasture yields at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott. The relative influence of each climate index on autumn pasture yield is indicated by the size of the standardized coefficient and the colour intensity indicates a positive (blue) or negative (red) impact. Coefficient values are the multiplicative factors that describe the size of effect each climate variable has on the yield.

		Wagga Wagga		Wagga Wagga with C4		Dookie		Hamilton		Ellinbank		Elliott	
		Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.
General climate	Rain fall	4	0.33	4	0.31	5	0.31	4	0.24	3	0.23	2	0.19
	T max	-397	-0.35	-264	-0.28	-380	-0.25	-248	-0.25	-296	-0.28	-218	-0.16
	T min	7	0.01	38	0.05	75	0.08	-42	-0.04	-25	-0.02	15	0.01
	CO_2	9	0.24	13	0.40	5	0.11	3	0.08	11	0.34	11	0.30
Extreme indices	Moderately dry months	-290	-0.16	-389	-0.26	-569	-0.23	-149	-0.07	-327	-0.17	-820	-0.32
	Severely dry months	-865	-0.28	-1125	-0.43	-189	-0.05	-545	-0.22	-534	-0.22	-564	-0.25
	Extremely dry months	N/A	N/A	N/A	N/A	N/A	N/A	-406	-0.14	N/A	N/A	-245	-0.07
	Moderately wet months	100	0.05	-29	-0.02	644	0.21	106	0.05	253	0.11	187	0.11
	Severely wet months	252	0.11	10	0.01	62	0.02	40	0.02	-269	-0.08	-175	-0.06
	Extremely wet months	90	0.02	-128	-0.04	313	0.06	N/A	N/A	-943	-0.23	N/A	N/A
	Frost days	1	0.00	12	0.06	-1	-0.01	-6	-0.02	14	0.02	0	0.00
	Hot days (>30 °C)	-25	-0.12	-21	-0.13	-87	-0.25	-32	-0.09	-79	-0.21	N/A	N/A
	R^2		0.70		0.72		0.58		0.37		0.52		0.41
	R^2 predicted		0.56		0.56		0.41		0.17		0.30		0.21
	Components		2		3		2		1		2		2
	X variance		0.37		0.50		0.43		0.19		0.35		0.38

Table 6. Summary of the PLS regression models fitted for summer pasture yields at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott. The relative influence of each climate index on spring pasture yield is indicated by the size of the standardized coefficient and the colour intensity indicates a positive (blue) or negative (red) impact. Coefficient values are the multiplicative factors that describe the size of effect each climate variable has on the yield.

		Wagga Wagga		Wagga Wagga with C4		Dookie		Hamilton		Ellinbank		Elliott	
		Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.	Coeff.	Std. coeff.
General climate	Rain fall	1	0.15	2	0.24	2	0.20	4	0.22	3	0.19	6	0.31
	T max	-38	-0.12	-51	-0.18	-71	-0.14	-138	-0.24	-148	-0.19	-387	-0.20
	T min	-17	-0.05	-9	-0.03	10	0.02	-87	-0.12	-163	-0.12	-72	-0.04
	CO_2	1	0.05	0	0.02	2	0.08	-1	-0.04	0	0.01	0	-0.01
Extreme indices	Moderately dry months	-46	-0.05	-84	-0.10	-102	-0.08	-55	-0.04	-121	-0.04	-194	-0.05
	Severely dry months	-44	-0.03	-36	-0.03	-90	-0.04	-10	0.00	47	0.02	-487	-0.12
	Extremely dry months	-69	-0.03	-109	-0.05	N/A	N/A	1	0.00	-284	-0.09	-303	-0.08
	Moderately wet months	-6	-0.01	112	0.14	25	0.02	181	0.10	123	0.07	435	0.15
	Severely wet months	167	0.10	130	0.09	337	0.22	163	0.08	470	0.11	747	0.18
	Extremely wet months	176	0.13	138	0.11	242	0.12	367	0.13	198	0.05	568	0.09
	Frost days	N/A	N/A	N/A	N/A	N/A	N/A	-34	-0.05	N/A	N/A	-39	-0.01
	Hot days (>30 °C)	-5	-0.13	-7	-0.18	-10	-0.15	-22	-0.20	-29	-0.16	-158	-0.08
	R^2		0.26		0.56		0.39		0.56		0.47		0.54
	R^2 predicted		0.03		0.47		0.18		0.41		0.36		0.43
	Components		1		1		1		1		1		1
	X variance		0.29		0.30		0.26		0.24		0.31		0.21

4.4. Discussion

The results of this study demonstrated that both general and extreme climate variables are important to explain the year to year pasture yield variability in SE Australia. The fitted PLS models at the five sites highlighted that general climate indices like annual rainfall, average maximum winter temperature and atmospheric CO_2 concentration increased annual pasture yield but increasing maximum spring temperature decreased the annual yield. Winter temperature increased pasture production in combination with the atmospheric CO_2 concentration mainly in the high rainfall cool temperate climates at Elliott and Ellinbank. Extreme climate indices however modified the positive effects of rainfall, revealing the negative relationships between the dry months severity classes and annual pasture yield mainly when they occurred during the winter and spring period. Further, hot days > 30 °C suppressed autumn and summer yields at almost all the sites except the coolest site at Elliott while increasing hot period length translated into lower pasture yields in the high rainfall sites affecting the summer production. Frost occurrences also decreased pasture yields in the spring season in medium rainfall sites despite the general trend of increasing temperature in the region. These results clearly showed that extreme climate indices modify the effects of general climate indices, most of which have negative impacts on annual and seasonal pasture production. Hence, any climate change impact study that accounts only the changes in the average climate (Hulme *et al.* 1999; Cullen *et al.* 2009) without considering the climate variability and associated extremes, risks underestimation of the actual climate change impacts (Thornton *et al.* 2014; Harrison *et al.* 2016).

4.4.1. Effect of rainfall indices

Across the sites simulated in SE Australia, rainfall was the key driver of the year to year pasture yield variation as indicated by annual and more specifically the spring rainfall in the fitted annual models. This was particularly prominent in the medium rainfall sites (Table 3-4). Higher pasture yield response to the spring rainfall was expected mainly because these systems become water limited in the mid to late spring and early summer months (latter part of the growing season) (Cullen *et al.* 2009) and the favourable spring temperature support pasture growth if the water is available (McKenzie *et al.* 1999).

Sanford *et al.* (2003) reported a similar finding showing that the length of the growing season accounted for a greater amount (30%) of variation in annual pasture growth among the factors influencing herbage accumulation in high rainfall zone of southern Australia. However, they observed annual rainfall as a poor predictor of pasture growth across sites.

Agreeing with the Sanford *et al.* (2003) the results of the present study indicated that, rainfall distribution had some negative impacts on pasture yield even though annual rainfall was a positive yield predictor in the fitted models. Dry month categories had a negative relationship with annual pasture production with some severity classes highlighting their particular importance. The impacts were greater when the dry months occurred in winter and spring months where larger proportion of annual herbage mass is produced. For example, in the medium rainfall sites of Dookie and Wagga Wagga, 10/10 and 13/15 extremely dry months over the simulated period occurred during winter and spring seasons. In Hamilton, 21/31 severely dry months have occurred during winter and spring months which had the greatest negative impact among all the climate indices. Likewise, in high rainfall sites of Ellinbank and Elliott, 11/18 extremely dry months and 24/41 moderately dry months have occurred during winter and spring seasons respectively (data not shown). These results concord with the previous work of Chapman *et al.* (2008) who showed that 7% of the years between 1900-1999 had extremely poor pasture yields in the Terang District due to the severe droughts experienced during the major pasture growing period. Analysing SPI-2 month time step from July to August, it has also been found that vulnerability (relative yield decrease) of rainfed maize systems in Bulgaria increased with increasing drought severity (Popova *et al.* 2014). Similarly, a comparison between SPI and crop yields (wheat, barley, maize and sunflower) in Bulgaria revealed that decreased yields were related to the severe droughts in the spring and summer months which were the major crop growing period (Nikolova 2013). Dry months during the key pasture growing period have many downside risks such as decreased pasture production, decreased quantity and quality of hay, increased water demand, land degradation, decreased carrying capacity (Malatinszky 2016), shifting seasons (Cullen *et al.* 2009; Moore and Ghahramani 2013) and low pasture persistence (Nie *et al.* 2004b; Poirier *et al.* 2012).

The results also highlighted varying responses of wet months (both positive and negative) on annual pasture production which was mainly due to the time of the year that these events occurred. At Wagga Wagga, even though extremely wet months have decreased the spring pasture yields, moderately wet months during winter and spring seasons (43/76) have translated into higher pasture yields. However, even the moderately wet months can produce negative impacts when it occurred in the major rainy period at high rainfall sites. For example, at Hamilton, moderately wet months caused lower annual pasture yields where 43/67 of these events have occurred during winter and spring months. Similarly, 18/25 severely wet months at Ellinbank have also occurred during winter and spring period which had translated to lower annual pasture production. Reduction of pasture growth during above average rainfall months could be mainly due to water logging of pastures. There are many consequences of water logging such as decreased pasture growth (McFarlane *et al.* 2003), nutritive quality (Lee *et al.* 2013), plant death due to soil anoxia (Woods *et al.* 1993), pasture compaction damage and poor subsequent regrowth (Nie *et al.* 2001). Time trend analysis indicated that total dry months have increased at Dookie while total wet months have decreased in Ellinbank and Hamilton ($P<0.05$) (Figure 2) reflecting a drying trend. However, other sites did not show any increasing or decreasing trend in rainfall extreme indices. In conclusion, both extremely dry and wet months have the potential to demote both pasture production and quality (Chang-Fung-Martel *et al.* 2017).

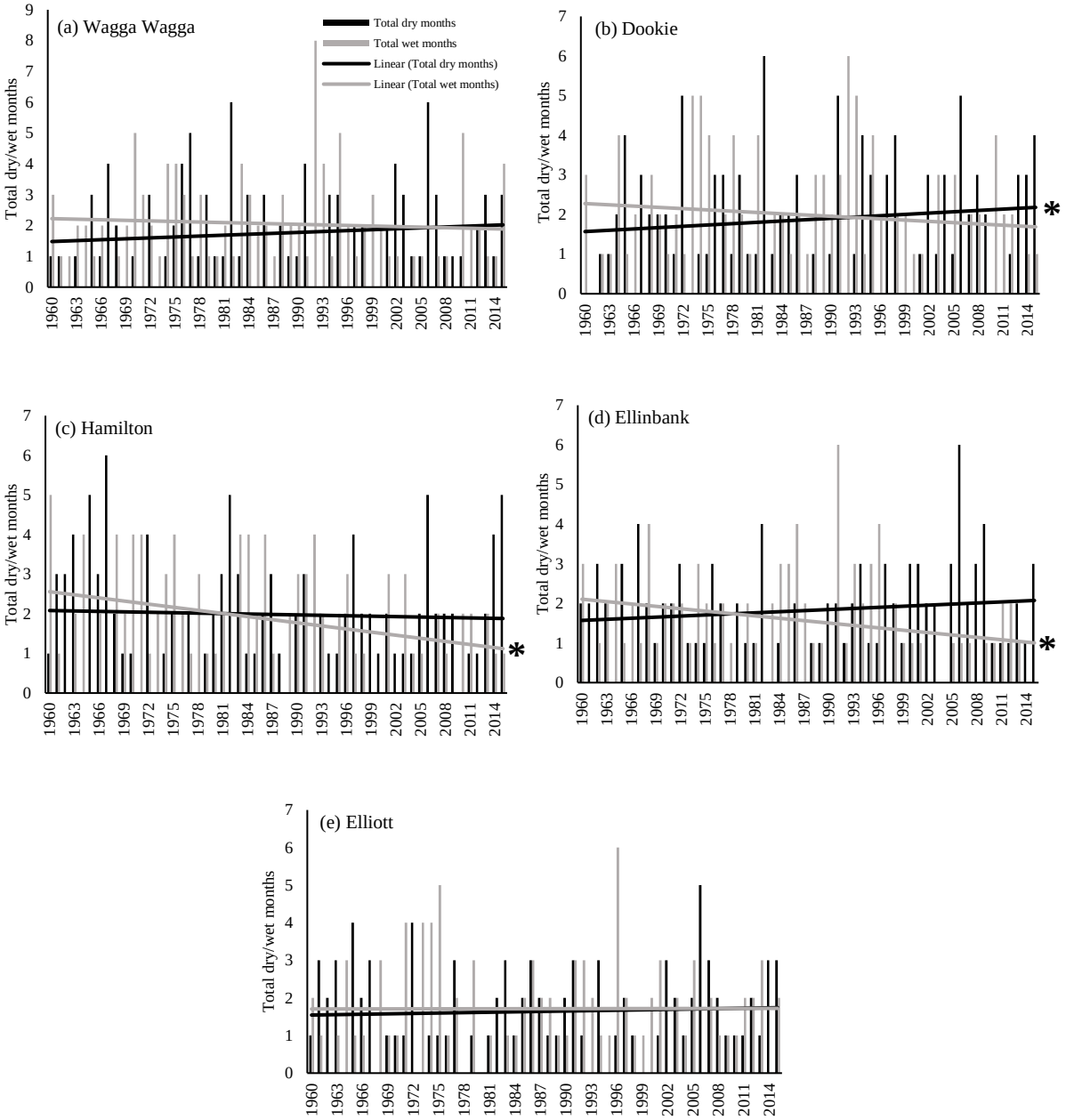

Figure. 2. Time trends of the total dry months (Black bars) and total wet months (grey bars) calculated from SPI-1 data from 1960-2015 at Wagga Wagga (a), Dookie (b), Hamilton (c), Ellinbank (d) and Elliott (e). Black line represents the linear trend of total dry months and grey line represents the linear trend of total wet months. Asterisk marks (*) represent significant trends form Mann Kendall test.

4.4.2. Effect of temperature indices

Apart from the positive effects of winter temperature on winter pasture production, average maximum spring temperature and all the temperature extremes such as number of hot days (>30 °C) and hot period length had shown down side risks on pasture yields. The optimum temperature range for temperate perennial pasture growth lies between 18 °C and 25 °C (Mitchell 1956; Duru 2000) and temperatures above and below this range can affect growth and physiological functions like photosynthetic capacity of a plant. The literature reports reduced growth and physiological functions of pastures due to extreme heat such as reduced biomass production (Milbau *et al.* 2005; Langworthy *et al.* 2015), reduction of photosynthesis rates, (Jiang and Huang 2001; Cui 2006), breakdown of cell membrane structure (Jiang and Huang 2001; Yang *et al.* 2014) and decreased energy available for cell maintenance through increasing respiration (Criddle *et al.* 1997). Further, prolonged periods of extreme temperatures in summer (during a heat wave) and concurrent occurrences of moisture stress can exacerbate the impacts by reducing the plants ability to recover from heat (Langworthy *et al.* 2018) resulting pasture mortality and reduced persistence. In this analysis Wagga Wagga, Hamilton, Ellinbank and Elliott sites showed significant increases in the maximum spring temperatures ($P<0.05$) (Figure 3) with the maximum of 2.8 °C increase recorded at Wagga Wagga in 2015 compared to 1960 (Figure 3,a). Further, hot period length has also increased significantly by 24 days at Wagga Wagga compared to 1960 (Figure 4) indicating that duration of heat stress for pastures in some parts of SE Australia has increased.

In addition to the warming trend, extremely cold nights (frost days) have reduced pasture production mainly during spring seasons at Dookie, Wagga Wagga and Elliott (Table 4). Frost occurrence has increased in Dookie by 29 days during winter-spring seasons (Figure 5) in the simulated period despite the fact that average maximum spring temperature and hot period length has increased by 0.92 °C and 10 days respectively (data not shown) This trend in in agreement with Matiu *et al.* (2016) and Cohen *et al.* (2012) who identified spatiotemporally coherent patterns of increasing frost, where annual and seasonal temperatures follow increasing trend, while temperature of some months have decreased, which is referred to as seasonal asymmetry.

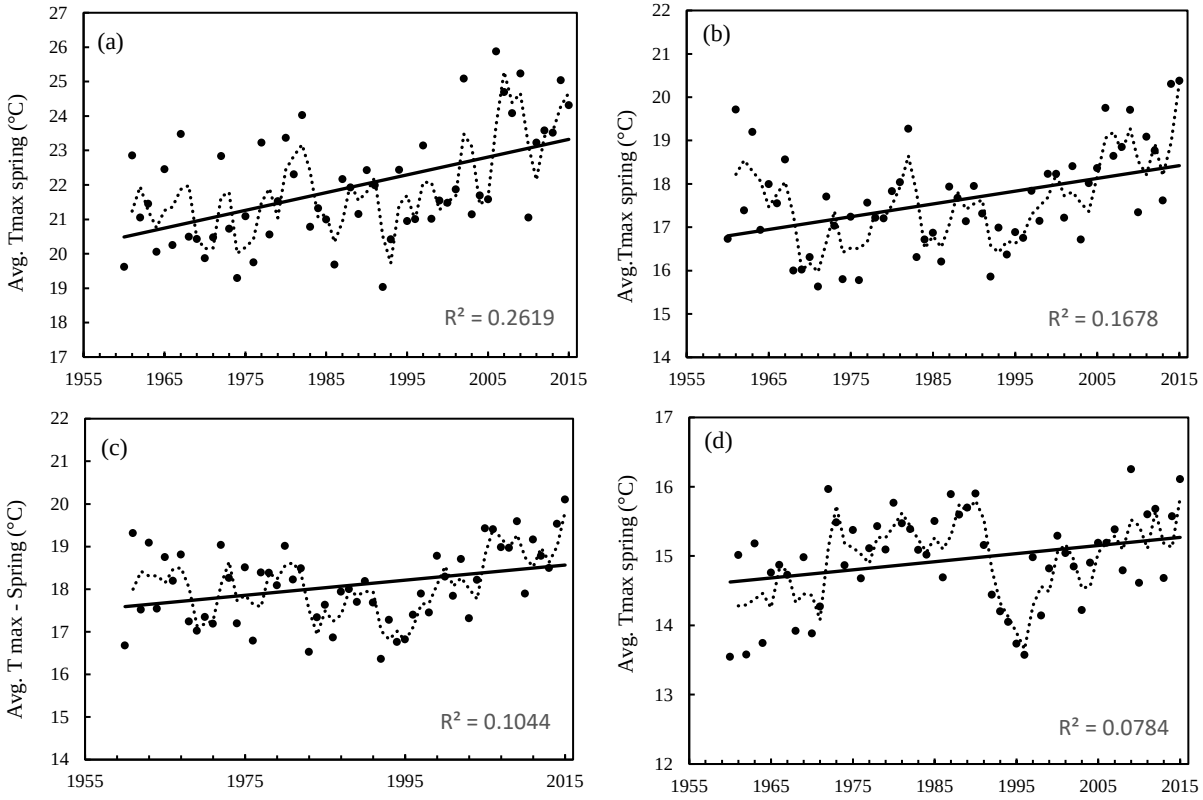

Figure. 3. Significant time trends (P < 0.05) of the average maximum spring temperatures at Wagga Wagga (a), Hamilton (b), Ellinbank (c) and Elliott (d) from 1960 to 2015.

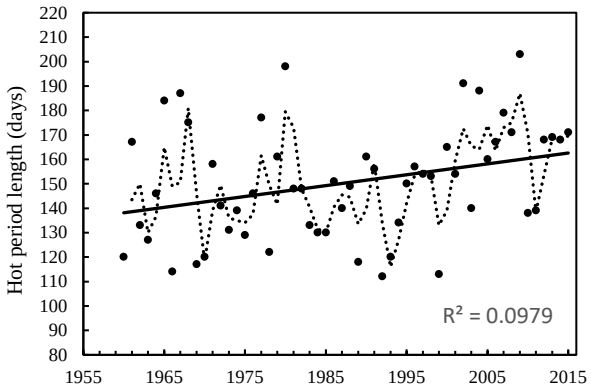

Figure 4. Time trend of the hot period length at Wagga Wagga from 1960 to 2015 (P < 0.05)

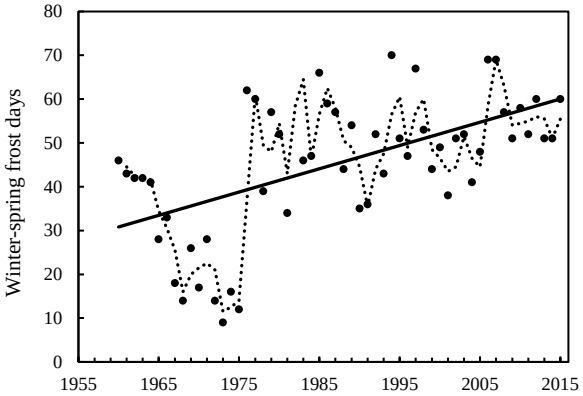

Figure 5. Time trend of the winter-spring frost days at Dookie from 1960 to 2015 ($P < 0.05$).

4.4.3. Response to gradual CO_2 increase

Understanding the role of CO_2 concentration for pasture production is important, because it needs to be considered in combination with moisture availability and temperature rather than considering as a single factor (Xu and Zhou 2006; Xu *et al.* 2014). In the fitted PLS models, gradual increase of CO_2 levels in the historical climate (1960-2015) translated into higher pasture yield responses at high rainfall cool temperate sites than in medium rainfall sites. For example, an extra 28 kg and 30 kg of pasture dry weight can be obtained per year per unit increase of CO_2 (1ppm) at Ellinbank and Elliott sites respectively (Table 3) while this amount is lower as 15 kg in the medium rainfall site at Wagga Wagga. However, this number needs further validation using field trials. Further, the yield response to CO_2 in the summer months was weak as available soil moisture is limited for pasture growth in summer. These responses were consistent with the results from controlled environmental studies where, elevated CO_2 enhanced the growth of C3 grasses when irrigation was provided, but declined drastically with severe drought (Xu *et al.* 2014). Similarly, for wheat crop, Dias de Oliveira *et al.* (2015) found yield increment with 2 °C warming and elevated CO_2, but yield declined with 4 °C warming and drought conditions. Further, Laing *et al.* (2002) observed a strong positive biomass response of perennial ryegrass to the elevated CO_2 under low temperature (12 °C) which is closer to the average maximum winter temperature in SE Australia (Table 2). Therefore, the higher pasture yield response to the gradually

elevated CO_2 levels in Elliott and Ellinbank could be due to the interaction of CO_2 with optimum soil moisture and temperature at these sites.

4.4.4. Limitations in the modelling approach

While the DairyMod software has been shown to realistically simulate pasture growth in SE Australia (Cullen *et al.* 2008), there are some limitations to how it models the impacts of extreme climate events on pasture plants. In particular, DairyMod does not simulate plant death, second, better parameterisation is needed for heat stress recovery function of pasture species. The model will further strengthen if the pasture persistence could be modelled. However, pasture persistence is governed by multiple complex interactive factors such as grazing intensity and interval (Cousins *et al.* 2003), pasture species composition (Tozer *et al.* 2011), insect and pests (Popay and Hume 2011) and weed infestation (Tozer *et al.* 2011), which are hard to model. The fitted PLS models need to be further validated using the actual pasture yields data against both general and extreme climate events in the future.

4.5. Conclusions

The fitted PLS models reported in this study highlighted that both general and extreme climate indices are important to assess the actual impacts of climate change on pasture systems in SE Australia. Further, improved seasonal forecasts to include extreme climate events will better equip farmers to manage these events. The relative importance of general and extreme variables from these models and their predicted future changes from GCMs can be used to identify the long-term adaptation practices required at each location to sustain the pasture production. Based on this analysis, it can be concluded that pasture production in SE Australia has been greatly challenged by changes in the dry and wet extremes in the rainfall distribution, increasing spring temperatures, and increasing hot period length in the past climate of SE Australia. While the identified model limitations deserve further model improvement efforts, this study demonstrates the importance of incorporating both general and extreme climate events in researching the impacts of climate variability and change in any agricultural production system.

Acknowledgement

Authors would like to thank Associate Professor Graham Hepworth, Statistical consultant center, The University of Melbourne for the statistical advice.

CHAPTER 5. Influence of El-Niño Southern Oscillation and Indian Ocean Dipole phases on annual pasture production in south eastern Australia

(Peer reviewed conference paper)

Perera R, Cullen B, Eckard R (2018) Influence of El-Niño Southern Oscillation and Indian Ocean Dipole phases on annual pasture production in south eastern Australia. In 'Proceedings 2018 Australasian Dairy Science Symposium (ADSS)'. 21–23 November 2018, Palmerston North, New Zealand. pp. 63–70. (Massey University and AgResearch: Palmerston North, New Zealand)

Available at: https://s3-ap-southeast-2.amazonaws.com/ap-southeast-2.accounts.ivvy.com/account34583/events/132130/files/5c47dfccd5e5e.p

Influence of El-Niño Southern Oscillation and Indian Ocean Dipole phases on annual pasture production in south eastern Australia

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Abstract

The synoptic scale climate drivers El-Niño Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) events can alter seasonal climate across south eastern (SE) Australia, but their influence on inter-annual variability of pasture production has not been fully described. Two indices were used to classify ENSO and IOD into three phases each in winter-spring period during 1950-2015. Statistical differences between ENSO and IOD phases (individually and combined) and annual pasture production, simulated at five sites (Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott) using DairyMod, were analysed using ANOVA. Mean annual pasture yields were substantially lower during El-Niño (EN) years at Wagga Wagga (7 t DM/ha.yr) and Dookie (6.4 t DM/ha.yr) than neutral and La-Niña (LN) years (~10 t DM/ha.yr) Similarly, IOD(+) years had lower yields at Wagga Wagga, Dookie and Elliott but not at Hamilton and Ellinbank. When combined ENSO-IOD phases were examined, the highest yields resulted when the LN phases coincided with IOD(-) or neutral, whilst the EN with IOD(+) phases led to the lowest yields. Analysis of sliding six-month windows revealed that yield difference started to emerge in March to August. This analysis highlights the importance of including combinations of large scale climate drivers to forecast pasture production with greater lead time.

Keywords: climate drivers; annual pasture production; DairyMod; yield forecasting

5.1. Introduction

In SE Australia, year to year climate variability poses a key challenge for managing pasture-based production systems. Frequent occurrences of unfavourable weather, such as severe drought, heat waves and extreme precipitation impact on pasture growth, quality and the key management decisions such as stocking rate, calving date and supplementary feeding (Cullen *et al.* 2009; Chapman *et al.* 2012b; Harrison *et al.* 2016). Synoptic scale climate drivers such as El-Nino Southern Oscillation (ENSO) and Indian Ocean Dipole (IOD) alone or in tandem can cause such anomalous weather, impacting on agricultural production in the key growing seasons (Potgieter *et al.* 2005; Hayman *et al.* 2010; Jarvis *et al.* 2018).

ENSO and IOD are two distinct modes of climate variability that alter seasonal weather conditions across Australia (Ashok *et al.* 2003; Wang and Hendon 2007). They develop by ocean (upwelling) and atmosphere (winds) interactions in the tropical Pacific and Indian oceans. ENSO phases usually swing between El-Niño(EN), La-Niña(LN) or neutral, and IOD changes between IOD(+), IOD(-) or neutral phases. EN and IOD(+) phases usually bring hot and dry conditions over Australia (Taschetto *et al.* 2011) while LN and IOD(-) phases support cool temperatures and above average rainfall (Ummenhofer *et al.* 2011). The conditions tend to be driest, when an EN event coincides with IOD(+) phase, while it could be extremely wet when a LN combines with IOD(-) (Ummenhofer *et al.* 2009). However, the impacts of each phase can vary in terms of their strength, temporal and spatial distribution across the region (Risbey *et al.* 2009; Risbey *et al.* 2013). A typical ENSO event starts in the first half of the year, peaks in the spring and gradually decays by the autumn but, LN phases can extend over several years. IOD events usually occur from May to November with their peaks occurring in the spring.

Several studies have investigated the influence of different phases of ENSO and IOD on agriculture in Australia. For example, LN events typically have higher wheat yield than EN (Nicholls 1985; Hayman *et al.* 2010), and IOD(+) phases have been linked to early maturity of wine grapes compared to IOD(-) phases (Jarvis *et al.* 2018). However, all these authors have reported varying

special impacts, which means their influence on the rainfall and agricultural yields vary between sites or the region. The influence of these climate drivers on pasture production has not been fully described, even though the impacts are acknowledged. Therefore, the objective of this study was to investigate the effects of ENSO, IOD and ENSO-IOD combinations on annual pasture yields in SE Australia and to test the ability of climate driver phases to forecast pasture growth.

5.2. Materials and methods

5.2.1. Pasture growth simulation

The DairyMod biophysical pasture model (Version 5.7.4) was used to simulate daily pasture growth rates for two medium rainfall sites (Dookie in northern Victoria and Wagga Wagga in southern NSW) and three high rainfall sites (Hamilton in south western Victoria, Ellinbank in Gippsland and Elliott in Tasmania) over the period 1950-2015. At the high rainfall sites, perennial ryegrass (*Lolium perenne* L.) was simulated with either white clover (*Trifolium repens* L.) or subterranean clover (*Trifolium subterraneum* L.). At the medium rainfall site at Dookie, a phalaris (*Phalaris aquatica* L.) and subterranean clover pasture was simulated, while at Wagga Wagga, a phalaris, subterranean clover and annual ryegrass (*Lolium rigidum* L.) mixture was simulated. Pastures were simulated under non-limiting nutrient conditions and without irrigation at all sites so that responses to climatic variation could be identified. Pasture was harvested to a residual mass of 1.4 t DM/ha at the end of each month. Daily weather data obtained from the Bureau of Meteorology SILO data base (Jeffrey *et al.* 2001) (rainfall in mm, maximum and minimum temperature in °C, radiation in MJ/m^2 and evaporation in mm), plus measured CO_2 concentrations at Cape Grim baseline air pollution station, were used.

5.2.2. Classification of ENSO and IOD events

Multivariate ENSO index (MEI) bimonthly ranks (Data source: https://www.esrl.noaa.gov/psd/enso/mei/rank.html) in June/July to October/November, which represents the major pasture growing period and the peak times of the ENSO phases, were used to classify years into different ENSO phases. If at least 3 out of 5 bimonthly ranks showed a distinct

ENSO signal, that year was categorised as either EN, neutral or LN, following the criteria used by Jarvis *et al.* (2018).

Dipole Mode Index (DMI) values calculated from the HadSST data set (Saji 2003) were used to identify IOD events from winter spring period. Based on the approach used by Cai *et al.* (2009) and Jarvis *et al.* (2018), the positive or negative IOD years were determined when the average DMI values (from June-November) were above or below +0.75 or -0.75 of its long term standard deviation, respectively. The years inside these thresholds were considered as neutral years. The years with different phases of ENSO and IOD and their composites are shown in Table 1. The average climate statistics at each site during ENSO and IOD phases are in Table 2.

5.2.3. Statistical analysis

Analysis of variance (ANOVA) was performed at each site using Minitab (V.17) to check whether the means of annual pasture yields differed significantly during ENSO, IOD and ENSO-IOD combined phases categorised in the June-November period. The significantly different phases ($P<0.05$) were then tested with Fisher's Least Significant Difference test to identify which phases were significantly different.

To investigate the ability of climate driver phases to forecast pasture growth, each year was categorised into ENSO, IOD and ENSO-IOD combined phases using sliding six monthly windows. Accordingly, six different periods were used (Jan-Jun, Feb-Jul, Mar-Aug, Apr-Sep, May-Oct, Jun-Nov). Mean annual pasture yields during those sliding windows were compared with ANOVA to identify significant yield differences between climate driver phases. Since the opposite phases of ENSO, IOD and their extreme phase combinations (EN/IOD+ and LN/IOD-) have shown the highest deviations from mean rainfall in most of the study sites in SE Australia (Table 2), (Risbey *et al.* 2009), yield differences were tested in those phases using 0.05 significance level. This approach allowed determination of the earliest time that the difference was significant and used it as an indication of forecast skill.

Table 1 Classification of ENSO, IOD and combined (ENSO-IOD) events from 1950-2015 using June-November values of MEI bimonthly ranks and DMI. Number of years that fall under each category is shown in parenthesis.

	IOD(+)	**IOD(Neutral)**	**IOD(-)**
El-Niño (EN)	1951, 1963, 1972, 1976, 1982, 1987, 1991, 1994, 1997, 2002, 2006, 2009, 2015 (13)	1957, 1965, 1977, 1979, 1986, 1993, 2004, 2014 (8)	(0)
Neutral	1961, 1983, 2000, 2003, 2012 (5)	1952, 1953, 1966, 1968, 1969, 1978, 1981, 1984, 1985, 1989, 1990, 1995, 2001, 2005, 2013 (15)	1958, 1959, 1960, 1980, 1992, 1996 (6)
La-Niña (LN)	1967, 1999, 2007, 2008, 2011 (5)	1950, 1955, 1962, 1970, 1971, 1973, 1974, 1975, 1988, 1998, 2010 (11)	1954, 1956, 1964 (3)

Table 2 Mean annual rainfall (mm) and annual average daily temperatures (°C) with standard deviations for the ENSO and IOD phases at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott. Coordinates of the sites were shown in parenthesis.

	El-Niño		Neutral		La-Niña		IOD(+)		Neutral		IOD(-)	
Site (location-Lat., Long.)	Rainfall (mm)	Annual average temperature (°C)	Rainfall (mm)	Annual average temperature (°C)	Rainfall (mm)	Annual average temperature (°C)	Rainfall (mm)	Annual average temperature (°C)	Rainfall (mm)	Annual average temperature (°C)	Rainfall (mm)	Annual average temperature (°C)
Wagga Wagga (-35.16, 147.46)	439±121	15.7±0.6	616±118	15.5±0.6	674±186	15.5±0.7	472±158	15.9±0.5	624±145	15.5±0.6	661±182	15.1±0.5
Dookie (-36.37, 145.70)	436±148	14.2±0.6	603±115	14.0±0.5	657±183	14.4±0.7	450±147	14.2±0.5	622±154	14.2±0.6	646±153	13.6±0.5
Hamilton (-37.83, 142.06)	610±105	13.0±0.5	723±111	13.0±0.6	704±152	13.0±0.5	615±124	13.3±0.6	708±115	12.9±0.5	751±140	12.8±0.4
Ellinbank (-38.25, 145.93)	962±193	13.7±0.4	1112±161	13.6±0.5	1078±170	13.7±0.4	942±187	13.8±0.3	1105±142	13.7±0.5	1150±195	13.3±0.4
Elliott (41.08, 145.77)	1038±168	11.4±0.5	1248±180	11.4±0.6	1323±276	11.4±0.7	1041±179	11.5±0.4	1269±212	11.5±0.6	1365±245	10.9±0.6

5.3. Results

The effects of ENSO only and IOD only phases during June to November on mean annual pasture yields are displayed in Figure 1. Wagga Wagga, Dookie and Elliott sites had lower yields during EN years, but no differences were observed between neutral and LN years. The yield reduction in EN years when compared with LN years, was greater at the medium rainfall sites of Dookie (4 t DM/ha) and Wagga Wagga (3 t DM/ha) than at high rainfall site, Elliott (1.7 t DM/ha). Similarly, mean pasture yields were not significantly different between IOD(-) and neutral years, but IOD(+) years resulted in lower yields. The yield reduction compared to IOD(-) years was greater at Wagga Wagga (3 t DM/ha) and Dookie (3.3 t DM/ha) than at Elliott (1.6 t DM/ha) following a similar pattern to ENSO events.

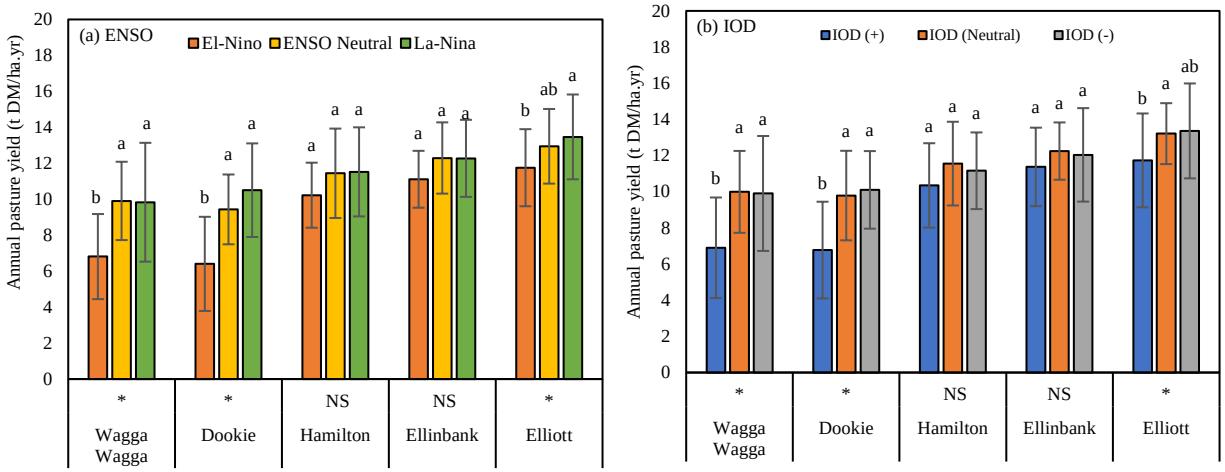

Figure 1. Mean annual pasture yield (t DM/ha) during El-Niño, La-Niña and Neutral phases (a) and IOD(-), IOD(+) and neutral phases (b) at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott sites. Significance of the ANOVA testing is displayed using asterisks at the bottom. The error bars indicate one-sided standard deviation and the significant differences are shown by different letters.

When analysed for the ENSO-IOD combined phases, mean annual pasture yields were significantly different (P<0.05) at the medium rainfall sites at Dookie and Wagga Wagga but not at the high rainfall sites (Figure 2). In general, annual yields tend to be the lowest when EN phases coincide with IOD(+) phases and this reduction was generally greater (Figure 2) than the reduction associated with each phase alone (Figure 1).

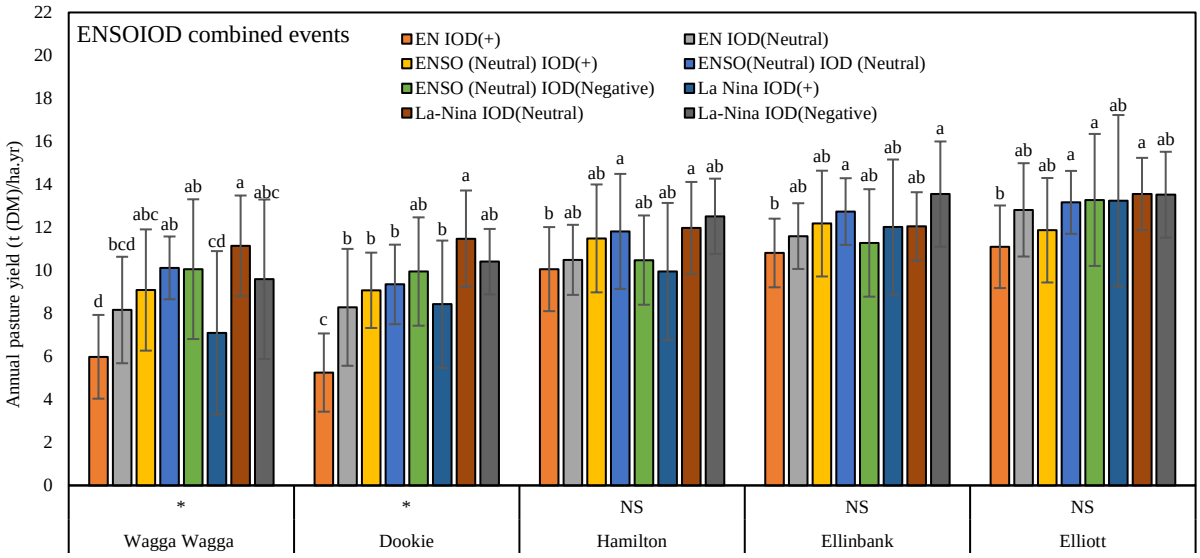

Figure 2. Mean annual pasture yield (t DM/ha) during ENSO-IOD combined events at Wagga Wagga, Dookie, Hamilton, Ellinbank and Elliott sites. Significance of the ANOVA testing is displayed using asterisks at the bottom. The error bars indicate one-sided standard deviation and the significant differences are shown by different letters.

The pasture yield differences of LN – EN, IOD(-) – IOD(+) and LN/IOD(-) – EN/IOD(+) phases tested at six monthly sliding windows are shown in Figure 3. These yield difference became significant from the March-August period. Yield differences were higher at Dookie (eg: LN - EN= 4t DM/ha.yr) and Wagga Wagga (LN - EN= 3 t DM/ha.yr) and lower at Elliott (LN- EN=1.7 t DM/ha.yr).

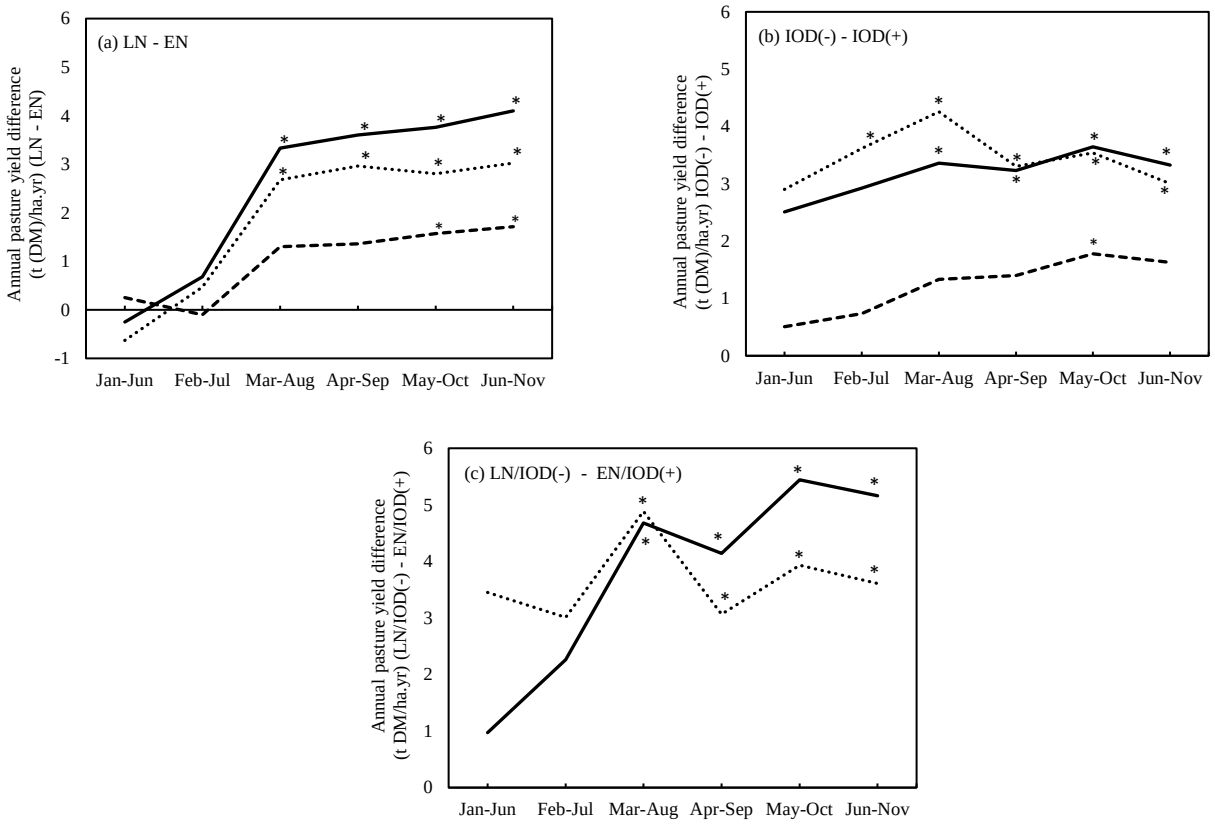

Figure 3. Difference in mean annual pasture yield (t DM/ha) between LN-EN (a), IOD(-) – IOD(+) (b) and LN/IOD- and EN/IOD+ (c) for Dookie (thick line), Wagga Wagga (dotted line) and Elliott (dash line) for the climate driver classifications using sliding six-month time windows. The significant mean differences ($P<0.05$) are shown near each data point using asterisks.

5.4. Discussion

Hot and dry phases of both ENSO and IOD events had significant negative impacts on predicted annual pasture yields, independently and in combination, especially at the medium rainfall sites (Figure 1,2). These results are consistent with the observed weather conditions during those climate driver phases in SE Australia (Table 2). The pasture yields during ENSO-IOD combined phases were influenced to a greater degree than when each phase occurred on its own because of the reinforcing effect of each climate driver phase when paired with the similar phase of the other driver (Risbey *et al.* 2009; King *et al.* 2014).

Understanding the impact of these climate driver phases will benefit those agricultural industries most affected by climate variability. Rainfed pasture production, which responds more strongly to rainfall variation, will benefit more if these event phases can be predicted before the key adapted management decisions are implemented (Ash *et al.* 2007). Management decisions to adapt to climate variability may involve planning for increased fodder conservation, early destocking or forward contracting of supplementary feed (Austen *et al.* 2002). However, accurate seasonal weather forecasting with sufficient lead time is still limited by the existing understanding of the complex ocean and atmospheric factors governing the strength and spatial extent of these phases (Henry 2006). A survey showed that farmers expected at least 70% forecast accuracy in order to use them in their decisions (Austen *et al.* 2002). Previous attempts have highlighted that the ENSO signal in the early season (March-May) is not often clear enough to influence farmers' decision making (Hayman *et al.* 2010). The results of this study are consistent with this finding, whereby the sliding six-month windows indicated that significant pasture yield differences did not emerge until the March to August period. This yield difference remained significant for the rest of the year indicating that the climate driver phase signal is reasonably well predicted at the end of winter. Detailed analysis of each of the phases further revealed that 70% of the ENSO and 85% of the IOD phases recognised in the March-August period remained unchanged for the rest of the year while the probability that any phase may reverse in direction after this window was very low or zero.

5.5. Conclusions

The synoptic scale climate drivers, ENSO, IOD and ENS-OIOD combinations can significantly affect annual pasture production. This effect is greater at medium rainfall sites. The ENSO and/or IOD signal in the March-August period provides a reasonable prediction of the nature of the climate driver for the rest of the pasture growing period. However, adaptive decision making using ENSO and IOD forecasts needs an appropriate lead time. Therefore, further understanding of the dynamics of these climate drivers will pave the way for better management of grazing systems in SE Australia.

CHAPTER 6. Growth and Physiological Responses of Temperate Pasture Species to Consecutive Heat and Drought Stresses (Journal paper)

Perera, R.S.; Cullen, B.R.; Eckard, R.J. Growth and Physiological Responses of Temperate Pasture Species to Consecutive Heat and Drought Stresses. Plants 2019, 8, 227.

doi:10.3390/plants8070227

plants

MDPI

Article

Growth and Physiological Responses of Temperate Pasture Species to Consecutive Heat and Drought Stresses

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Received: 25 June 2019; Accepted: 14 July 2019; Published: 16 July 2019

Abstract: Heat and drought are two major limiting factors for perennial pasture production in south eastern Australia. Although previous studies have focused on the effects of prolonged heat and drought stresses on pasture growth and physiology, the effects of short term recurring combined heat and drought stresses and the recovery from them have not been studied in detail. A controlled environment experiment was conducted to investigate the growth and physiological responses of perennial ryegrass (*Lolium perenne* L.), cocksfoot (*Dactylis glomerata* L.), tall fescue (*Festuca arundinacea* Schreb.) and chicory (*Cichorium intybus* L.) plants exposed to two consecutive seven day heat (control = 25/15 °C day/night; moderate = 30/20 °C day/night and severe = 35/25 °C day/night) and/or drought stresses each followed by a seven day recovery period. During the first moderate and severe heat and drought treatments, maximum photochemical efficiency of photosystem II (Fv/Fm), cell membrane permeability and relative leaf water content decreased in chicory and tall fescue compared to perennial ryegrass and cocksfoot. However, during the second moderate heat and drought treatment, all species showed less reduction in the same parameters suggesting that these species acclimated to consecutive moderate heat and drought stresses. Chicory was the only species that was not affected by the second severe heat and drought stress while physiological parameters of all grass species were reduced closer to minimum values. Irrigation mitigated the negative effects of heat stress by cooling the canopies 1–3 °C below air temperatures with the most cooling observed in chicory. All the species exposed to moderate heat and drought were fully recovered and those exposed to severe heat and drought recovered partially at the end of the experiment. These findings suggest that chicory may be a potential species for areas subject to frequent heat and drought stress.

Keywords: perennial pastures; combined heat and drought stress; membrane permeability; maximum photochemical efficiency of PS II; acclimation

1. Introduction

Global mean temperature is increasing at a rate of 0.2 °C per decade and projected to increase by 1.5 °C above pre-industrial levels (1850–1900) by 2050 if global warming continues at the current rate [1]. In conjunction with global temperature rise, mean temperature in Australia has increased by about 1 °C since the start of the 20th century [2]. At the same time, the frequency, magnitude and duration of extreme climate events such as heat waves and droughts are also increasing [2]. These climatic conditions are highly likely to challenge the production and persistence of perennial pastures in south eastern (SE) Australia, mainly in summer months (December–February). This in turn affects the profitability of the livestock industry since home grown pasture is the cheapest source of feed for livestock [3].

Heat stress is defined as a state where the temperatures are hot enough to cause impairment of physiology, metabolism and productivity of plants [4], where the impacts are mainly dependent on the duration and severity of the stress [5]. Drought stress is a period of sub-optimal water supply to plants that reduces water potential, turgor pressure and subsequently inhibits normal plant functions [6]. During prolonged severe drought, plants could be irreversibly damaged [7]. Heat and drought stress can act individually or in combination. Combinations of heat and drought stresses often cause more detrimental impacts on plants than individual stresses, such that when temperature increases, vapor pressure deficit rises allowing more transpiration per unit of CO_2 uptake. This in turn reduces the water use efficiency [8] and increases the rate of water deficit stress development in plants. During water deficit stress, plant water status (water potential or relative water content) decreases affecting turgor pressure [6]. The first response to drought stress in plants is the reduction of leaf expansion. Since herbage mass is the primary target of pasture production, decreasing leaf expansion growth directly affects the forage dry matter production [9]. In SE Australia, rainfed perennial ryegrass pasture production in summer months is often as low as 5–10% of the annual yields, because of the suboptimal water availability and high temperature [10]. Reduction of leaf elongation rates due to water deficit stress has been widely reported for cool season temperate pasture species such as tall fescue and cocksfoot [11], perennial ryegrass [12,13] and Italian ryegrass [14]. In addition to that, water deficit largely impacts on stomatal opening and CO_2 diffusion into the leaves, affecting photosynthetic carbon fixation [15–19].

The downregulation of photosynthesis due to heat stress occurs through reduction in Rubisco activity and impairment of photochemistry [20,21]. Optimal temperature for shoot growth of temperate cool season grasses range between 15–23 °C [22,23] and reduction in photosynthesis and growth beyond this range has been reported in several studies. It was found that photosynthesis of Kentucky bluegrass decreased at temperatures above 25 °C [24]. For tall fescue, reduction in photosynthesis has been reported at much higher temperatures (30 °C) [25–27].

Photosystem (PS) II is the most heat labile component in the photosynthesis process and is responsible for the impairment of photochemistry under heat stress [28–30]. Chlorophyll fluorescence has been developed as a non-destructive measurement to analyze abiotic stresses like heat and drought [31]. Measurement of fluorescence in dark adapted leaves provides an estimate of the maximum photochemical efficiency of PS II (Fv/Fm = variable fluorescence/maximum fluorescence) and gives important information on how much incoming light is used for the photochemistry. Fv/Fm in healthy leaves under optimum conditions is around 0.83 [32–36]. However, reductions of Fv/Fm have been reported under heat and drought stresses for pastures [24,25,32,37].

Downstream effects of heat stress include production of reactive oxygen species (ROS) [38] and peroxidation of membrane lipids. As a result, cell membranes lose their integrity and electrolyte leakage occurs [39]. Increased production of ROS like hydrogen peroxide and superoxide in tall fescue [40] and high lipid peroxidation in tall fescue and perennial ryegrass [25,41] have been observed under high temperature stress. However, variations exist among and within species with respect to their ability for thermotolerance. For instance, tall fescue and cocksfoot were reported to have higher membrane thermotolerance than perennial ryegrass [11,41,42].

Plants often evolve strategies to modify their responses to abiotic stresses using the previous stress memory, referred to as a priming effect [42]. Many studies have investigated the modified plant responses by exposing plants to non-lethal heat treatments [41,43]. Thermotolerance is acquired through reorganizing the lipid compositions of cell membranes [44] and modifying biochemical processes [45]. It has been reported that heat acclimated tall fescue and perennial ryegrass showed decreased water loss, membrane damage and lipid peroxidation relative to non-heat acclimated plants [41].

Growth and physiological responses of temperate pastures under prolonged heat and drought stresses have been studied previously [32,33,46]. However, heat and drought are likely to increase with the increased frequency of extreme climate events due to climate change [47]. Physiological

responses of temperate grasses to recurring heat and drought stresses, and their ability to acclimate to the previous stresses have not been studied in detail. Therefore, the objectives of this study were to 1. investigate the growth and physiological responses and recovery potential of four temperate perennial pasture species that are commonly grown pasture species in SE Australia to consecutive heat and/or drought stress alone or in combination and 2. to identify pasture species more tolerant to recurring heat and drought stresses. To test these objectives, an experiment was conducted where plants were exposed to consecutive moderate (30/25 °C, day/night) and severe (35/30 °C, day/night) heat stresses under well-watered and drought conditions, with a one-week recovery period in between.

2. Results

2.1. Relative Soil Water Content (RSWC)

There was little difference in RSWC in well-watered treatments (Figure 1a–c) but it declined from the initial level of ~1 to about 0.6 on average at the end of the first combined heat and drought treatments. There was a difference between chicory and the grasses during the second drought treatment whereby chicory had higher RSWC than grasses at every temperature (Figure 1d–f). Soil water was restored in all the species during the recovery phases and the species differences were seldom significant at the end of each recovery phase (Table 1).

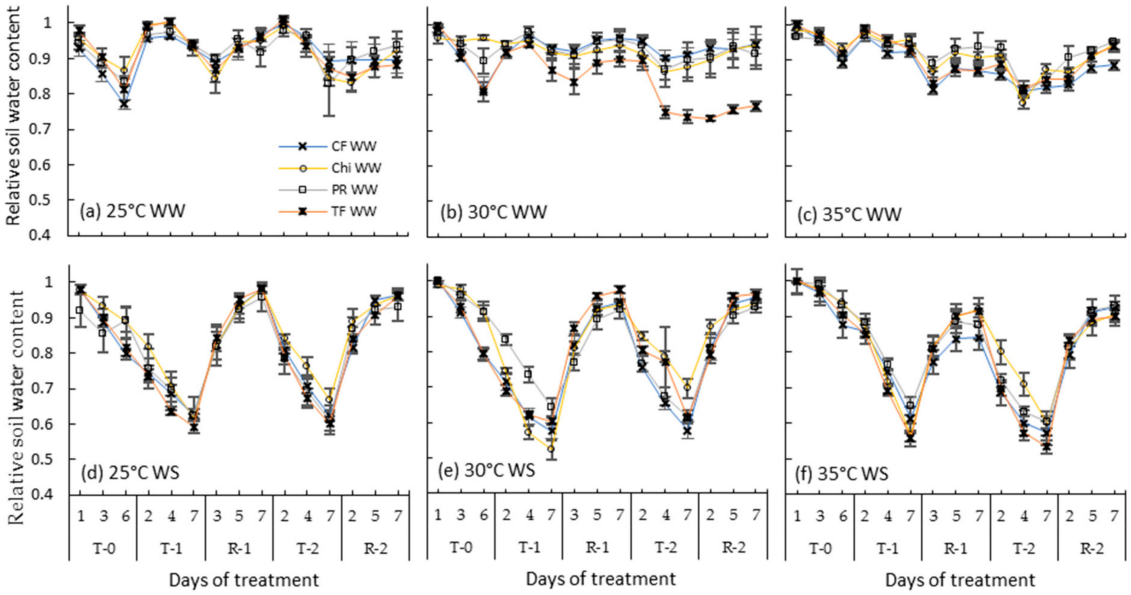

Figure 1. Relative soil water content of pots containing perennial ryegrass (PR), cocksfoot (CF), tall fescue (TF) and chicory (Chi) during consecutive heat and drought treatments and subsequent recovery periods. (**a**), (**b**) and (**c**) represent well-watered (WW) plants grown at control, moderate and severe heat stresses, respectively, while (**d**), (**e**) and (**f**) represent corresponding water stressed (WS) plants. T-0 denotes pre-treatment, T-1 and T-2 denote treatments and R-1 and R-2 denote recovery periods. Mean values (n = 5) are provided with error bars representing ± standard error

Table 1. Level of significance of the main factors and their interactions in relative soil water content.

Main Factors and Interactions	Pre-Treatment			Treatment 1			Recovery 1			Treatment 2			Recovery 2		
	Day 1	Day 3	Day 6	Day 2	Day 4	Day 7	Day 3	Day 5	Day 7	Day 2	Day 4	Day 7	Day 2	Day 5	Day 7
Temperature	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water status	NS	NS	NS	***	***	***	*	NS	NS	***	***	***	*	NS	*
Species	*	***	***	***	***	*	NS	NS	NS	*	NS	*	*	NS	NS
Temperature × Water status	NS	NS	NS	**	***	NS	NS	NS	NS	NS	**	NS	NS	NS	NS
Temperature × Species	NS	NS	**	**	**	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water status × Species	NS	NS	NS	**	***	NS	*	*	NS	*	*	NS	*	NS	*
Temperature × Water status × Species	NS	NS	NS	NS	*	*	NS	NS	NS	NS	*	*	NS	NS	NS

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

2.2. Maximum Photochemical Efficiency of Photosystem II (Fv/Fm)

There was little difference in Fv/Fm ratio between species under well-watered conditions however, chicory had a higher Fv/Fm ratio compared to the other three grass species (Figure 2). Significant interactions between species, temperature and water status were observed at the end of the first treatment period then again after day 6 of the second treatment (Table 2). During the first moderate heat and drought, the maximum reduction of the Fv/Fm was observed in chicory (72% of the control), followed by tall fescue (38%), cocksfoot (17%) and perennial ryegrass (7%) on day 2 of recovery 1 (Figure 2). Similar patterns were observed for the first severe heat and drought treatment. However, reduction of Fv/Fm during the first severe heat and drought stress treatment was slower in pasture species than the first moderate stress. This may have been due to the high relative humidity (RH%) (>80%) observed during the first two days in the severe heat and stress-imposed growth chamber. High RH% may have reduced the rate of water loss from plants via transpiration and maintained plant functions longer into the stress.

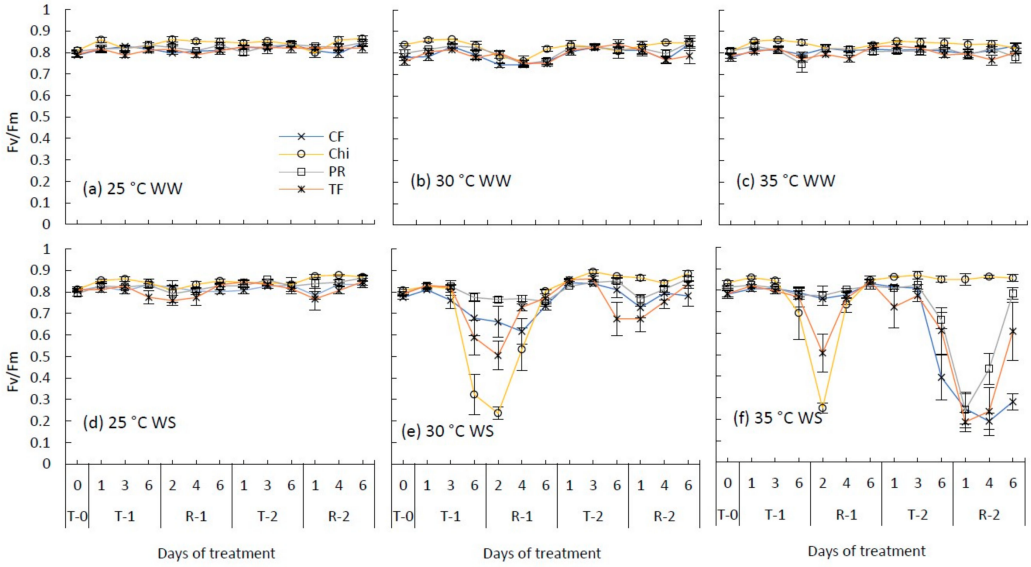

Figure 2. Maximum photochemical efficiency of photosystem II (Fv/Fm) during consecutive temperature and drought treatments and subsequent recovery of cocksfoot (CF), chicory (Chi), perennial ryegrass (PR) and tall fescue (TF). (**a**), (**b**) and (**c**) represent well-watered (WW) plants grown at control, moderate and severe heat stress, respectively, while (**d**), (**e**) and (**f**) represent corresponding water stressed (WS) plants. T-0 denotes pre-treatment, T-1 and T-2 denote treatments and R-1 and R-2 denote recovery periods. Mean (n = 3–5) values are provided with error bars representing ± standard error.

During the second moderate heat and drought stress treatment, Fv/Fm was higher in all species compared to the first moderate heat and drought treatment (Figure 2e). For example, tall fescue had a reduction of 38% after the first treatment and it was only 17% after the second treatment. In contrast, in the second severe heat and drought treatment, the Fv/Fm of all species except chicory declined more significantly and extensively than the first severe heat and drought stress treatment. For example, perennial ryegrass had a reduction of 5% at the end of the first severe treatment compared to 71% at the end of the second severe treatment. During the recovery phase, perennial ryegrass almost fully recovered (94%) and cocksfoot only partially recovered (33%).

The significant interaction of the temperature × water status × species on day 6 of treatment 2 in Fv/Fm is shown in Figure 3. It showed that water stressed perennial ryegrass, cocksfoot and tall fescue plants in the severe temperature treatment (35 °C) had lower Fv/Fm values than the well-watered control. In contrast, chicory maintained a higher Fv/Fm value (similar to non-stressed control = 0.85). Chicory was the only species that did not show any reduction throughout the second heat and drought stress and recovery after stress, indicating no heat induced damage to chicory.

Table 2. Level of significance of the main factors and their interactions on each day for maximum photochemical efficiency of photosystem II (Fv/Fm).

Main Factors and Interactions	Pre-Treatment	Treatment 1			Recovery 1			Treatment 2			Recovery 2		
	Day 0	Day 1	Day 3	Day 6	Day 2	Day 4	Day 6	Day 1	Day 3	Day 6	Day 1	Day 4	Day 6
Temperature	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water status	NS	NS	NS	**	***	***	NS	NS	*	***	***	***	***
Species	***	***	***	*	***	NS	***	*	***	***	***	***	***
Temperature × Water status	NS	NS	*	*	***	*	NS	NS	*	***	NS	***	***
Temperature × Species	NS	NS	NS	**	***	*	NS	NS	NS	***	*	***	***
Water status × Species	NS	NS	NS	***	***	*	NS	NS	NS	**	NS	***	***
Temperature × Water status × Species	NS	NS	NS	**	***	NS	NS	NS	NS	**	NS	***	***

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

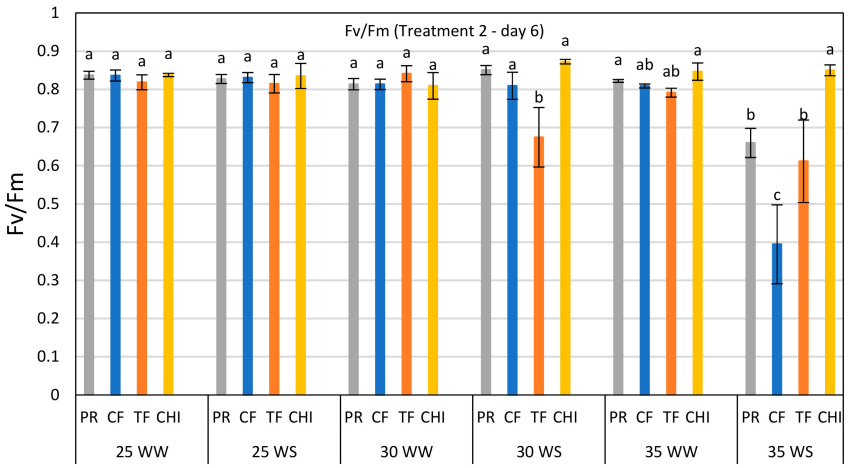

Figure 3. Comparison of Fv/Fm ratio of perennial ryegrass (PR), cocksfoot (CF), tall fescue (TF) and chicory (CHI) on day 6 of the second heat and water stress treatment. Each bar represents mean (n = 3–5) Fv/Fm value with ±SE. Significant differences are shown by different letters. The values in this bar graph can also be read from the day 6 of T-2 in each graph of Figure 2.

2.3. Cell Membrane Permeability

Electrolyte leakage (EL%), an indicator of cell membrane damage, did not increase under well-watered conditions (Figure 4a–c). However, chicory maintained slightly higher EL% (~16% on average) compared to other species (~10%). At the control temperature, drought stressed plants of chicory showed a gradual increase of EL% up to 60% in the first treatment but there were no marked variations in the EL% in any species during the second drought stress treatment at 25 °C.

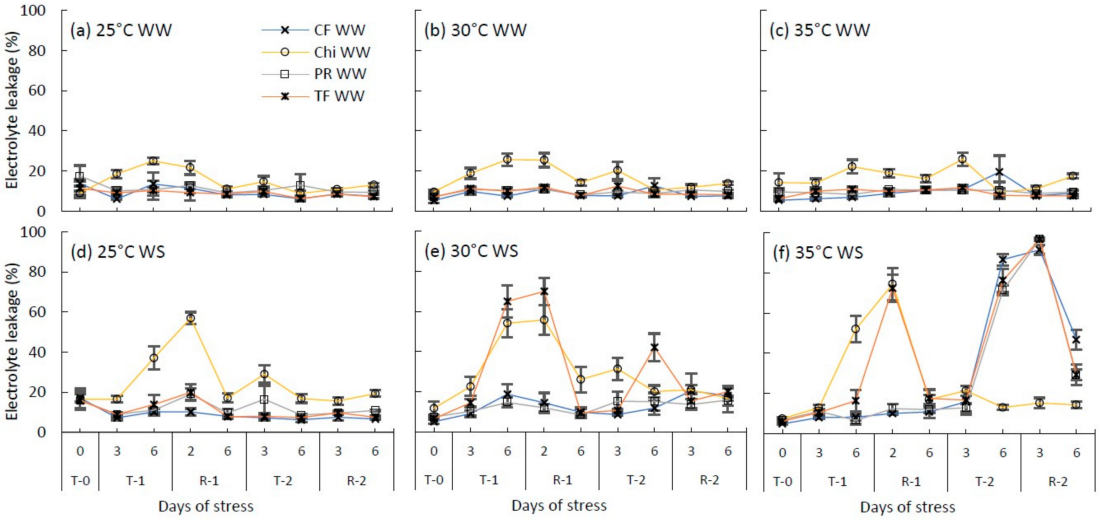

Figure 4. Changes to the cell membrane permeability (measured using electrolyte leakage %) of cocksfoot (CF), chicory (Chi), perennial ryegrass (PR) and tall fescue (TF) during the consecutive temperature and water treatments and subsequent recovery phases. (**a**), (**b**) and (**c**) represent well-watered (WW) plants grown at control, moderate and severe heat stress, respectively, while (**d**), (**e**) and (**f**) represent corresponding water stressed plants (WS). T-0 denotes pre-treatment, T-1 and T-2 denote treatments and R-1 and R-2 denote recovery periods. Mean values (n = 3–5) are provided with error bars representing ± standard error.

During the first moderate heat and drought stress treatment, chicory and tall fescue showed significant membrane damage up to 56% and 70%, respectively, extending the effect to the second day of the recovery phase. Similarly, during the first severe heat and drought stress treatment, the EL% of

chicory and tall fescue increased significantly up to 74% and 72% but did not increase in perennial ryegrass or cocksfoot.

During the second moderate heat and drought treatment, electrolyte leakage of the tall fescue and chicory was lower compared to the first treatment. In contrast, cell membranes of all the grass species were significantly damaged (>90%) during the second combined severe heat and drought stress treatment and the effect extended to the recovery phase, but chicory was not affected. Chicory produced new leaf after the first stress period and these new leaves did not show EL above 15% during the second treatment period, indicating no heat induced membrane damage. At the end of the recovery phase, the grass species were partially recovered (Table 3), reporting EL% of 47% in cocksfoot and 30% in perennial ryegrass and tall fescue species.

2.4. Leaf Elongation Rates

Leaf elongation rates showed variations between species and ranged from 1.7 cmd^{-1} in cocksfoot to 2.2 cmd^{-1} in chicory on average under control temperature and well-water treatment (Figure 5a). Chicory showed a transient increase in leaf elongation rates under well-watered conditions soon after the temperature was increased (Figure 5b,c). However, heat stress alone decreased the leaf elongation rates of other grass species, particularly at the severe heat stress treatment (Figure 5c). For example, during the second severe heat treatment, leaf elongation rate of cocksfoot, perennial ryegrass and tall fescue decreased by 68%, 65% and 55%, respectively, compared to the control. Under water stress treatment (control temperature), leaf elongation rates of all the species decreased substantially and fluctuated around 0.3–0.5 cmd^{-1}. At the end of both moderate and severe heat stresses, leaf elongation of water stressed plants stopped completely. In contrast, leaf elongation rate of chicory during the second combined moderate/severe heat and drought stresses did not reach zero but remained less than well-watered treatments. At the end of the recovery period, all plant species subjected to each temperature and drought treatment restored their leaf elongation rates to the control levels (Table 4) and tall fescue increased even above the control level.

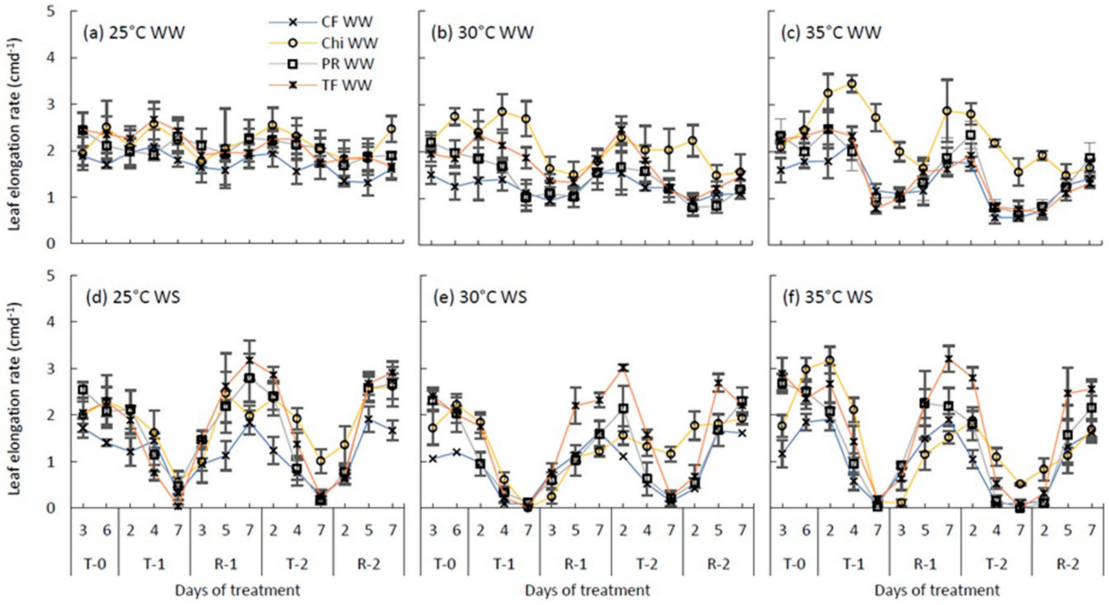

Figure 5. Leaf elongation rates of perennial ryegrass (PR) cocksfoot (CF), tall fescue (TF) and chicory (Chi) measured as cmd^{-1} during the consecutive temperature and drought treatments and subsequent recovery phases. (**a**), (**b**) and (**c**) represent well-watered (WW) plants grown at control, moderate and severe temperatures, respectively, while (**d**), (**e**) and (**f**) represent corresponding water stressed (WS) plants. T-0 denotes pre-treatment, T-1 and T-2 denote treatments and R-1 and R-2 denote recovery periods. Mean values (n = 3–5) are provided with the error bars representing the ± standard error.

Table 3. Level of significance of the main factors and their interactions on each day for cell membrane permeability.

Main Factors and Interactions	Pre-Treatment	Treatment 1		Recovery 1		Treatment 2		Recovery 2	
	Day 0	Day 3	Day 6	Day 2	Day 6	Day 3	Day 6	Day 3	Day 6
Temperature	NS	NS	NS	NS	NS	NS	NS	***	NS
Water status	NS	NS	***	***	**	*	***	***	***
Species	NS	***	***	***	***	***	***	***	NS
Temperature × Water status	NS	NS	***	***	NS	NS	***	***	***
Temperature × Species	NS	NS	***	***	NS	NS	***	***	***
Water status × Species	NS	NS	***	***	NS	NS	***	***	***
Temperature × Water status × Species	NS	NS	***	***	NS	NS	***	***	***

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

Table 4. Level of significance of the main factors and their interactions on each day for leaf elongation rate.

Main Factors and Interactions	Pre-Treatment		Treatment 1			Recovery 1			Treatment 2			Recovery 2		
	Day 3	Day 6	Day 2	Day 4	Day 7	Day 3	Day 5	Day 7	Day 2	Day 4	Day 7	Day 2	Day 5	Day 7
Temperature	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water status	NS	NS	*	***	***	***	NS	NS	NS	***	***	***	***	***
Species	***	***	***	***	***	NS	**	*	***	***	***	***	*	***
Temperature × Water status	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS
Temperature × Species	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	*	NS	NS
Water status × Species	NS	NS	NS	NS	***	***	NS	***	***	NS	NS	NS	*	*
Temperature × Water status × Species	NS	NS	NS	NS	***	NS	NS	NS	NS	NS	NS	NS	NS	NS

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

2.5. Relative Leaf Water Content (RLWC)

Well-watered plants maintained higher RLWC >0.8 at all temperature treatments (Figure 6a–c). However, chicory displayed lower RLWC than grasses from the start of the experiment. At the end of the first treatment, the RLWC of chicory and tall fescue declined significantly to below control levels under all the temperature and drought stressed treatments with the lowest RLWC of 0.16 observed in tall fescue at moderate heat stress. During the second treatment, reduction in the RLWC in control and the moderate temperatures was much lower than the first treatment and chicory maintained a RLWC of ~0.8 which was closer to its non-stressed control value. The largest reductions of RLWC were observed at the end of the second severe heat and drought stressed treatment where the RLWC of all the grass species declined to ~0.2 but chicory maintained a greater RLWC of >0.7 All the grass species were almost recovered at the end of the second recovery period (Table 5), restoring the RLWC > 0.75.

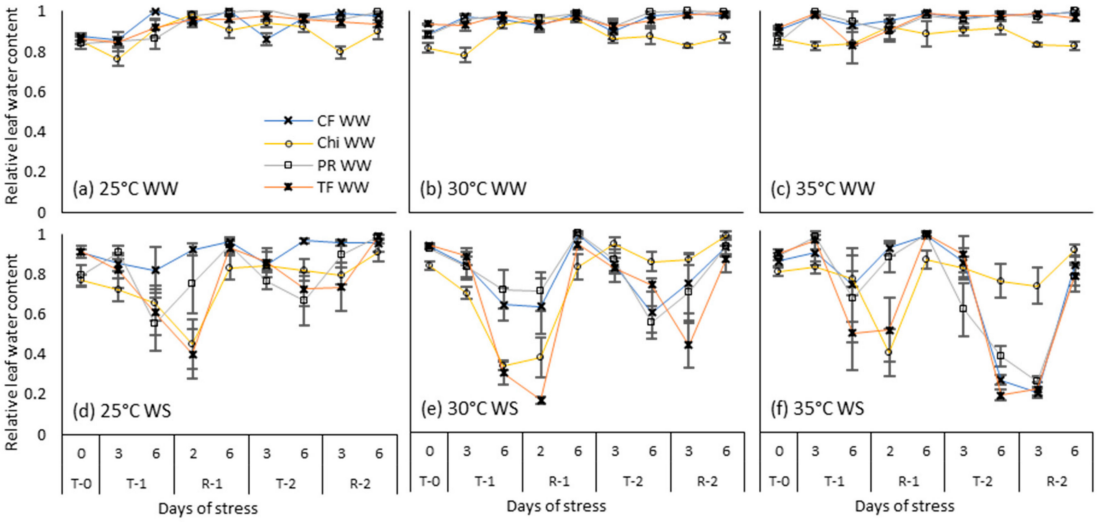

Figure 6. Relative leaf water content during consecutive temperature and drought treatments and subsequent recovery phases of cocksfoot (CF), chicory (Chi), perennial ryegrass (PR) and tall fescue (TF). (**a**), (**b**) and (**c**) represent well-watered (WW) plants grown at control, moderate and severe temperatures respectively while (**d**), (**e**) and (**f**) represent corresponding water stressed (WS) plants. T-0 denotes pre-treatment, T-1 and T-2 denote treatments and R-1 and R-2 denote recovery periods. Mean values (n = 3–5) are provided with error bars representing ± standard error.

2.6. Canopy Temperature Depression (CTD)

CTD of well-watered plants during treatment 2 were often positive at all temperature treatments (Figure 7a–c) indicating that the canopy was cooler than air temperature. Chicory showed the highest CTD at day 2 with cooling of 1.6 °C, 1.8 °C and 3 °C at control, moderate and severe heat stresses, respectively. In contrast all water stressed plants at day 4 and 7 were hotter than well-watered plants. At day 2, the canopy temperature of control and moderate heat stress were closer to air temperature, but at 35 °C, canopies were still 1 °C cooler. Furthermore, temperature and watering interaction was significant at day 7 (Table 6) indicating that the difference between well-watered and water stressed plants became higher when the severity of the high temperature stress increased.

Table 5. Level of significance of the main factors and their interactions on each day for relative leaf water content.

Main Factors and Interactions	Pre-Treatment	Treatment 1		Recovery 1		Treatment 2		Recovery 2	
	Day 0	Day 3	Day 6	Day 2	Day 6	Day 3	Day 6	Day 3	Day 6
Temperature	NS	NS	NS	NS	NS	NS	NS	NS	NS
Water status	NS	*	***	***	*	***	***	***	***
Species	***	***	*	***	***	NS	***	*	NS
Temperature × Water status	NS	NS	NS	*	NS	NS	***	***	***
Temperature × Species	NS	NS	NS	NS	NS	NS	***	***	NS
Water status × Species	NS	NS	NS	***	NS	*	***	***	***
Temperature × Water status × Species	NS	NS	NS	NS	NS	NS	***	**	*

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

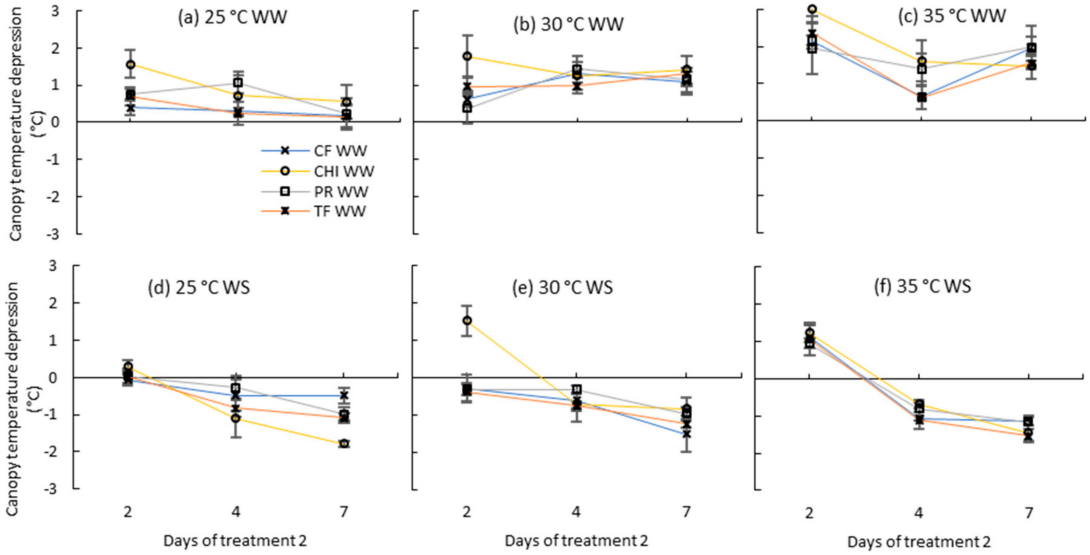

Figure 7. Canopy temperature depression (Ta-Tc) of perennial ryegrass (PR), cocksfoot CF), tall fescue (TF) and chicory (CHI) during day 2, 4 and 7 of the second treatment period. (**a**), (**b**) and (**c**) represent well-watered (WW) plants grown at control, moderate and severe temperatures, respectively, while (**d**), (**e**) and (**f**) represent corresponding water stressed (WS) plants. Means are shown (n = 3 or 5) with error bars representing ± standard error.

Table 6. Level of significance of canopy temperature depression measured on day 2, 4 and 7 in the second treatment period.

Main Factors and Interactions	Treatment 2		
	Day 2	Day 4	Day 7
Temperature	NS	NS	NS
Water status	***	***	***
Species	***	*	NS
Temperature × Water status	NS	NS	***
Temperature × Species	NS	NS	NS
Water status × Species	NS	NS	NS
Temperature × Water status × Species	NS	NS	NS

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

2.7. Top Dry Weight (Green, Senesced), Root Dry Weight and Root Length

Dry matter yields of green leaves and roots showed clear differences between well-watered and water stressed plants and between species at the end of the experiment (Table 7, Figure 8a,c). Dry weight of green leaves and roots were greater in well-watered plants compared to water stressed plants. Further, higher temperatures (moderate and severe heat stress) increased the dry weight of green leaves compared to the control under well-watered conditions, but water stress counteracted this positive response. In contrast, the weight of the senesced leaves was greater in the water stressed plants and the highest senesced leaf weight was observed in combined severe heat and drought stress treatment. Even though root dry weight declined with increasing temperature and drought stress, root lengths did not show much variations across treatments. All grass species had root lengths of ~80 cm and chicory fluctuated around 65 cm.

Table 7. Level of significance of the top weight (green), top weight (senesced), root weight and root length measured at the end of the experiment.

Main Factors and Interactions Terms	Top Dry Weight (Green)	Top Dry Weight (Dead)	Root Dry Weight	Root Length
Temperature	NS	NS	NS	NS
Water status	***	***	***	**
Species	***	*	NS	***
Temperature × Water status	***	***	NS	NS
Temperature × Species	*	***	NS	*
Water status × Species	**	*	**	NS
Temperature × Water status × Species	NS	***	NS	NS

NS = Non-significance, * $p < 0.05$, ** $p < 0.005$ and *** $p < 0.001$.

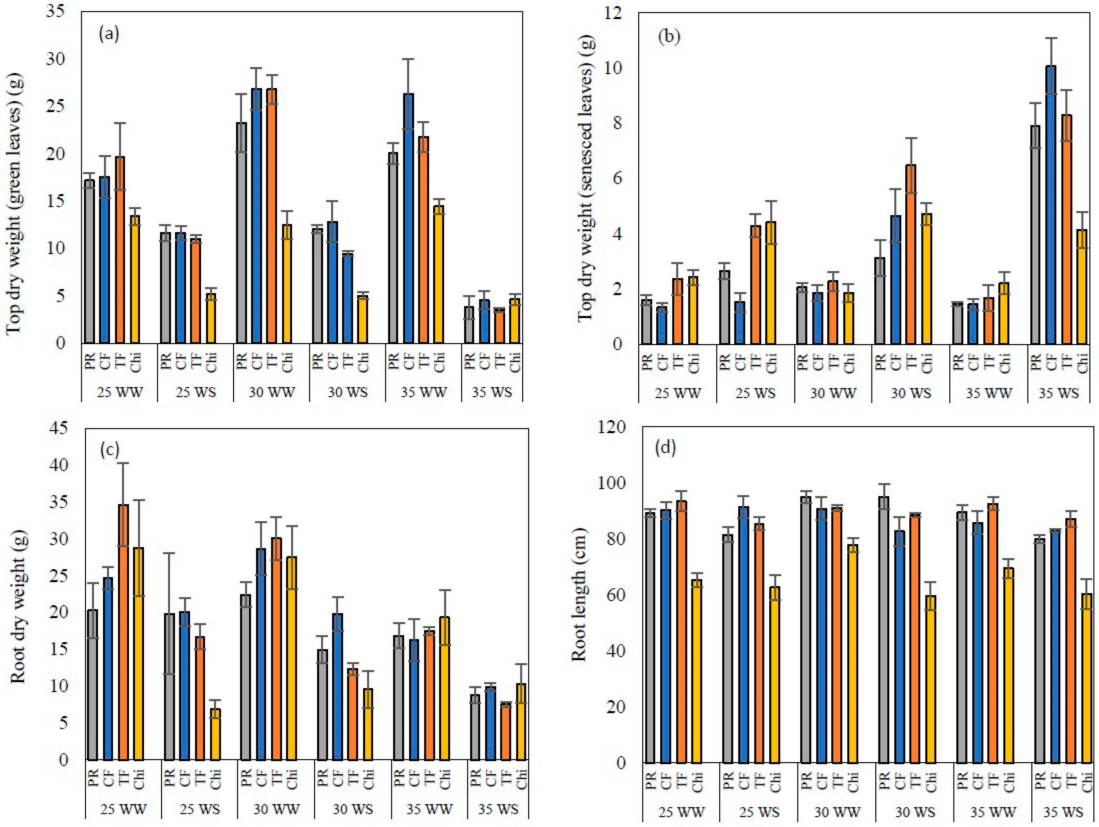

Figure 8. Top dry weight of green (**a**) and senesced leaves (**b**), root dry weight (**c**) and root length (**d**) of perennial ryegrass (PR), cocksfoot CF), tall fescue (TF) and chicory (Chi) measured at the end of the experiment. Mean values $n = 5$ are shown with the error bars representing standard error.

3. Discussion

In this study, all the species acclimated to a combination of moderate heat and drought, but only chicory acclimated to the combination of severe heat and drought stresses. Chicory not only tolerated consecutive severe heat and drought stress but also maintained growth as indicated by greater Fv/Fm, leaf elongation rates, RLWC and cell membrane stability at the end of the second severe heat and drought stress. This superior heat and drought tolerance of chicory is consistent with previous findings that showed chicory survived under supraoptimal temperatures (38/25 °C, day/night) and drought stresses for 18 days while other grass species including perennial ryegrass and cocksfoot died after 12 days of the same stress [33,48]. However, it is also important to note that the grasses did recover (partially) at the end of the experiment in the present study, suggesting that the consecutive heat and

drought stresses of this magnitude were not severe enough to challenge the survival of the tested temperate grass species.

3.1. Individual Stresses

3.1.1. Effects of Heat Stress

Leaf elongation rates of all species were significantly affected by the severe heat stress in this study, confirming that growth rate of the youngest leaf is sensitive to the temperature changes in its growing environment [49]. A rapid decline of shoot growth of perennial ryegrass under high temperatures above 30 °C with complete cessation of growth at temperatures above 35 °C has been observed previously [50]. However, other physiological parameters such as Fv/Fm, EL% and RLWC of the four species were not affected by seven day moderate or severe heat stresses alone. A previous study has reported similar results that most of the cool season pastures in SE Australia (including pasture species used in this study) maintained Fv/Fm values near 0.83 (similar to unstressed plants) during heat stress treatment of 38/25 °C, day/night [33]. Similarly, Jiang and Huang [32] reported that leaf water content and EL% of perennial ryegrass and tall fescue was not affected by exposing plants only to heat stress of 35/30 °C, day/night for 12 days. Maintenance of the physiological functions under heat stress can be ascribed to the cooling effect of plants due to increased transpiration rate when there is enough soil moisture available. For instance, Jiang and Huang [32] observed transient increase of transpiration rates of perennial ryegrass and tall fescue plants during the first nine days of the heat stress compared to control plants. In the present study, canopy temperature depression of irrigated plants under high temperature treatments were often positive indicating that the canopies were cooler than surrounding air temperatures. Canopy temperatures at the control treatment were closer to air, but canopies were about 1.5 °C cooler under moderate heat stress and about 2 °C cooler under severe heat stress treatments. Chicory maintained the coolest canopies (3 °C cooler than air) under severe heat stress on day two of the severe heat stress treatment. Effective cooling of chicory relative to the grasses may be the reason for the lower reduction of leaf elongation rates of chicory during the second severe heat stress than grasses.

3.1.2. Effect of Drought Stress

In this study, leaf elongation rates of all pasture species decreased soon after drought stress was imposed and was below 0.5 cmd^{-1} at the end of both consecutive droughts (Figure 5d). For all the species, this pattern of decrease was more closely related to the pattern of RSWC (Figure 1d) rather than RLWC. This observation coincides with the results of Volaire and Lelièvre [11] who found a linear relationship between leaf extension and the fraction of soil water reserve available for plants. Michelena and Boyer [51] and Van Volkenburgh and Boyer [52] have also observed that the leaf elongation rates of maize decreased with increasing soil moisture deficit while there was no change in the turgor pressure in the growing points of leaves. Likewise, Meyer et al. [53] related the reduction of soybean hypocotyl growth rate from 1.6 to 0.2 mmh^{-1} with decline in soil water rather than hypocotyl turgor pressure. Since expansion of cells is not only related to turgor pressure but also to the supply of water to the growing area [54], declining soil water content could be the likely reason for the observed decline in leaf elongation rates of pasture species.

In this study, cocksfoot maintained relatively higher leaf water content compared to other species during consecutive drought stresses. This may be related to better water uptake of cocksfoot at low soil moisture levels and delay of dehydration. In a comparison study between tall fescue and cocksfoot, Volaire and Lelièvre [11] found that leaf area and water potential of tall fescue decreased earlier than cocksfoot along with the increased cell membrane damage, indicating that cocksfoot possess higher dehydration control under drought stress than tall fescue.

Other physiological parameters like Fv/Fm and EL% were not affected significantly during drought stresses in the tested species. Many other studies also agreed with these results indicating that short-term moderate water deficit had no effect on Fv/Fm [18] and cell membrane stability [55].

3.2. *Effect of Combined Stresses and Acclimation to Previous Stress*

Physiological parameters that were not affected by either heat and drought stress alone were severely affected when plants were exposed to combined heat and drought. Fv/Fm values for plants exposed to the first combined heat and drought treatments (at both moderate and severe temperatures) decreased below the values for non-stressed plants (0.83) suggesting physiological impairments of photosystem II, particularly in tall fescue and chicory. This pattern was consistent in the EL% and the RLWC in these two species; however, perennial ryegrass and cocksfoot were less affected during the first heat and drought stresses. Previous studies have shown that tall fescue has superior heat and drought tolerant capacity than perennial ryegrass [32], which is mainly related to a dehydration avoidance mechanism, from its efficient uptake of water from the deeper soil layers by the deep root system [56–58]. However, in this study, the roots of all the grass species reached the full length >75cm of the growing tubes and there was no difference of root dry weights between perennial ryegrass and tall fescue in moderate and severe heat and drought stress treatments. This result strongly suggests that under similar rooting conditions, tall fescue has no superior heat and drought tolerance compared to perennial ryegrass. Confirming this result, Wallner et al. [59] also found that tall fescue was no more heat tolerant than perennial ryegrass under in vitro conditions as assessed by cell membrane thermostability. In another study conducted in shallow pots (with restricted root growth), Milbau et al. [46] reported a reduction of Fv/Fm in both perennial ryegrass and tall fescue to around 0.2 after seven days of a heat wave of 35.8 ± 3.8 °C, in combination with drought stress, indicating no difference between tall fescue and perennial ryegrass in stress tolerance. Further, plants used in this study were raised from seeds and they were only eight weeks old when the treatments were imposed. Plants used in a similar study which resulted no substantial reduction Fv/Fm in chicory throughout the experiment, were about 8 months old [33] and those used by Jiang and Huang [32], who observed tall fescue perform better than perennial ryegrass, were 4 year old sod pieces.

In comparison with the first treatment, the second heat (both moderate and severe) and drought treatment affected pasture species differently. During the second moderate heat and drought stress treatment, Fv/Fm, EL% and RLWC were less affected in all species compared to the first treatment. This is likely to be due to the stress acclimation of plants. Many studies have demonstrated that plants can adapt to environmental stresses like heat and drought by modifying their membrane structure and functions and the production of heat stress proteins [41,60,61]. It has been shown that previous stress memory not only protects plants from subsequent stresses but also allows better performances [62,63]. The results of the current study are supported by Xu et al. [41], who reported that heat acclimation pretreatment (30 °C for three days) alleviated cell membrane damage and water loss from perennial ryegrass and tall fescue plants exposed to 38 °C.

Unlike in the second moderate heat and drought stress treatment, the second severe heat and drought treatment had detrimental impacts on all pasture species except chicory. During this time period, Fv/Fm values of all grass species decreased by 90% of the control, electrolyte leakage exceeded 90% and RLWC decreased below 20%, and these parameters only partially recovered at the end of the recovery period. In contrast, chicory's tolerance of consecutive combined heat and drought stresses may be due to the maintenance of viable green leaf area. This is evidenced by high relative water content (>0.7) and high Fv/Fm values closer to 0.83 indicating that chicory can produce new biomass with the remaining viable new leaf area produced after the first stress treatment and supply photo assimilates to replenish diminishing carbohydrate reserves during the second stress.

These results demonstrate that the plant species used in this study were better able to acclimate to consecutive moderate heat stress combined with drought stresses. This is an important characteristic in the cool season grasses to produce biomass under warmer and drier climates predicted for the

coming decades in SE Australia. These results also suggest that tall fescue has similar stress tolerance compared to perennial ryegrass, which is in contrast with field studies that demonstrate that tall fescue is more persistent in pastures in south eastern Australia [64]. Greater persistence of tall fescue in field conditions might be due to its deeper roots and that this greater root depth is what confers greater survival under drier and hotter conditions [57,58]. The results of the current study support this by showing no difference between tall fescue and other grasses when the roots are the same length, suggesting that root depth is the key reason for its greater persistence under field conditions. This finding also highlights the importance of selecting or breeding deep-rooted species as an adaptation for the more variable future climates with frequent dry and hot conditions expected in southern Australia. Deeper rooting has been identified as a promising trait for drought adaptation in crops. For instance, in rice crops, cloning of *DEEPER ROOTING 1* (*DRO1*) gene to shallow rooting rice cultivar improved drought avoidance by modifying root system architecture through downward bending of roots [65]. In the current study, the likely reason for chicory's superior heat and drought tolerance was its ability to maintain more viable and photosynthetically active leaf area however, other mechanisms relating to drought survival linked with root characteristics need further research. Further, species with Mediterranean origins may have different responses to combined heat and drought stresses and this is another future research direction. The current study focused only one cultivar from each species and in future research, the use of several genotypes with more than one cultivar would be helpful to screen more drought and heat tolerant species. Among all the species used in this study, chicory may be a potential summer active pasture species that is capable of tolerating more severe heat and drought stress and at the same time producing more livestock feed than grasses in SE Australia.

4. Materials and Methods

4.1. Plant Materials and Establishment

The physiological responses of four summer active temperate pasture species including three grasses; perennial ryegrass (*Lolium perenne* cv. Base AR37), cocksfoot (*Dactylis glomerate* cv. Savvy), tall fescue (*Festuca arundinacea* cv. Quantum II Max P) and a herb; chicory (*Cichorium intybus* cv. Puna II) to heat and drought stress were evaluated in this study. All cultivars are commercially grown and popular among farmers in SE Australia. Quantum II max P is a commercial tall fescue cultivar bread in New Zealand (NZ) with higher summer production and drought tolerance [66]. Cocksfoot cv. savvy originated from continental Europe and is well known for drought tolerance and production under low soil fertility. Perennial ryegrass is less tolerant to drought than tall fescue and cocksfoot however, cv. base AR37 was bread in Australia from drought tolerant plants to enhance late season production. Perennial ryegrass is commercially grown in areas where annual rainfall is over 650 mm [67]. Chicory cv. puna II was selected from a commercial NZ line where it has higher summer production, drought resistance and persistence than grasses [68].

The experiment was conducted in the glass house and growth cabinet facilities at the Faculty of Veterinary and Agricultural Sciences, the University of Melbourne (37.7964°S, 144.9612°E). The experiment was conducted between 21 December 2017 and 3 April 2018. Plants were grown in polyvinyl chloride (PVC) tubes (diameter 10 cm, height 75 cm). A soil media consisting of a 3:1 (v/v) mixture of sand and soil. Soils (Red Chromosol) were collected from Dookie campus, the University of Melbourne. Before plant establishment, five poly vinyl chloride tubes were filled with the air-dried soil medium and then irrigated until free drainage occurred from the bottom of the tube and weighed (fully wet soil). These soils were oven dried at 80 °C for 10 days and dry weight was measured (oven dry soil), to be used later to calculate soil moisture content (described in Section 4.3). Plants were established by sowing six seeds in each tube. Plants were well watered daily to field capacity during the establishment period until the treatments commenced. Liquid fertilizer, aquasol (NPK 23:3.95:14) was applied every two days at seedling concentration (1 g/L:100 mL/plant) at the early stages of growth and increased gradually up to 5 g/L:100 ml/plant until the sixth week after sowing. At week six,

osmocote (NPK 14:1.3:14.9 including iron magnesium and trace elements), a slow release fertilizer, was applied at a rate of 2 kg/m^3 (nearly 12 g/pot). Plants were thinned out to retain three plants/pot at week six and a light grazing was simulated by clipping the plants to 2/3 height to encourage tiller growth. After eight weeks, plants were assigned to three separate growth chambers with 25 °C/15 °C day/night temperature, 12 h photoperiod, 900 μmolm^{-2}s^{-1} light intensity and 70% RH for two weeks, to allow plants to adjust to the growth chamber conditions prior to imposing heat and drought treatments.

4.2. Treatments and Experimental Design

Heat and drought stress treatments commenced 70 days after sowing, following the acclimation period. Plants were exposed to three temperature regimes (control, moderate and severe heat stress) with or without watering as explained below. The stress levels were selected as moderate and severe at 30 °C and 35 °C, respectively, because the onset of heat stress occurs in the key pasture species (perennial ryegrass) at 30 °C and growth stops at 35 °C [50]. Treatments consisted of consecutive seven-day heat and drought stresses each followed by a seven-day recovery period. Conditions during the pretreatment and recovery periods were the same as the control. The heat stress treatments were designed to mimic the summer heat waves experienced in southern Victoria, Australia, where successive heat events are common [69]. Three heat treatments were imposed in separate growth cabinets as follows:

- Control: Plants were grown at 25 °C/15 °C day/night temperatures for the duration of the experiment.
- Moderate heat stress: Plants were grown at control conditions during pre-treatment week. A moderate heat stress was simulated by increasing the cabinet temperatures to 30 °C/20 °C day/night for a seven-day period followed by a seven-day recovery period (by resetting the growth chamber temperatures to the control conditions). The second seven-day heat stress was imposed in the same way followed by another seven-day recovery period.
- Severe heat stress: Two consecutive heat stresses and subsequent recovery periods were given in the same way to the moderate heat stress, but with increased temperatures (35 °C/25 °C day/night).

The diurnal pattern of the temperature variation was simulated in the growth chambers by changing the temperatures gradually between day and night. Environmental conditions of the three growth chambers during the experiment are shown in Figure 9.

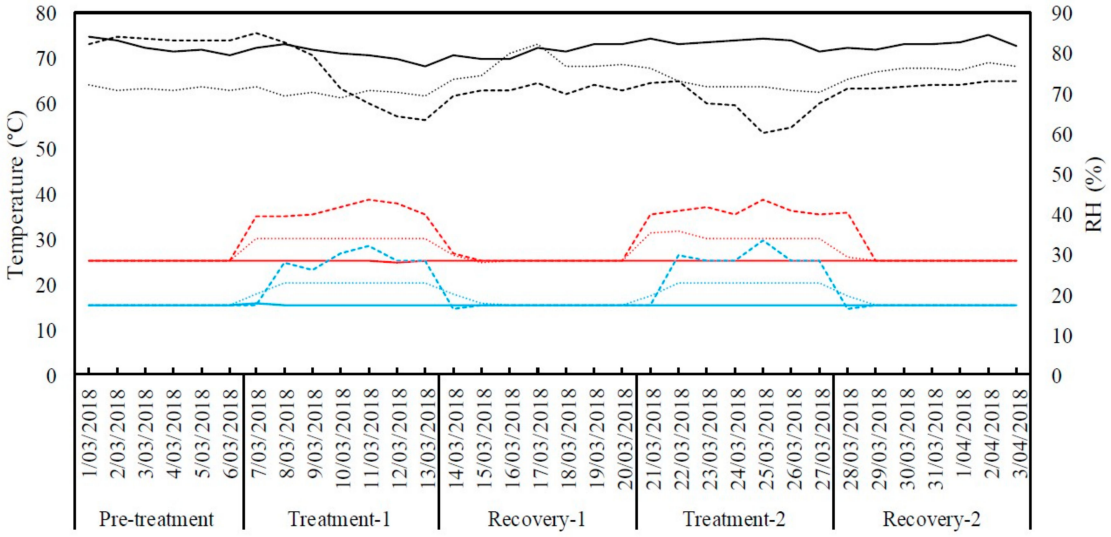

Figure 9. Daily maximum (red), minimum (blue) temperatures and average relative humidity (RH %) (black) inside the growth chambers for the duration of experiment. The thick line represents control (25 °C/15 °C day/night) treatment, the dotted line represents moderate heat stress treatment (30 °C/20 °C day/night) and the dashed line represents severe heat stress treatment (35 °C/25 °C day/night).

Two watering treatments were applied in each growth chamber. One set of plants was irrigated each day to the field capacity for the entire duration (well-watered). Irrigation was withheld in another set of plants during the period of high temperature stress (drought). All plants were well-watered during the pre-treatment and the recovery periods.

The current study carried out inside growth chambers fairly resembles the natural environment in several ways. Pasture plants were grown in 75 cm long PVC tubes to allow more root growth into deep layers of the potting media. Further, diurnal variation of the temperature change was simulated by gradually increasing and decreasing the temperature between day and night. Finally, light intensity was maintained at 19.4 MJm^{-2} (~900 $\mu molm^{-2}s^{-1}$) which is in the range of radiation intensity during heat waves in the SE Australia. For example, at Ellinbank, analysis of climate parameters indicated that the radiation intensity of days with a maximum daily temperature >30 °C reach on average 25 ± 5 $MJm^{-2}d^{-1}$ (data not shown).

There were 40 pots per growth chamber (two irrigation treatments × four species × five replicates) arranged in eight rows and five columns (blocking structure). Well-watered and drought stressed treatments were simulated in alternative rows of plants (eight in all). Five replicate plants of each species were randomly allocated in each watering treatment and the experimental design was randomized in row and column wise directions within each growth chamber.

4.3. Measurements

Key physiological measurements such as maximum photochemical efficiency of PS II (Fv/Fm), cell membrane permeability (electrolyte leakage %), leaf elongation rate (cmd^{-1}), leaf relative water content and the canopy temperature (°C) were measured at two to three-day intervals. Relative soil moisture content of the pots was also measured at one-day intervals. At the end of the experiment, plants were harvested and the dry weight of the canopy (green and senesced) (g), root length (cm) and root dry weight (g) were measured.

Relative soil water content (RSWC) was calculated for each species to monitor soil dryness with time. Pots were weighed to measure the weight of soil with water. RSWC was calculated using Equation (1) [46].

$$RSWC = \frac{Actual\ weight\ of\ water\ in\ tubes\ (Weight\ of\ soil\ with\ water - weight\ of\ oven\ dried\ soil)}{Potential\ weight\ of\ water\ in\ tubes\ (weight\ of\ fully\ wet\ soil - weight\ of\ oven\ dried\ soil)} \quad (1)$$

Chlorophyll fluorescence was measured using a MINI PAM (pulse amplitude modulation), portable chlorophyll fluorometer (Heinz Walz GmbH, Effeltrich, Germany). The maximum photochemical efficiency of PSII, Fv/Fm (Genty parameter) [70] was measured in dark-adapted leaves by selecting the youngest fully expanded leaves on the plant using the leaf clip holder 2030-B. The distance between the leaf and the fiberoptic was maintained at 15 mm during measurements. The angle between the fiberoptic axis and the leaf was 60°. Plants were subjected to darkness by turning lights off inside growth cabinets for one hour (in between 17.00–18.00) before taking measurements. Mode menu-5 (ML-BURST function) of the MINI PAM was used for the measurements to reduce the intensity of measuring light to 1/5 and clear any false signals in the fluorescence measurement.

Cell membrane damage induced by heat and drought stresses was measured by testing the percentage electrolyte leakage (EL%) in leaves as described by Jiang and Huang [32]. Fully grown leaves were collected destructively from each pot and cut into small pieces of about 1 cm. Those leaf pieces were rinsed three times with distilled deionized water to wash out surface adhered electrolytes and those on the cut surfaces. Leaf pieces (5–10) were placed in test tubes and filled with 15 ml distilled deionized water. Test tubes were then shaken for 18 h in a mechanical shaker before measuring the initial conductivity (C_1). Leaf samples were then autoclaved at 121 °C and 0.1 MPa for 15 minutes to kill the leaf tissues and the final conductivity (C_2) was measured. EL% was computed as $(C_1/C_2) \times 100$.

To calculate leaf elongation rates, a tiller with three fully expanded leaves and one emerging leaf was randomly selected from each pot and marked with a plastic wire ring at the base of the tiller. The

length (cm) of the youngest elongating leaf was measured from tip to ligule of the youngest fully expanded leaf [71]. Leaf elongation rate was calculated by dividing the difference of the leaf length by the number of days and given as cmd^{-1}. New tillers were selected every 2–4 days or when a new leaf started to emerge from the same tiller.

Relative leaf water content (RLWC) was measured according to the method used by Barrs and Weatherley [72] and Jiang and Huang [32]. First, the middle part of a fully-grown leaf was excised from each plant and fresh weight was recorded. Then the leaf was put into a water filled test tube and kept in the dark for five hours to reach full hydration. After five hours, the surface water was blotted dry using tissue paper and turgid weight was measured. Leaves were kept inside the oven at 60 °C for 48 h and dry weight was measured. RLWC was calculated using following equation.

$$RLWC = \frac{Fresh\ Weight - Dry\ weight}{Turgid\ weight - Dry\ weight} \quad (2)$$

Canopy temperature was measured using infrared camera (FLIR T-series; model B 360) during the second, fourth and seventh day of the second treatment period. Thermal images of 3–5 plants in each species were captured using the white colored wall of the growth chamber as the background. The thermal images had a resolution of 320 × 240 pixels. Each pixel represents a specific temperature value of the picture. Thermal images were analyzed using a custom code developed using MATLAB R 2014b software [73]. Pixels from the background and the pot were excluded by selecting the maximum and minimum temperature value within the canopy and the pixels within the canopy were averaged to calculate canopy temperature. Air temperature inside growth chambers was measured using a mercury thermometer during the capture of each thermal image to get the accurate air temperature inside the cabinet. The difference between canopy temperature and air temperature (canopy temperature depression, CTD) was calculated as T canopy − T air.

At the end of the experiment, plants were harvested from the base near the soil surface and leaves of each plant were separated into green and senesced portions. Leaves were dried in the oven at 80 °C until constant weight achieved. Dry weight of the dead and green leaves was measured.

Remaining soil column with roots was removed from the PVC tubes and roots were carefully washed to remove the trapped soil particles. Root system length was measured in each plant and roots were oven dried at 80 °C until a constant weight achieved. Dry weight of the roots was measured.

4.4. Statistical Analysis

Data were statistically analyzed using linear mixed models, using GenStat statistical software. Rows and columns in each chamber were used as random effects in the model, while temperature, water status (irrigated or drought stressed) and species were used as fixed effects. Mixed models were used in this analysis because it could account for the lack of balance in the experimental design. Physiological measurements on each day were analyzed to reveal the differences between temperature, water and species and their interactions.

5. Conclusions

This study demonstrated that temperate cool season pasture species can acclimate to combined moderate heat and drought stresses, but chicory is the only species that maintained growth under combined severe heat and drought stress. The results further showed that tall fescue has no superior drought and heat tolerance compared to perennial ryegrass under similar rooting conditions. Therefore, the ability of tall fescue to tolerate drought stress under field conditions may be largely due to its deep rooting and effective water uptake from the deeper soil layers. Individual stresses had no significant impacts on physiological functionality of pasture species, but the leaf elongation rates were affected by either stress alone. Irrigation mitigated the negative impacts of heat stress by cooling the pasture canopies 1–3 °C through transpirational cooling, with chicory having the coolest canopy temperature. While the specific mechanisms of chicory's greater heat and drought tolerance compared to grasses

deserve further research, it can be concluded that chicory is a potential pasture species to provide livestock feed under more challenging hot and dry summer months in SE Australia.

Author Contributions: Conceptualization, R.S.P., B.R.C. and R.J.E.; Data curation, R.S.P.; Formal analysis, R.S.P. and B.R.C.; Funding acquisition, B.R.C.; Investigation, R.S.P.; Methodology, R.S.P., B.R.C. and R.J.E.; Project administration, B.R.C. and R.J.E.; Resources, B.R.C.; Supervision, B.R.C. and R.J.E.; Validation, R.S.P.; Visualization, B.R.C.; Writing—original draft, R.S.P.; Writing—review and editing, R.S.P., B.R.C. and R.J.E.

Funding: This research received no external funding.

Acknowledgments: The authors acknowledge the kind support of the Steven Elefteriadis, Glasshouse Complex Manager, Faculty of Veterinary and Agricultural Sciences (FVAS)/School of Biosciences, The University of Melbourne for allocating glass house space, growth chamber facilities and providing equipment to conduct this experiment. The authors would also like to thank Associate Professor Graham Hepworth, Statistical consultant center, The University of Melbourne for the statistical advice, the technical staff of the soil science laboratory of the FVAS for the assistance given in using the equipment and Mahil Pathirana, Department of Infrastructure Engineering, The University of Melbourne for the technical assistance.

Conflicts of Interest: The authors declare no conflict of interest.

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CHAPTER 7. Using leaf temperature to improve simulation of heat and drought stresses in a biophysical model (Journal paper)

Perera, R, Cullen, B, Eckard, R (2020) Using Leaf Temperature to Improve Simulation of Heat and Drought Stresses in a Biophysical Model. *Plants* **9**, 8. doi:10.3390/plants9010008

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Using Leaf Temperature to Improve Simulation of Heat and Drought Stresses in a Biophysical Model

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Received: 2 November 2019; Accepted: 13 December 2019; Published: 19 December 2019

Abstract: Despite evidence that leaf temperatures can differ by several degrees from the air, crop simulation models are generally parameterised with air temperatures. Leaf energy budget is a process-based approach that can be used to link climate and physiological processes of plants, but this approach has rarely been used in crop modelling studies. In this study, a controlled environment experiment was used to validate the use of the leaf energy budget approach to calculate leaf temperature for perennial pasture species, and a modelling approach was developed utilising leaf temperature instead of air temperature to achieve a better representation of heat stress impacts on pasture growth in a biophysical model. The controlled environment experiment assessed the impact of two combined seven-day heat (control = 25/15 °C, day/night, moderate = 30/20 °C, day/night, and severe = 35/25 °C, day/night) and drought stresses (with seven-day recovery period between stress periods) on perennial ryegrass (*Lolium perenne* L.), cocksfoot (*Dactylis glomerata* L.), tall fescue (*Festuca arundinacea* Schreb.) and chicory (*Cichorium intybus* L.). The leaf temperature of each species was modelled by using leaf energy budget equation and validated with measured data. All species showed limited homeothermy with the slope of 0.88 ($P < 0.05$) suggesting that pasture plants can buffer temperature variations in their growing environment. The DairyMod biophysical model was used to simulate photosynthesis during each treatment, using both air and leaf temperatures, and the patterns were compared with measured data using a response ratio (effect size compared to the well-watered control). The effect size of moderate heat and well-watered treatment was very similar to the measured values (~0.65) when simulated using T leaf, while T air overestimated the consecutive heat stress impacts (0.4 and 0). These results were used to test the heat stress recovery function (Tsum) of perennial ryegrass in DairyMod, finding that recovery after heat stress was well reproduced when parameterized with T sum = 20, while T sum = 50 simulated a long lag phase. Long term pasture growth rate simulations under irrigated conditions in south eastern Australia using leaf temperatures predicted 6–34% and 14–126% higher pasture growth rates, respectively at Ellinbank and Dookie, during late spring and summer months compared to the simulations using air temperatures. This study demonstrated that the simulation of consecutive heat and/or drought stress impacts on pasture production, using DairyMod, can be improved by using leaf temperatures instead of air temperature.

Keywords: energy budget; leaf temperature; air temperature; simulation modelling; heat stress recovery; DairyMod; pasture

1. Introduction

Climate change projections for Australia indicate increasing frequency and magnitude of extreme climate events such as heat waves, droughts, extreme precipitation and frost occurrences in the coming decades [1], which are likely to reduce productivity and profitability of pasture-based systems [2]. A recent study conducted in southeastern (SE) Australia showed that the anticipated changes to

the pasture growth patterns under future climate change reported by [3,4] are already occurring under current climate change, including increased pasture yield variability over the major growing seasons (autumn and spring) and a decreased spring season growth leading to shorter growing season lengths [5]. These changes were more prominent in the most recent period (2002–2015) compared to the periods before and were mainly caused by the increased occurrences of heat and drought stress [5].

The optimal temperature range for growth of temperate pasture species lies between 15 °C and 23 °C [6,7]. Beyond this range, growth and physiological processes decrease in plants. Net photosynthesis reduction of perennial ryegrass (*Lolium perenne*) and Kentucky blue grass (*Poa pratensis)* starts at temperatures above 25 °C [8,9]. For cocksfoot (*Dactylis glomerata)*, the optimum temperature range for maximum net canopy photosynthesis is between 19 and 22 °C and the values declining to lowest at 31 °C [10]. Physiological impairments due heat stress occurs in plants mainly due to reduction of Rubisco activity [11,12], reduction of maximum photochemical efficiency of photosystem II [13,14], reduction of apparent electron transport rate of photosystem I [15], production of reactive oxygen species (ROS) [16,17] and subsequent damages to the cell membranes [18]. Since high temperature stress often coincides with moisture limitation under field conditions, the combined impacts could be over and above the effects of individual stresses [13,14,19].

Accurate assessment of the effects of heat and drought stresses on crop processes is important to identify correct management and adaptation strategies in order to stabilize production. Many crop simulation models incorporate heat and drought stress impacts on growth and developmental processes. For example, the Agricultural Production Systems sIMulator (APSIM) simulates leaf senescence of wheat (*Triticum aestivum* L.) due to heat stress between 32 °C and 34 °C (daily maximum temperatures) [20,21]. Ecosys simulates heat stress impacts on seed set of wheat above 33 °C during anthesis and post anthesis periods [22]. Likewise, grain filling in wheat crop stops when the maximum temperature exceeds 38 °C in STICS (Simulateur mulTIdisciplinaire pour les Cultures Standard) model [23]. However, many of the biophysical models are parameterized with air temperatures taken from the meteorological data assuming that air temperature is a fair representation of the environment at which crops are grown. It is well known that leaf temperature can differ from air temperatures [24], depending on the structural and physiological characteristics of the leaf. Under well-watered conditions, it has been observed that plant leaves are generally cooler than air at above optimum temperatures and hotter than air at below optimum temperatures [25–27]. This phenomenon is called "limited homeothermy" and considered as an adaptive response of plants to maintain leaf temperatures within the optimum range for photosynthesis [25].

Ignoring this leaf-to-air temperature difference may cause uncertainties in assessing heat and drought stress impacts by crop simulation models [28]. It may also result in parameterizing heat stress functions with unrealistic temperature threshold values [28,29] and in turn predicting unrealistic results [30]. Use of leaf/canopy temperatures would reduce such uncertainties and improve the simulations. For example, canopy temperature measured during the anthesis of the rye canopy (*Secale cereal* L.) was 2 °C cooler than the air when irrigated and it was 7 °C warmer than the air under rainfed conditions [28]. Based on this observation, heat stress effects on rye grain number observed in controlled experimental conditions were able to reproduce well under field conditions when only the stress thermal time ((STT) temperature sums accumulated above high temperature stress threshold during the heat sensitive growth stage of the crop [31]) was calculated using canopy temperatures, but not using air temperatures. Similarly, the use of canopy temperature calculated using energy balance slightly improved heat stress effects of wheat than using air temperature in wheat models [29].

Leaf energy balance provides a process-based approach to incorporate canopy temperature effects into crop simulation models [24,25,29]. In an energy balance approach, the summation of net radiation (absorbed–emitted), latent heat flux (energy required to evaporate water) and sensible heat flux (energy required to warm or cool the leaf) at the leaf surface should be equal to zero. The latent heat is proportional to the transpiration rate and the sum of boundary layer and stomatal conductance to water, while sensible heat flux is proportional to the difference between leaf and air temperature and

boundary layer conductance to heat. Therefore, leaf temperature can be derived from the sensible heat flux term. Using these thermodynamic principles and linearization techniques used by Penman [32], Campbell and Norman [24] derived an equation to determine leaf temperature in a straightforward way, using air temperature, wind speed, radiation and vapor pressure deficit, which enables the calculation of the leaf temperature using the recorded weather data and crop specific parameters.

DairyMod is a mechanistic biophysical pasture model developed to predict grazing dynamics across a range of climates, soil types, forage species and management under conditions in Australian and New Zealand [33]. In the DairyMod model, temperature response to photosynthesis describes the growth of pasture species using minimum and optimum temperatures where growth limitation occurs at temperatures above and below the optimal temperatures. Additionally, growth restrictions under high temperatures are simulated in the model using an empirical function referred to as the high-temperature stress coefficient, which is a scale ranging from 0 (full stress) to 1 (no stress). The model reduces photosynthesis and subsequent growth if the maximum daily temperature exceeds the high temperature onset and approaches maximum when it reaches full stress [34]. High temperature stress thresholds (onset and full) for perennial ryegrass have been parameterized using experimental evidence [35]; however, there is little data available to parameterize the recovery from heat stress (T sum) in the model.

The broad objective of this study was to evaluate whether the use of leaf temperature compared to air temperature can better simulate the impact and recovery of consecutive heat and drought stresses leading to improved prediction of heat and drought impacts in biophysical models. The specific objectives were: (1) to test the limited homeothermy hypothesis for four temperate pasture species commonly grown in SE Australia; (2) to validate the leaf energy budget equation using leaf temperature data measured under well-watered (WW) and water-stressed (WS) conditions at three temperature levels; (3) to parameterize the high temperature stress recovery function in DairyMod, and finally, (4) to model leaf temperature using the leaf energy budget equation and use these in simulations in DairyMod to estimate the uncertainty associated with use of air temperature to predict pasture growth at two sites in SE Australia.

2. Results

2.1. Test for the Limited Homeothermy of Pastures

The slope of the relationship between leaf and air temperature for irrigated plants was 0.88 (R^2 = 0.95). This slope was significantly less than 1 (P = 0.001) and greater than 0 ($P < 0.001$) (Figure 1), therefore the pasture species used in this study would be classified as limited homeotherms, with the ability to buffer leaf temperature against the variation in the ambient air temperature.

In general, leaf temperatures were cooler than air temperatures under well-watered (WW) conditions, while leaves were warmer than air temperatures under water-stressed (WS) conditions (Figure 1). The difference between WW and WS plants at each temperature on each day was significant at $P = 0.05$ level, except for the moderate heat stress on day 2. The difference between WW and WS plants was smaller on day 2 of the stress treatment and it increased as the combined heat and drought stresses progressed through time. For instance, the difference between WW and WS plants on day 2 was 1.1 °C under severe heat stress (35 °C), but increased to 2.3 °C on day 7 ($P < 0.001$).

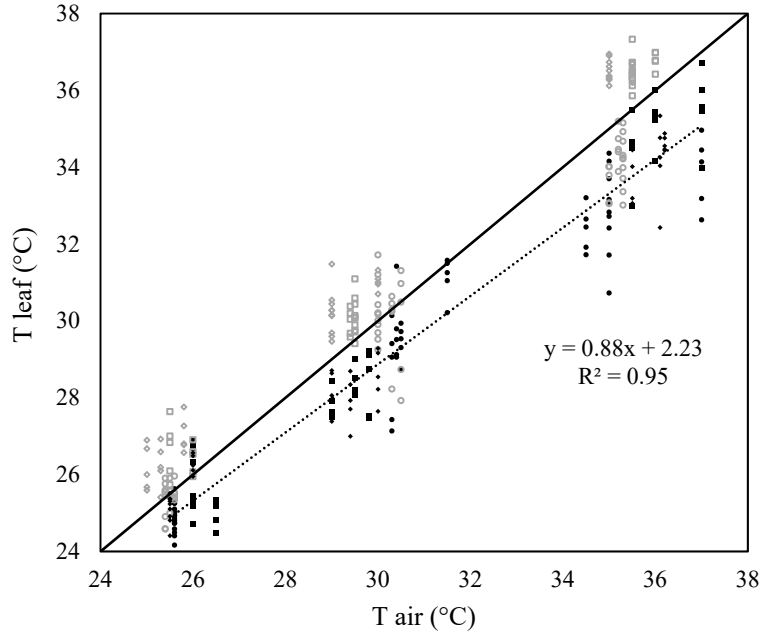

Figure 1. Relationship between air temperatures inside the growth chambers and leaf temperatures (measured using infra-red thermal images) of perennial ryegrass, cocksfoot, tall fescue and chicory at three temperatures (25 °C, 30 °C and 35 °C) and two watering levels during day 2(●), 4(■) and 7(♦) of the second combined heat and drought stress treatment. Filled black symbols represent well-watered plants and open grey symbols represent water-stressed plants. The thick line refers to the 1:1 reference line and dotted line represents regression line for well-watered plants. n = 294.

2.2. Ability of the Leaf Energy Budget Equation to Model Leaf Temperature

The measured leaf temperature is compared with modelled temperatures using the leaf energy budget for each pasture species in Figure 2 with summary statistics presented in Table 1. The mean bias indicates that there is an overprediction of 0.98 °C on average for all the data (Table 1). Chicory showed the highest mean bias of 3.06 °C while grasses had mean bias less than 0.5 °C. Mean prediction error was also less than 5% for grasses indicating excellent model prediction but was 10.8% for chicory. Similarly, modelling efficiency was above 0.9 for the grass species, while for chicory it was 0.37. Bias correction factor (C_b) and Variance Ratio (V) were above 0.9 for all the categories, indicating that there were only small deviations from 1:1 reference line and that variance in measured and modelled data were similar in all the categories. In general, the leaf energy budget equation predicted the leaf temperature more accurately for grasses (with higher R^2, Pearson's correlation coefficient (r), modelling efficiency (MEF), concordance correlation coefficient (CCC) and lower mean prediction error (MPE)) than chicory.

Table 1. Summary statistics calculated to assess the adequacy of the leaf energy budget equation in modelling leaf temperature (all data, for perennial ryegrass, cocksfoot, tall fescue, chicory, well-watered and water-stressed plants). Cb, bias correction factor; CCC, concordance correlation coefficient.

Model Statistics	All Data	Perennial Ryegrass	Cocksfoot	Tall Fescue	Chicory	Well-Watered	Water-Stressed
Mean (measured)	30.02	30.05	29.83	30.23	29.93	29.32	30.74
Mean (calculated)	31.00	30.18	30.31	30.61	32.99	30.37	31.65
Mean bias	−0.98	−0.13	−0.48	−0.39	−3.06	−1.05	−0.91
R2 (Coeff. of determination)	0.89	0.95	0.97	0.96	0.94	0.86	0.91
r (Pearson's correlation coeff.)	0.94	0.98	0.99	0.98	0.97	0.93	0.95
Mean Prediction Error (MPE)	5.88%	3.18%	3.03%	2.86%	10.79%	6.38%	5.36%
Modelling Efficiency (MEF)	0.80	0.94	0.95	0.95	0.37	0.76	0.83
Variance Ratio (V)	0.92	0.94	0.93	0.97	0.96	0.91	0.91
Cb	1.00	0.97	1.00	1.00	1.00	1.00	1.00
CCC	0.94	0.95	0.98	0.98	0.97	0.92	0.95
n	294	76	69	79	70	150	144

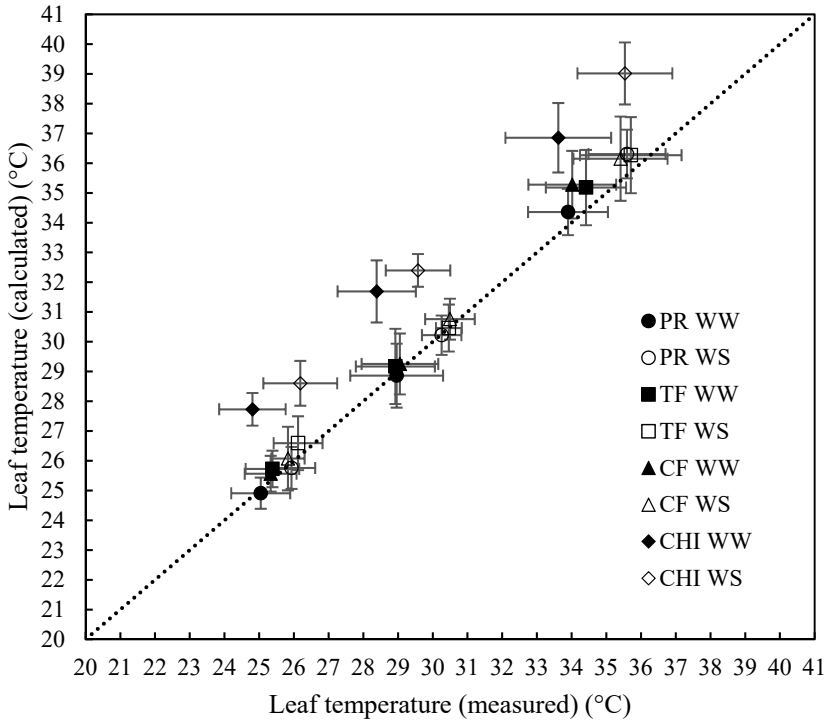

Figure 2. Measured (using infra-red camera) and modelled (using leaf energy budget equation) leaf temperature values of perennial rye grass (PR), cocksfoot (CF), tall fescue (TF) and chicory (CHI) at three temperature (25 °C, 30 °C and 35 °C) and two watering levels (well-watered (WW) - filled symbols, water-stressed (WS) - open symbols) during the second combined heat and WS treatment. Means (3–5 plants) of each species are presented with error bars representing ± standard deviation. The dotted black line is the 1:1 reference line.

2.3. Use of T Leaf and T Air to Simulate Photosynthesis

Perennial ryegrass showed a significant decrease in the measured leaf photosynthesis rates at the end of consecutive WS treatments by 74% and 65%, respectively, compared to the WW plants at the control temperature (25 °C) (Figure 3a). Heat stress at 30 °C only decreased leaf photosynthetic rates by 35% and 27% during consecutive treatments (Figure 3b). In contrast, photosynthetic rates reached zero (100% reduction) when the heat (30 °C) and drought stresses were imposed together (Figure 3b). At both temperatures, perennial ryegrass fully recovered from combined heat and WS treatments at the end of each recovery phase.

DairyMod simulated photosynthetic rates of perennial ryegrass using T-air versus T-leaf and Tsum 50 versus Tsum 20 (Figure 3c–h) followed a similar pattern to the measured photosynthesis data (Figure 3a,b). Correlation coefficients showed that there was a strong ($r > 0.85$) ($P < 0.05$) correlation between measured and modelled data in WS treatments, while no such significant pattern was observed in WW plants (Table 2). Recovery of photosynthesis after heat stress was reproduced well when the DairyMod model was parameterised using Tsum = 20, while there was a long lag phase in the recovery period at combined severe heat and drought treatments when Tsum 50 was used. For instance, photosynthesis rates recovered only by 50% (Figure 3e) when Tsum 50 was used irrespective of the leaf temperature or air temperature used. Even though no photosynthetic data were available at 35 °C, other physiological data such as maximum photochemical efficiency of photosystem II, leaf elongation rates and relative water contents measured in this same experiment provide evidence that perennial ryegrass fully recovered from severe heat and drought stress at the end of the seven-day recovery period [14], which was well simulated when Tsum 20 was used (Figure 3h).

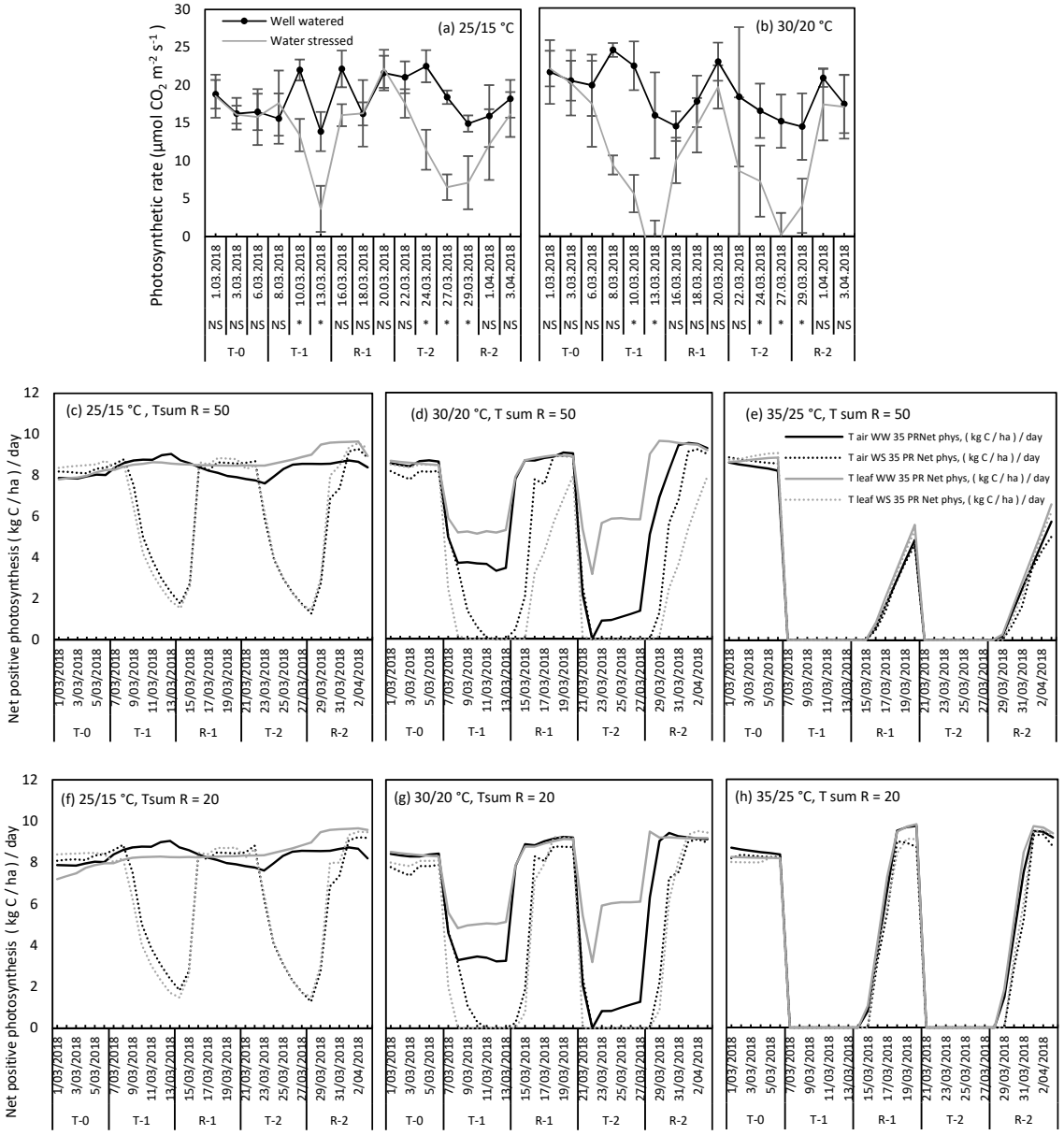

Figure 3. Net photosynthetic rates (µmol CO_2 m^{-2} s^{-1}) measured under control and moderate heat stress (**a**,**b**) and net positive photosynthesis ((kg C / ha) / day) modelled using DairyMod biophysical model (**c–h**). Middle graphs (**c–e**) represent modelled data with T sum = 50 and the bottom graphs (**f–h**) represent modelled data with T sum = 20. In graphs a and b, black line indicates WW and grey lines indicate WS plants with significant differences between WW and WS at each day is shown in asterisk marks. NS = Not Significant. In Figure c–h, black lines represent simulations run using air temperatures and grey lines represent simulations run using leaf temperatures. Thick lines denote well-watered plants while dotted lines denote water-stressed plants. T-0 represents pre-treatment period, T-1 and T-2 represent 7-day treatments and R-1 and R-2 represent 7-day recovery periods.

Effect size (calculated as response ratio) of each temperature and watering treatment compared to the WW control was shown for measured and simulated data (using Tsum 20) in Figure 4. Response ratios calculated for measured data were well reproduced by both DairyMod simulations (using air temperature and leaf temperature) in WS plants at control and moderate temperatures. However, simulations with leaf temperature performed better than air temperature in simulating the effect size of WW plants under moderate heat stress (Figure 4b). For instance, response ratio calculated using leaf temperature simulations was reduced from 1 to 0.6 during the first treatment period (T-1) which was

very similar to the actual reduction of response ratio (from 1 to 0.65) in the measured data, but it was reduced to 0.37 in the simulations with air temperature. During the second treatment, reduction in response ratio calculated with simulations run with leaf temperature decreased to 0.38 on day 2 of the treatment but recovered quickly to 0.7 on day 4, which is again similar to the measured reduction (0.7). In contrast, response ratios calculated using simulations run with air temperature reached minimum values of zero. Likewise, at both consecutive moderate heat stress treatments under WW conditions, DairyMod simulations with air temperature overestimated the actual impacts of moderate heat stress on perennial ryegrass. This was also confirmed by the evaluation statistics shown in Table 3, where under moderate heat stress and WW treatment (Figure 4b), RMSE was larger (0.54) for simulations run with air temperature, while it was much smaller (0.36) for simulations run with leaf temperature. Likewise, MAE was also higher for air temperature (0.42) and lower for leaf temperature (0.25) (Table 3).

Table 2. Correlation coefficients between measured and simulated (with air temperature versus leaf temperature and Tsum = 50 versus Tsum = 20) photosynthetic rates of perennial ryegrass at control (25 °C) and moderate heat stress (30 °C) under WW and WS treatments. Correlation coefficients (r) shown in bold are significant (P = 0.05).

		Tsum R = 50		Tsum R = 20	
		T Air	T Leaf	T Air	T Leaf
25 °C	WW	−0.39	−0.22	−0.39	−0.14
	WS	**0.87**	**0.86**	**0.86**	**0.86**
30 °C	WW	0.18	−0.07	0.09	−0.09
	WS	**0.88**	**0.93**	**0.86**	**0.87**

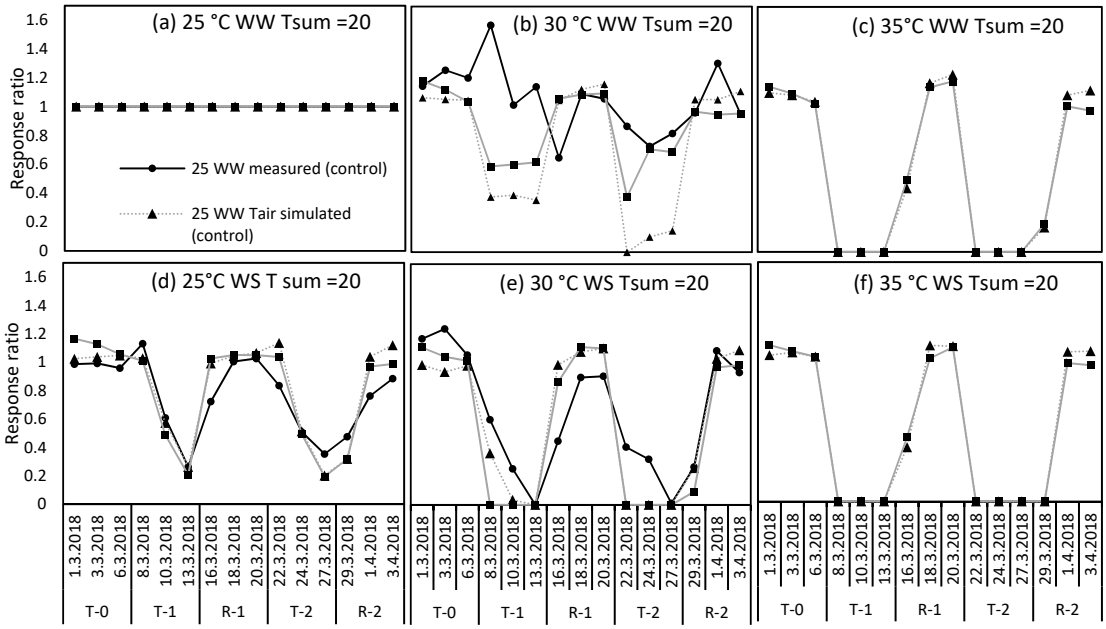

Figure 4. Response ratios (effect size compared to well-watered control) of perennial ryegrass for well-watered (WW, **a**,**b**,**c**) and water-stressed plants (WS, **d**,**e**,**f**) at three temperature levels (25 °C, 30 °C, 35 °C) calculated using photosynthesis rates of measured data (●) and simulated data using air temperature (▲) and leaf temperature (■) during the experiment. T-0 is the pretreatment period, T-1 and T-2 are treatments and R-1 and R-2 are recovery periods.

Table 3. Root mean square error (RMSE) and mean absolute error (MAE) comparisons for response ratios between measured data and simulated data with air temperature and leaf temperature at 25 °C WW and 30 °C, WW and WS plants.

	(RMSE)		(MAE)	
	Tair	**Tleaf**	**Tair**	**Tleaf**
25 °C WS	0.16	0.15	0.12	0.13
30 °C WW	0.54	0.36	0.42	0.25
30 °C WS	0.24	0.26	0.19	0.20

2.4. Uncertainty in Perennial Ryegrass Growth at Ellinbank and Dookie when Using Air Temperature in the Simulations

When applying a leaf energy budget to calculate leaf temperature, the modelled leaf temperatures of perennial ryegrass under irrigated conditions were generally cooler than air at both Ellinbank and Dookie sites above maximum air temperatures of 18 °C and 16 °C, respectively (Figure 5). Below these temperatures, modelled leaf temperatures were warmer than air agreeing with the limited homeothermy hypothesis as tested with the measured data. Modelled leaf temperatures scattered more widely around the 1:1 reference line at both sites under rainfed situations. This was due to the presence of both wet and dry days within a year where leaf temperatures are cooler when there is enough soil moisture to transpire, while leaf temperatures tend to be warmer when there is limited soil moisture.

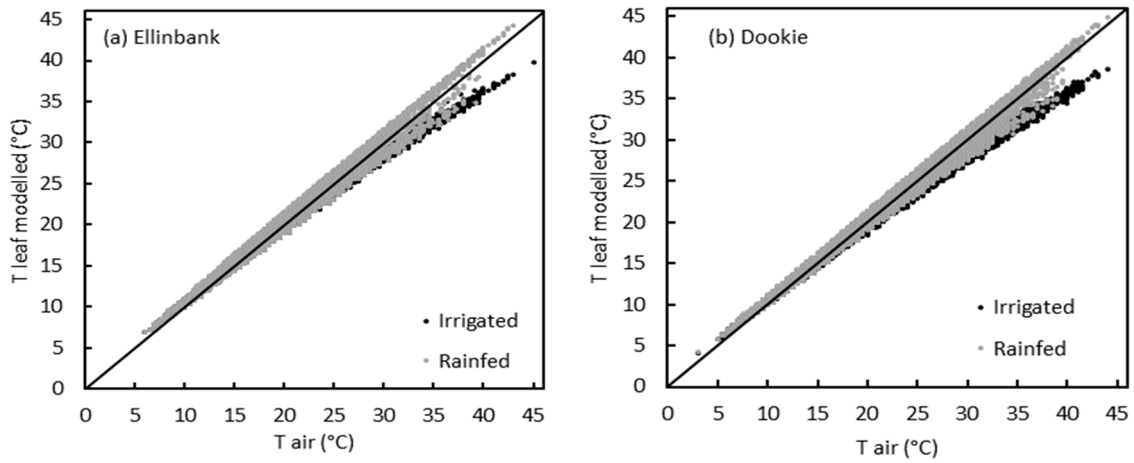

Figure 5. Relationship between air temperature and modelled perennial ryegrass leaf temperature at Ellinbank (**a**) and Dookie (**b**) under irrigated (black) and rainfed (grey) conditions. Black line = 1:1 reference line.

DairyMod simulated no significant yield difference between using leaf temperature and air temperature under rainfed situations at either site. However, when pasture paddocks were irrigated, there was a significant ($P < 0.05$) increase in predicted pasture growth rates simulated using leaf temperature from November through to March at both sites, compared to air temperature. For instance, simulated perennial ryegrass production at Ellinbank in Nov, Dec, Jan, Feb and Mar increased by 6%, 10%, 22%, 34%, and 23%, respectively, while at Dookie the simulated pasture production increased by 14%, 52%, 88%, 126% and 60%, respectively, when simulated using leaf temperature compared to air temperature (Figure 6).

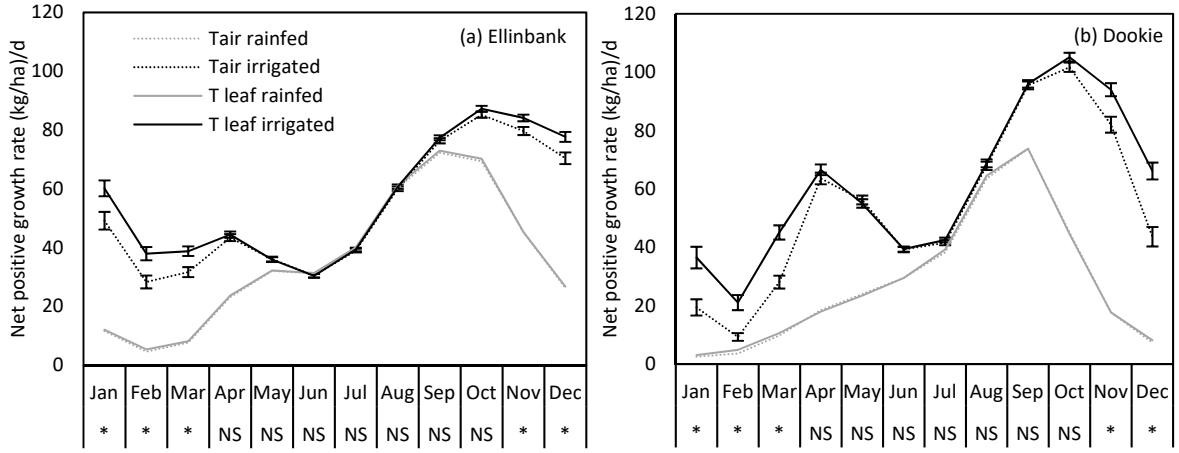

Figure 6. Simulated pasture growth rates (net positive growth rate, kg DM/ha.day) of perennial ryegrass under irrigated (black) and rainfed (grey) conditions at (**a**) Ellinbank and (**b**) Dookie. Simulations using air temperature are shown with dotted lines while those with leaf temperature are shown with thick lines. Mean pasture growth rates for each month (1960–2015) are shown with error bars representing ± standard errors. Significant differences (P = 0.05) between air temperature and leaf temperature in each month for irrigated simulations are shown in the X axis using (*). NS = not significant.

3. Discussion

This study demonstrated that the impacts of heat and water stresses on perennial pasture plants could be better simulated in a biophysical model using leaf temperature, rather than air temperature, because it captures the interactions between air temperature and water status of the plant. The four pasture species used in this study showed limited homeothermy under irrigated conditions indicating that pastures can buffer temperature variations in their surrounding environment through transpirational cooling. Leaf temperature values modelled with a leaf energy budget equation were in good agreement with the measured data for grasses as indicated by higher modelling efficiency (~0.95) and lower mean prediction error (~3%). Leaf temperatures better simulated the effects of moderate heat stress on photosynthetic rates of perennial ryegrass while simulations with air temperatures overestimated the impacts. The pattern of photosynthesis recovery after heat stress was well reproduced by DairyMod when Tsum = 20 was used while T sum = 50 simulated longer lag phase between stress and full recovery. When the modelled leaf temperature was used, both Dookie and Ellinbank sites simulated under irrigated conditions predicted higher pasture growth rates in late spring and summer periods compared to the simulations run with air temperatures. These results confirmed that uncertainty in simulating heat and drought stress on pasture growth in DairyMod can be reduced by using leaf temperature in the simulations and parameterizing high temperature stress recovery function with T sum = 20.

The slope of WW plants (considering all pasture species) (Figure 1) was 0.88, which was significantly less than 1. Using leaf temperatures from 62 species measured at an air temperature gradient of 50 °C, a slope of 0.67 was reported in a previous study [25]. The slope of the grass species observed in this study was greater than that observed by [25], hence the difference was small in the leaf-to-air temperature. This is because the grasses have narrow leaves and smaller leaf characteristic dimensions compared to broad leaves. According to the energy balance equation, narrow leaves have a greater convective energy exchange rate compared to the broader leaves, hence grass leaves maintain temperature nearer to air temperature [24].

Well-watered plants often maintained cooler canopies than air through transpirational cooling (Figure 1) at all temperature levels. Photosynthesis and respiration enzymes in plants have a narrow thermal tolerance range. Therefore, cool canopies help plants to remain physiologically active in the periods of high air temperatures [13,25]. Transpirational cooling may also help to reduce the temperature at the crown (plant–soil interface) [36]. During vegetative growth, apical meristems are

at the crown level [37–39] and they produce phytomers, which are the repeating units of vegetative growth [40]. Supra optimal temperatures at the crown area could damage the apical meristems and in turn challenge plant survival [41]. Therefore, transpirational cooling helps plants to maintain growth and physiological functions as well as plant survival.

Compared to the WW plants, WS plants had warmer leaves at all temperature levels. This was mainly due to the gradual decrease in stomatal conductance and development of greater leaf to air vapor pressure deficits with time as the combined stresses progressed (Figure 7). This result is consistent with a previous study conducted with wheat under WW and WS conditions where the warmer canopies occurred under WS due to decreased transpiration rates associated with lower stomatal conductance [42].

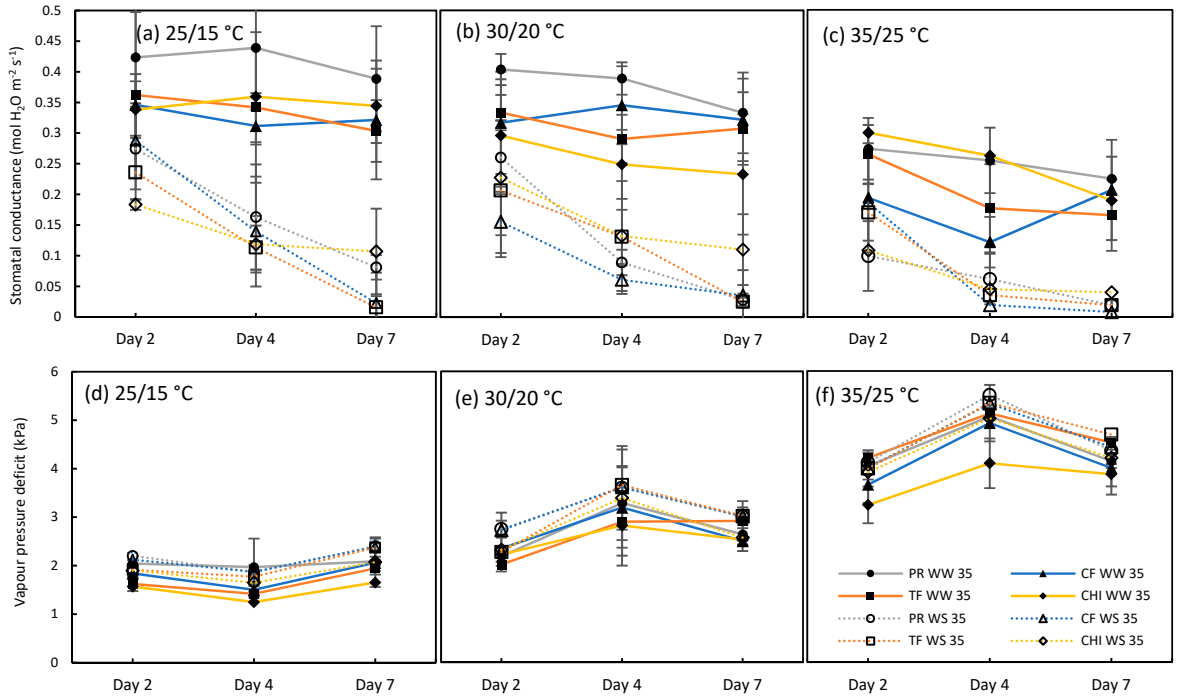

Figure 7. Stomatal conductance (**a**–**c**) and leaf to air vapour pressure deficits (**d**–**f**) of perennial ryegrass (PR), cocksfoot (CF), tall fescue (TF) and chicory (CHI) at control (25/15 °C, day/night), moderate heat stress (30/20 °C, day/night) and severe heat stress (35/25 °C, day/night) respectively during the day 2, 4 and 7 of the second heat and drought treatment. Filled symbols and thick lines represent WW plants and the open symbols and dotted lines represent WS plants. Mean (n = 3–5) is provided with the error bars representing standard deviation.

Leaf temperatures calculated using leaf energy budget equation were in good agreement with measured values for grasses but, the equation did not work well for chicory. Chicory, being a dicot plant has stomata only in one side of the leaf (hypostomatic dicot) and in contrast, grasses possess stomata on both sides (amphistomatic monocots) [43]. Grasses show greater conductance for vapor than chicory because conductance occurs from both sides of the leaves in grasses. Lower vapor conductance in chicory might cause accumulation of incoming radiation loads inside the leaf leading to more over prediction (mean bias > 3 °C) compared to grasses (mean bias < 0.5 °C) (Figure 2). The slight but consistent over prediction observed for other grass species could be due to mutual shading experience by the surrounding leaves. Since the equation does not simulate this effect, the calculated leaf temperatures could be slightly higher than the measured values.

The difference between air and leaf temperature in plants has been well known for many years [26,44,45]; however, this relationship has not been used in the crop simulation models until recently [29]. Incorporation of leaf temperature in DairyMod simulations showed that even a small leaf to air temperature difference can cause a substantial impact when the temperatures are near

to the upper end of supraoptimal temperature tolerance of a pasture species. For example, the leaf temperatures of WW perennial ryegrass under moderate heat stress was 1.3 °C cooler than air (Figure 8). This temperature difference prevented the perennial ryegrass leaves reaching the threshold temperature for heat stress impacts in DairyMod (30 °C) in the moderate heat stress treatment. However, DairyMod simulations that used air temperature started to simulate high temperature stress because air temperature reached the onset of high temperature stress threshold. When comparing the effect size on photosynthesis using response ratio, it was lower in the leaf temperature simulation which was in a good agreement with the measured data as indicated by the low RMSE and MAE than air temperature.

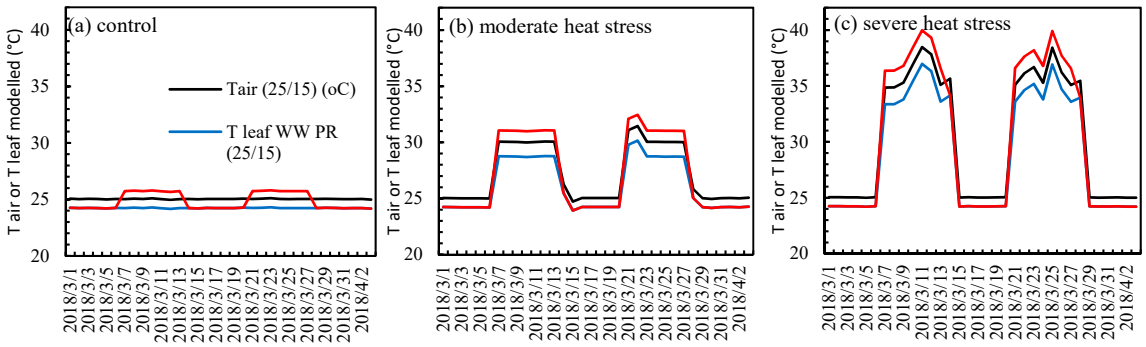

Figure 8. Maximum air temperatures (black line) and leaf temperatures of perennial ryegrass under well-watered (blue line) and water-stressed conditions (red line) on each day during the experiment at (**a**) control, (**b**) moderate heat stress and (**c**) severe heat stress treatments.

The use of leaf temperature in simulations is increasingly important for regions like south eastern Australia, where maximum temperature during the late spring and summer months is likely to pass the onset of heat stress threshold of perennial ryegrass (30 °C) on some days, while soil moisture is still available for plant growth. Under such situations, transpirational cooling is likely to reduce leaf temperature and use of leaf temperatures would realistically simulate the high temperature response of pastures. Use of leaf temperature is equally important for simulating heat stress impacts of other crops. For example, in wheat, grain sterility due to heat stress occurs at 31 °C [46,47], but there is no impact at 30 °C. At 30 °C, a 1 °C increase in canopy temperature due decreased transpirational cooling associated with soil dryness can cause grain sterility. In contrast, at 31 °C, canopy temperature drops by 1 °C due to transpirational cooling can eliminate the impact of heat stress on grain sterility [29]. In this way, large over or underestimation errors in simulating grain yields are likely to occur when the leaf temperatures are ignored in the simulation. Further, high yielding wheat genotypes have been found to have cooler canopies associated with effective water uptake from the deep soil profile [48,49]. Similarly among temperate pastures, tall fescue and chicory have shown lower crown temperatures than perennial ryegrass under supra-optimal temperatures after cutting at different stubble heights [36], and the authors hypothesize that this cooler canopy would partly explain why tall fescue and chicory outperform perennial ryegrass in hot summers.

The approach of using soil moisture stress index (GLF_water) to allocate stomatal conductance on each day for the energy budget developed in this study is similar to other studies that attempted to integrate canopy temperatures into crop models [29]. For example, in SIMPLACE<Lintul2> and SIMPLACE<Lintul5> models, soil water stress index was used to interpolate canopy temperatures between the high (no transpiration) and low (full transpiration) limits. In APSIM wheat, canopy temperatures were considered up to 6 °C warmer and 6 °C cooler than air under water-stressed and well-watered conditions, respectively, with canopy temperature change between those limits computed according to the relationship between canopy to air temperature difference and the ratio between actual and potential evapotranspiration [44,50]. However, in approach used in this study, the model has to be run using air temperature first to get the GLF_W data as this information is not available

directly without running the model. Stomatal conductance values were then allocated to GLF_W value in each day to estimate the leaf temperature on each day.

Based on the results, it is confirmed that the DairyMod model default values of high temperature stress recovery function (T sum = 100) for perennial ryegrass was too high because it takes more days to recover from high temperature stress than observed values [14]. Both values of T sum = 50 and T sum = 20 tested in this study simulated photosynthesis recovery pattern reasonably well after combined stresses at 25 °C and 30 °C but, T sum = 50 was still too high for recovery after severe heat (35 °C) and WS. However, T sum = 20 accurately reproduced the recovery pattern and the number of days taken to fully recover from heat and drought stress at all temperature levels as observed in the measured data. The recovery from high temperature stress (T sum) function in DairyMod is also used for simulating summer dormancy in addition to the recovery of summer active species following short term heat stresses. For areas where prolonged summer droughts create accumulated soil moisture deficits above 700 mm, summer dormant species like phalaris (*Phalaris aquatica* L.) are more persistent than perennial species that lack summer dormancy [51]. In DairyMod, summer dormancy is simulated by allowing long recovery periods after heat stress (T sum = 200) so that those species spend the whole summer period without simulating any growth until next autumn where there are no more days reaching the high temperature stress threshold. However, for areas where summer droughts are not so severe, summer active species like perennial ryegrass are more productive and the high temperature stresses that occur in such areas are usually short term [52]. It has been shown that the summer active pasture species can recover such conditions [14,53]. Therefore, parameterizing this high temperature recovery function is very important for the accurate estimation of summer pasture production and when conducting climate change impact studies under future climate scenarios.

Comparison of DairyMod predicted pasture growth rates using air and leaf temperatures indicated that there was a large uncertainty in yields when the leaf temperatures were ignored particularly at the medium rainfall warm temperate climate at Dookie. Yield increase when simulating with leaf temperature ranged from 14–126%, compared to air temperatures at Dookie during late spring and summer months. This could be due to leaf temperatures getting closer to optimum for photosynthesis at higher temperatures and transpirational cooling avoiding the high temperature threshold of 30 °C in irrigated simulations. In a study comparing different sterility functions of rice models, van Oort et al. [54] reported similar observations showing that ignoring the transpirational cooling effect overestimated the spikelet sterility by 14–73%.

While many studies have shown that the air temperature is a poor predictor in terms of plant production [55,56], most crop simulation models still using air temperature to represent canopy/leaf temperature. This could be mainly due to the complexity of using energy budget and the requirement of more detailed weather and plant (stomatal conductance) data for the energy budget estimation. In this study, energy budget for leaf was used for the estimation of leaf temperature but the most applicable component for plant population would be the canopy temperature. Canopy temperature calculation requires more information such as heat storage in the soil and canopy conductance which were not measured in this study. While further research is required to simplify the approach and find better ways to integrate leaf/canopy temperature into crop simulation models, this approach improved the simulation of perennial ryegrass under consecutive combined heat and drought stresses.

4. Materials and Methods

4.1. Validation of Leaf Energy Budget Equation

4.1.1. Experimental Description

A controlled environment experiment was conducted to collect the information required to validate leaf energy budget equation and simulation approach used in this study. Full experimental details, including the experimental design, treatments, and pasture species, were provided in [14] and only a short description is provided here. Four temperate perennial pasture species including three

grasses; perennial ryegrass (*Lolium perenne* cv. Base AR37), cocksfoot (*Dactylis glomerata* cv. Savvy), tall fescue (*Festuca arundinacea* cv. Quantum II Max P) and a broad leaf; chicory (*Cichorium intybus* cv. Puna II) were grown in poly vinyl chloride tubes (height 75 cm and diameter 10 cm) inside a glasshouse in the Faculty of Veterinary and Agricultural Sciences, The University of Melbourne. Plants were well-watered and fertilised during the initial growing stage in the glass house. After eight weeks of vegetative growth, plants were transferred into three separate growth chambers and allowed to adapt to conditions for two weeks. The first week before the treatments were imposed was considered as the pre-treatment period. Plants in each chamber were then exposed to consecutive seven-day heat and water stress treatments each followed by a seven-day recovery period. Three temperature levels were allocated to three growth chambers including control = 25/15 °C, day/night, moderate heat stress = 30/20 °C, day/night and severe heat stress = 35/25 °C, day/night. At each temperature level, a group of plants were fully irrigated daily to the field capacity throughout the experiment (well-watered, WW) and irrigation was arrested during consecutive seven-day temperature treatments in the water-stressed (WS) plants. All pots were well watered during the pre-treatment and the recovery periods to the field capacity.

Each growth chamber contained 40 plants (4 species × 5 replicates × 2 irrigation treatments) arranged in eight rows and five columns. Watering treatments (WW and WS) were allocated in alternative rows in each chamber. Species were randomised in both row- and column-wise directions.

4.1.2. Measurements

Diurnal variation of temperature was implemented inside growth chambers by gradually increasing and decreasing air temperature changing between night time minimum to day time maximum over a period of 3 hours. Temperature inside the chambers were recorded every minute by a data logger in each growth chamber. Relative humidity (RH%) inside the chambers were set at 70% and light intensity was maintained at 900 $\mu molm^{-2}s^{-1}$ (range of 844–1030) using high pressure sodium lamps and incandescent lights. Maximum leaf widths of 10 leaves were recorded from each pasture species and averaged to calculate leaf characteristic dimension (d = 0.72 × maximum leaf width in the direction of wind flow).

The leaf photosynthetic rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) of the youngest fully expanded leaf was measured in perennial ryegrass three times per week throughout the experiment using Li-6400 portable gas exchange system (LI-COR Inc., Lincoln, USA) under the given lighting conditions of the chamber and CO_2 concentration set at 400 ppm. Modulated chlorophyll fluorescence was also measured in alternative days throughout the experiment. Since the grasses have a narrow leaf, the whole leaf chamber was not covered by leaves. Therefore, every leaf inside the LI-COR leaf chamber was photographed using a digital camera (keeping equal distance between leaf chamber and camera) when taking photosynthesis measurements to compute the leaf area within the leaf chamber. The leaf area was analyzed using ImageJ software [57]. Photosynthesis was recomputed for the calculated leaf area using LI-6400 simulator 5.3.2. Stomatal water conductance and the leaf-to-air vapor pressure deficit values over day 2, 4 and 7 were also extracted from the LI-COR 6400 after recomputing the data, as shown in Figure 7. Photosynthesis data from perennial ryegrass were statistically analyzed using linear mixed models in GenStat (16^{th} edition) taking rows and columns in each chamber as the random effects and temperature, watering treatment and time as fixed effects. Three-way interaction was significant ($P < 0.05$), however to reduce the complexity of the analysis, only the means between WW and WS plants at each temperature on each day are presented in this study (Figure 3a,b).

Thermal images of 3–5 plants in each species were captured using infra-red camera (FLIR T series; model B 360) keeping the plants inside the chamber during the days 2, 4 and 7 of the second heat and WS treatment. In each thermal image, pixels of the pot and the background were eliminated by selecting the maximum and minimum temperatures within the plant canopy using a code written in MATLAB R 2014b [58]. Pixels selected within the canopy were then averaged to calculate the average leaf temperature of each plant. Air temperature values inside chambers were also recorded when capturing

each thermal image using a mercury thermometer in addition to the recorded temperatures inside chambers to get the accurate air temperature reading at that point time. Average leaf temperatures of species were analyzed using two sample *t*-tests at each temperature level to test the hypothesis; H0: mean leaf temperature of WW plants = mean leaf temperature of WS plants.

4.2. Leaf Temperature Calculation Using Energy Budget Equation

Temperatures of pasture leaves were calculated using air temperature, radiation, leaf characteristic dimension [24,59], wind speed, relative humidity (RH%) and stomatal conductance using leaf energy budget for wet/humid operating systems (Chapter 14. Equation (14.6)) [24] on days 2, 4 and 7 of the second heat and WS treatment consistent with the timing of the leaf temperature measurements (using infra-red images). The leaf energy budget can be written as in Equation (1).

$$Tl = T_a + \frac{\gamma^*}{s + \gamma^*} + \left[\frac{R_{ni}}{g_{Hr} Cp} - \frac{D}{P_a \gamma^*}\right] \quad (1)$$

where Tl is leaf temperature (°C), T_a is air temperature (°C), γ^* is apparent psychrometer constant (C^{-1}), s is slope of saturation mole fraction function, R_{ni} is isothermal net radiation (Wm^{-2}), g_{Hr} is sum of boundary layer (gHa; mol m^{-2} S^{-1}) and radiative (gr; mol m^{-2} S^{-1}) conductance, Cp is specific heat of air (J mol^{-1} C^{-1}), D is vapor pressure deficit (kPa) and P_a is atmospheric pressure (kPa). R_{ni} was used for leaf temperature modelling because it does not depend on the leaf surface temperature. R_{ni} was calculated using Equation (2).

$$R_{ni} = SWR_{abs} + LWR_{in} - LWR_{out,i} \quad (2)$$

where SWR_{abs} is absorbed short wave radiation, LWR_{in} is incoming long wave radiation and $LWR_{out,i}$ is isothermal outgoing long wave radiation.

Monocot plants (grasses) have stomata on both sides of the leaf (amphistomatous), while dicots (chicory in this study) have stomata only on one side (hypostomatous). To account for this feature, vapour conductance was calculated for grasses and chicory separately in the energy budget equation. For chicory, only the first half of Equation (3) was used.

$$g_v = \frac{0.5\, g_{vs}^{ab}\, g_{va}}{g_{vs}^{ab} + g_{va}} + \frac{0.5\, g_{vs}^{ad} g_{va}}{g_{vs}^{ad} + g_{va}} \quad (3)$$

where g_v is the vapor conductance, g_{vs}^{ab} is abaxial stomatal conductance, g_{vs}^{ad} is adaxial stomatal conductance and g_{va} is boundary layer conductance for vapour. g_v is used to calculate γ^*. Step by step calculation of the leaf temperature can be found in [24].

A range of statistics were calculated to test the adequacy of the leaf energy budget equation to predict the leaf temperatures of four pasture species with sufficient accuracy, based on methods reported in Tedeschi [60]. The statistics include; mean bias (the difference between measured and modelled data), the regression estimate of coefficient of determination (R^2); Pearson's correlation coefficient (r), mean prediction error (MPE) where <5% represents excellent model prediction, 5–10% represents very good, 10–20% represents moderate and more than 20% represents poor model prediction [61]; for the modelling efficiency (MEF), where above 0.5 is ideal and lower than zero indicates that the model predictions are worse compared to measured values; variance ratio with 1 indicating same amount of variation in measured and modelled data; bias correction factor (Cb) with 1 indicating best fit and lower than 1 indicating bias from the 1:1 reference line, and finally, the Concordance Correlation Coefficient (CCC), which is also known as reproducibility index that simultaneously account for the accuracy and precision with 1 indicating the best fit.

4.3. Simulation of Photosynthesis Pattern; Comparison Between Tair and Tleaf

Net positive photosynthesis rates of perennial ryegrass were simulated using the DairyMod biophysical model during consecutive heat and water stresses to compare the pattern with the measured data. Data for perennial ryegrass was used in this comparison as it is the most commonly grown pasture species in SE Australia. Six simulations were built to represent the three temperature and two watering levels separately. To run the simulations, climate files required for DairyMod were prepared using the data recorded in each growth chamber including light intensity (μmol m^{-2} s^{-1}), maximum and minimum daily temperatures (°C); RH%, vapor pressure (kPa) and wind speed (used a constant value of 2 ms^{-1}). One set of simulations were run using the measured climate data including the maximum daily air temperature. Another set of simulations were run substituting the maximum daily temperatures with the leaf temperatures calculated for each day using leaf energy budget equation. Maximum air temperatures inside each growth chamber and leaf temperatures for WW and WS simulations are shown in Figure 8. Canopy net positive photosynthesis values (kg C/ha.d) from DairyMod were used for the analysis. While net negative photosynthesis values were predicted by DairyMod during the combined heat and water stresses due to growth and maintenance respiration, these days were given the value of zero in this study consistent with the net positive pasture growth rates (Figure 6). Patterns of net positive photosynthesis using leaf temperature and air temperature were then compared with the measured leaf photosynthesis data.

Since measured and modelled photosynthesis values were in different units, they were transformed to comparable scales using response ratio (RR). RR was calculated as $Psis_i$ / $Psis_{control}$ where $Psis_i$ is the photosynthesis value on i^{th} day and $Psis_{control}$ is the corresponding control value. RR gives the effect size of each temperature and watering treatment on each day compared to the WW control treatment (25 °C WW). The RR of the 25 °C, WW treatment in both measured and modelled data sets were always equal to one as the value of each day is divided by the same value. RR was calculated for both measured and modelled photosynthesis values separately and then used for the comparisons. Several regression model evaluation statistics were used, such as residual mean squared error (RMSE) and mean absolute error (MAE) to calculate the error rate of modelled data. Photosynthesis data measured only at controlled and moderate heat stress treatments were used in the analysis. Photosynthesis data measured at the severe heat stress treatment was not used for comparisons due to instrumental error occurred during measurement. However, the pattern of photosynthesis was modelled for all three temperature levels and photosynthesis pattern at severe temperature treatment (35/25 °C, day/night) was visually compared with the pattern of heat and/or drought stress responses of other growth and physiological measurements such as maximum quantum yield of photosystem II, relative leaf water content and the leaf elongation rate described in [14].

4.4. Parameterization of High Temperature Stress Recovery (T-sum) Function

Perennial ryegrass in the DairyMod biophysical model experience high temperature stress (high temperature stress-onset) at 30 °C and the stress become maximum (high temperature stress-full) at 35 °C. Recovery of pasture species from high temperature stress is modelled using an empirical function called T-sum recovery. The model default T sum for perennial ryegrass is 100 [34]. This means if the summation of 25 and the mean daily temperature after the high-temperature stress period reaches 100, the perennial ryegrass will fully recover from heat stress. For example, if the mean temperature of the following day is 20 °C, five heat units accumulated in that day. After 20 days of mean temperatures of 20 °C, the perennial ryegrass will fully recover from heat stress. This function was not well-parameterized in the model. The model uses arbitrary values for each species when modelling high temperature stress effects on pastures. In this study, T-sum recovery for perennial ryegrass was adjusted to match the days to recover after stress relief using the measured photosynthesis data.

4.5. Evaluating Effects of Using Leaf Temperature Compared to Air Temperature on Pasture Growth Rate

To evaluate the effects of leaf temperature on pasture production compared to air temperature, perennial ryegrass was simulated using both approaches (Tair and Tleaf) separately at two contrasting sites in south eastern (SE) Australia (high rainfall cool temperate site at Ellinbank (Lat. −38.25°, Long. 145.93°) and medium rainfall warm temperate site at Dookie (Lat. −36.37°, Long-145.70°)) spanning the period from 1960–2015. Climate data for each site (solar radiation in MJ/m^{-2}, maximum and minimum temperatures in °C, rainfall in mm, evaporation in mm and RH%) were obtained from the SILO database service [62]. Soil type details of the two sites were extracted from [5]. Simulations were managed as a cutting trial where pastures were harvested to a residual level of 1.4 t DM/ha at the end of each month. Pastures were grown under nutrient nonlimiting conditions. Rainfed and irrigated pastures were simulated for each site separately. The rainfed simulation was run to capture the water limiting growth of pastures during dry months where transpirational cooling does not occur and thereby increasing leaf temperatures of plants occurs. In the irrigated simulation, irrigation was applied as required all year so that no water stress was simulated. The irrigation rule used in DairyMod was to apply 50 mm of water when the rainfall deficit (cumulative PET—rainfall) exceeded 25 mm over a five-day interval.

During simulations, the effect of transpiration on pasture growth was incorporated using modelled leaf temperature in two-step process. First, the model was run using the described climate data (obtained from SILO database) and growth limiting factor water (GLF_W) values on each day over 1960-2015 were extracted from export file for each site. GLF_W was then used to incorporate the transpirational cooling effect by adjusting stomatal conductance in the leaf energy budget, using a similar approach to a previous study [29]. GLF_W range from 0 to 1 where 1 means there is no limitation to growth while 0 means total limitation. For each GLF_W value, a corresponding stomatal conductance was allocated based on the measured values for perennial ryegrass as shown in Figure 7. Maximum stomatal conductance of 0.4 mol H_2O m^{-2}s^{-1} was allocated to GLF_W = 1 to simulate maximum transpiration and it was progressively decreased to 0.005 mol H_2O m^{-2}s^{-1}, which is equal to GLF_W = 0 to simulate little or no transpiration. Stomatal conductance values allocated for a range of GLF_W are shown in Table 4. These stomatal conductance values were within the range of measured values under different soil water status and mid-day leaf water potential values for perennial ryegrass reported by [63]. As the next step, leaf temperature was calculated for each day using leaf energy budget equation using radiation, vapor pressure, wind speed, and maximum daily temperature from the climate file, and the stomatal conductance values allocated to GLF_W on each day. The calculated leaf temperature was then used as the maximum daily temperature values in the second run of the model. In the irrigated simulation, GLF_W was always equal to 1. To account for this feature, leaf temperature for irrigated plants were calculated using the maximum stomatal conductance of 0.4 mol H_20 m^{-2}s^{-1} to represent maximum transpirational cooling. Using this approach, the environment experienced by the canopy due to transpirational cooling was incorporated into the model rather than using air temperature. The monthly pasture growth rates (kg DM/ha.day) simulated using air temperature and leaf temperature were analyzed using two sample *t*-tests for both irrigated and rainfed conditions and uncertainty was computed as percentage difference of net positive growth rates compared to air temperature.

Table 4. Stomatal conductance values of perennial ryegrass used in the leaf energy budget equation when calculating leaf temperatures for each day at Dookie and Ellinbank. Stomatal conductance values used in this table came from the measured values shown in Figure 7 and they are allocated to different ranges of GLF_water values.

GLF Water Range	Stomatal Conductance mol m^{-2} s^{-1}
0.91–1	0.4
0.81–0.9	0.225

Table 4. *Cont.*

GLF Water Range	Stomatal Conductance mol m^{-2} s^{-1}
0.71–0.8	0.18
0.61–0.7	0.11
0.51–0.6	0.05
0.41–0.5	0.035
0.31–0.4	0.025
0.21–0.3	0.01
0.11–0.2	0.008
0–0.1	0.005

5. Conclusions

The four pasture species used in this study showed limited homeothermy under WW conditions, suggesting that pastures can buffer temperature variations in a range of ambient air temperatures. A leaf energy budget equation modelled temperatures of the grasses better than chicory under different temperatures and watering levels. The leaf temperature modelled using an energy budget equation better simulated the heat stress impacts on perennial ryegrass compared to the air temperature, suggesting that the uncertainty of using air temperature can be reduced if leaf temperatures were used in crop simulation models. Weather variables available from the meteorological stations (radiation, maximum and minimum temperatures, vapor pressure, RH% and wind speed) together with crop-specific variables (leaf characteristic dimension, stomatal conductance) and the soil moisture stress index (GLF_water) allows for the approximation of leaf temperature using the leaf energy budget. When using this approach in DairyMod, simulations using leaf temperature under irrigated conditions showed increased pasture growth rates during the late spring and summer months at the Ellinbank and Dookie sites, with the highest increase predicted at the medium rainfall site at Dookie. This approach can be used to model pasture production in other temperate and Mediterranean climates of the world where high temperature stress is an ongoing problem. While further research is required to better represent the canopy temperature in crop simulation models using an energy budget approach, this study demonstrated that leaf temperature can better simulate pasture responses under consecutive combined heat and water stresses.

Author Contributions: Conceptualization, R.S.P., B.R.C. and R.J.E.; Data curation, R.S.P.; Formal analysis, R.S.P.; Funding acquisition, B.R.C.; Investigation, R.S.P.; Methodology, R.S.P., B.R.C. and R.J.E.; Project administration, B.R.C. and R.J.E.; Resources, B.R.C.; Supervision, B.R.C. and R.J.E.; Validation, R.S.P.; Visualization, B.R.C.; Writing—original draft, R.E.P.; Writing—review & editing, R.S.P., B.R.C. and R.J.E. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: The authors acknowledge the kind support of the Steven Elefteriadis, Glasshouse Complex Manager, Faculty of Veterinary and Agricultural Sciences (FVAS)/School of Biosciences, The University of Melbourne for allocating glass house space, growth chamber facilities and providing equipment to conduct this experiment. The authors would also like to thank Associate Professor Graham Hepworth, Statistical Consultant Center, The University of Melbourne for the statistical advice, and Dr. Mahil Pathirana, Department of Infrastructure Engineering, The University of Melbourne and Dr. Himali Balasooriya, Faculty of Veterinary and Agricultural Sciences, The University of Melbourne, for technical assistance.

Conflicts of Interest: The authors declare no conflicts of interest.

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CHAPTER 8. General discussion

8.1. Key findings and original contributions

The major objective of this research was to better understand the impacts of climate variability and extreme climate events on pasture systems in SE Australia using simulation modelling and controlled environmental experimental approaches. The thesis addressed five specific research questions as below. The key findings and novel contribution of each chapter is described in the first paragraph under each question and the findings are discussed in detail in the following paragraphs.

Are pasture growth patterns changing under the increasing climate variability and extreme events experience in recent decades? If so, which seasons show the most year to year variability in pasture growth and what does this mean for adaptation? (Chapter 3)

The results of the Chapter 3 provide clear evidence that pasture growth patterns have changed, with increased winter growth, decreased spring production and increased year to year yield variability in the autumn and spring seasons during the most recent period (2002-2015) compared to the periods before (1960-2001). These changes are linked to the increasing trend in variability and extreme events observed in the historical climate. Although similar results reported in this study have been expected in future under climate change projections for 2030 (Cullen et al. 2009; Moore and Ghahramani 2013), this research showed that these changes are already occurring highlighting the urgent need to take adaptation measures to stabilize production. Based on the results of chapter 3, climate change impact studies on pasture systems in the future should incorporate further changes to rainfall, temperature and CO2 and their impacts should be assessed with simulation models properly parameterized for heat and drought stress functions and tiller deaths as emphasized in chapter 7. Future studies should also incorporate the effects of decreased rainfall, increased temperature and elevated CO_2 during millennium drought on pasture systems in the SE Australia.

SE Australia receive majority of its annual rainfall during winter and spring months (CSIRO and BOM 2015). This cool season rainfall pattern is favorable for the growth of temperate pasture species

in the region. However, seasonal and year to year pasture yield variability has become a key challenge in managing the pasture based systems in SE Australia. Among the many factors governing pasture yield variability, year to year variation in rainfall is a key factor (Chapman *et al.* 2013) because most pasture lands do not have access to irrigation. Recent changes observed in the climate in SE Australia show that climate variability has increased with decreased rainfall in the cooler months of the year since 1990's (Timbal 2009; Braganza *et al.* 2011) including nearly 20% reduction of rainfall in Victoria (Hennessy *et al.* 2016) and increased occurrences of extreme climate events (CSIRO and BOM 2015). In Chapter 3, simulated pasture growth rates (using DairyMod biophysical software) from 1960-2015 at five sites in SE Australia were analyzed dividing the simulation period into 14-year time windows and found that pasture growth patterns have changed during the most recent period (2002-2015) compared to the periods before (1960-2001). These changes are in line with the observed changes in the climate in the same period. Cross site analysis revealed that spring pasture growth rates have decreased by 26% ($P<0.001$) in the most recent period (2002-2015) compared with 1988-2001, winter pasture production has increased steadily by 10% from the start of the simulation period, and year to year pasture yield variability (CV%) has increased in the key growing seasons (both autumn and spring) with spring variability being more than doubled across the region (62% in 2002-2015 compared with ~30% in 1988-2001). Increased occurrences of heat and moisture stresses together with increased CSSSMD during the most recent period were closely related to these changes. These findings are consistent with the effects of recent changes to climate on other major crops nationally and globally (Brisson *et al.* 2010; Hochman *et al.* 2017). It was found that in Australia, despite genetic improvement, wheat yields have stagnated since 1990's and the water limited reduction of yield from 1990-2015 was around 27% (Hochman *et al.* 2017). Similarly, the temperature of the world's major wheat growing regions has increased more than one standard deviation from the historical variation and that has caused 5.5% yield decline in wheat (Lobell *et al.* 2011).

The changes to the pasture systems reported in this study highlight the urgent need to take adaptation measures to stabilize production. Incorporation of deep rooting and heat tolerant characters to

perennial ryegrass are some suitable adaptation options as shown by Cullen *et al.* (2014b) and these traits would be beneficial to extend production at the end of the growing season when the soil moisture is diminishing. Further, in a future climate change modelling study, Ghahramani and Moore (2013) reported that increasing soil fertility by adding phosphorus fertilizer, growing summer-active species (such as lucerne) on part of the farm and confinement feeding in summer as the best adaptation options to recover from the negative impacts of climate change. Simulations conducted with these adaptations resulted full profit recovery at some areas across southern Australia in 2030. Incorporation of native C4 grasses was also tested at Wagga Wagga in Chapter 3 as a possible adaptation strategy to cope with the warming and drying trend. Even though C4 grasses produced greater herbage mass compared to C3 species in summer months, their winter production was still lower compared to C3 species. while there is a general southward movement of weather systems, climate change does not automatically mean a switch from winter rainfall to summer rainfall in SE Australia, so switching from a winter-active pasture (C3) to a summer active (C4) pasture, that needs summer rainfall, is only likely to benefit the margins of the season. Therefore, under current climate change, total replacement of C3 with C4 will not be a beneficial option to counteract the climate change impacts in SE Australia, but has potential to be incorporated to a part of the farm to secure summer feed supply. Other than that, livestock production systems should target more towards conservative stocking rates, breeding for heat tolerant animal breeds, and shifting the calving/lambing cycles to coincide with higher pasture producing months (Ash et al. 2007; Chapman et al. 2013). These adaptation options need to be prioritized because the changes to the pasture patterns predicted to occur by 2030 (Cullen et al. 2009; Moore and Ghahramani 2013) appear to have already occurred. Other than long term strategic decisions, tactical and operational level decisions may also be useful to manage climate variability but they need frequent monitoring. Such options involve fodder conservation in high producing years, supplementary feeding, applying nitrogen fertilizer strategically to take the best use of available soil moisture, and animal destocking in poor pasture producing years before animal conditions decline (Austen *et al.* 2002).

Can year to year pasture yield variability be better explained using both average and extreme climate indices rather than using only the average climate variables? Which climate variables are more important in explaining the year to year pasture yield variability? (Chapter 4)

To investigate this research question, a methodology was developed in chapter 4 to explain year to year pasture yield variability using both general and extreme climate indices. General climate indices are the annual and seasonal averages of climate at each site while the extreme indices were designed to reflect extreme wet and dry and hot and cold spells. Results showed that in addition to an overarching effect of the general climate indices such as rainfall and temperature on pasture growth, extreme climate indices such as increasing number of dry months, number of hot days (>30°C), hot period length during the year and the number of frost days during winter and spring months all translated into lower pasture yields.

Chapter 3 highlighted the changes to the pasture growing patterns occurred in the historical climate in SE Australia and an approach was developed in Chapter 4 to explain the observed year to year variability (reported in chapter 3) using climate indices (general and extreme). The climate indices represent the climate variability observed in SE Australia, including the rainfall distribution (both wet and dry months categorized based on SPI dry/wet severity classes; one monthly time scale), hot days (days with Tmax >30 °C, where perennial ryegrass experience heat stress (Mitchell 1956)), hot period length and winter spring frost occurrences. Previous modelling studies have employed a fixed level of atmospheric CO_2 over the historical simulation period set at 380 ppm (Cullen *et al.* 2009); however, in this study, the atmospheric CO_2 concentrations measured from 1960-2015 were also used to make the simulations more realistic.

It was found that both average and extreme climate indices are important to explain the year to year pasture yield variability in the historical climate with medium rainfall sites more sensitive to key climate indices (Wagga Wagga R^2 = 89%) than high rainfall sites (Elliott R^2 =70%). In addition to the effect of rainfall and temperature on pasture growth, this study identified that extreme climate indices such as dry months, number of hot days (>30°C), hot period length during the year and the number of frost days during winter and spring months decreased pasture yields. More importantly,

the rainfall distribution (dry and wet months) modified the generally observed positive effects of total rainfall on pasture growth depending on the season in which they occurred. All dry month categories (moderately, severely and extremely dry months) translated into low pasture yields when they occurred during the winter and spring. For example, at Wagga Wagga and Dookie sites, 13/15 and 10/10 extreme dry months occurred during the winter and spring months, respectively, all of which translated into lower pasture growth. Likewise, extreme precipitation amounts received in the same months (winter-spring season) cause water logging which can lead to reduced pasture yields due to soil saturation. Similar relationships between climate and pasture growth rates reported in this study were observed previously in pasture areas in Australia where 7% of the years between 1900 and 1999 had very low pasture yields in the Terang district due to very low rainfall in the major pasture growing season (Chapman *et al.* 2008). Hot days and hot period length during summer and frost occurrences during winter and spring seasons appeared as negative factors for pasture production. These effects were not accounted for when only the average climate change was considered in the previous research (Cullen *et al.* 2009), even though it is acknowledged that decreasing rainfall and increasing temperature are the major limiting factors of pasture production (Cullen *et al.* 2009; Chapman *et al.* 2013; Moore and Ghahramani 2013). Farmers will benefit if these events can be predicted earlier so that they can be prepared for the downside risks of climate extremes such as low pasture production, low quality and quantity of hay, lower carrying capacity (Malatinszky 2016) and decreased pasture persistence (Nie *et al.* 2004b; Chapman *et al.* 2011). These findings demonstrate that extreme climate events should be considered in any analysis of climate change impacts on agricultural systems. Even though seasonal climate forecasts will be increasingly valuable in this regards (Ash *et al.* 2007), their lack of accuracy and insufficient leading time currently prevent their effective use in agricultural decision making (Hayman *et al.* 2010). Therefore, it is an urgent need to accurately predict the anticipated magnitude and the frequency of extreme climate events in the future climate scenarios.

How do the large scale climate drivers of ENSO, IOD and ENSO IOD combined phases influence annual pasture production in SE Australia? (Chapter 5)

The effects of these drivers have been studied previously for other crops and cereals (Hayman et al. 2010; Jarvis et al. 2018), the study described in Chapter 5 is the first of its kind for pasture systems. The findings revealed that the hot and dry phase of each Large-Scale Climate Driver (El-Nino and IOD+) were responsible for lower pasture yields. The most negative impacts were observed when the hot and dry phase of one driver coincided with the hot and dry phase of the other (i.e. El-Nino and IOD+). Forecast analysis revealed that the yield differences between the opposite climate driver phases can be clearly identified only at the end of winter period. However, this is not a sufficient leading time for farmers to make key management decisions, so further research is warranted to increase the forecast skills of climate driver phases to enable more proactive pasture management decisions.

What are the growth and physiological responses of commonly grown temperate pasture species to consecutive heat and drought stresses? (Chapter 6)

The controlled environmental chamber experiment (Chapter 6) revealed some important heat and drought resistance mechanisms of pasture plants that could inform future pasture breeding programs. This study found that the pasture species studied (perennial ryegrass, tall fescue, cocksfoot and chicory) can acclimate to moderate heat and drought stress through previous exposure (termed as priming effect). Since the frequency of heat waves (CSIRO and BOM 2015; Perkins Kirkpatrick et al. 2016) and droughts (Westra et al. 2016) are predicted to increase under future climate change scenarios in SE Australia, the ability of pasture plants to acclimate to the previous heat and drought is a beneficial trait to maintain growth and physiological functions under short term moderate stress conditions.

Even though all pasture species showed acclimation to moderate heat and drought stress, all grasses showed a decline of their growth and physiological functions under severe heat and drought stress.

Chicory was the only species that maintained physiological functions during the second severe heat and drought stress. This was mainly due to the maintenance of viable green leaf area with high relative leaf water content and higher photochemical efficiency of PS II (as indicated by Fv/Fm values closer to 0.83). Superior heat and drought stress tolerance of chicory is in agreement with the previous findings of Langworthy et al. (2018) who reported that chicory survived supraoptimal temperature (38/25 °C, day/night) and drought for 18 days while other plants (including all grass species used in this study) died after 12 days of the treatment. Therefore, chicory may be a potential pasture species for areas in SE Australia with hot and dry summer conditions.

During individual stresses (drought or heat), the immediate response of all species was the reduction of leaf elongation rates indicating that the growing points of plants are sensitive to heat stress (Williams and Biddiscombe 1965) as well as cell expansion growth is sensitive to moisture stress (Volaire and Lelièvre 2001). Since green foliage is the economically important part of pastures, reduction of foliage growth significantly decreases pasture production under heat and drought. This response is frequently observed during hot and dry summers in SE Australia with pasture yields during this time of the year as low as 5-10% of the total annual pasture yields (Özkan *et al.* 2015). However, other physiological responses such as Fv/Fm, cell membrane permeability were not significantly affected by the 7-day individual stresses alone. This is particularly important for pasture species to survive stressful events because growth can resume after the stress has ceased if the physiological processes were not affected. Transpirational cooling is a key mechanism by which plants maintain physiological functions (Fv/Fm, cell membrane permeability, turgor pressure) during severe heat stress under irrigated conditions (Michaletz *et al.* 2015). All pasture species tested in this study showed cooler canopies under WW conditions indicating the importance of irrigating the plants to prevent serious injuries to physiological functions. However, the majority of the key pasture regions in SE Australia do not have access to irrigation.

The reduction of leaf growth was found to be more related to the pattern of RSWC rather than the pattern of RLWC. Even though plants maintained higher RLWC during the short-term stress, leaf elongation rates decreased closely following the pattern of soil water reduction. A similar response

was observed by Volaire and Lelièvre (2001) who found a linear relationship between available soil moisture fraction and the leaf extension rate of grasses under drought stress. Since the cell expansion rate is not only related to turgor pressure but the rate at which the water is supplied to the growing area of the leaf (Lockhart 1965), moisture status of the soil is more important for pasture growth than the actual amount of water in the tissues. This implies the importance of having enough soil moisture or having roots deep enough to reach water in the deep layers of the soil profile, for pasture production particularly at the end of spring and summer months, where pasture growth is often become limited by the low rainfall. However, pasture species like cocksfoot may have advantage under limited soil moisture because of its ability to uptake soil moisture effectively at low soil moisture and thereby delay dehydration when drought progress (Volaire and Lelièvre 2001).

The importance of incorporating deep rooting characters into pasture species through breeding programs suggested in Chapter 3 was further confirmed from the findings of Chapter 6. Under field conditions, tall fescue is more drought tolerant and this trait is more related to its deep root system. However, Chapter 6 results showed that tall fescue was drought sensitive when grown under similar rooting conditions with other pasture species like perennial ryegrass. Therefore, the drought tolerant nature of tall fescue under field conditions could be more related to the deeper root system which may allow plant to transpire and cool the canopies under extreme heat and drought stresses. Langworthy *et al.* (2019) also observed that the crown temperatures of tall fescue were cooler than perennial ryegrass after cutting into shorter stubble heights under high temperatures and the authors assume that the ability of tall fescue to tolerate drought more than perennial ryegrass could be partly due to cooler crown temperatures.

All pasture species acclimated to 7-day combined moderate heat and drought stress. However, chicory was the only species that acclimated to the 7-day combined severe heat and drought stress. Previous stress memory can produce heat stress proteins and modify metabolic functions which protect the plants from subsequent stresses, referred to as a priming effect. This is a beneficial trait that can be utilized in breeding better heat and drought tolerant cultivars. Therefore, in future studies, field experiment protocols should focus on measuring plant growth and physiological responses not

only under a single heat stress events, but over repeated events, because results could be different due to acclimation of plants to subsequent stresses.

Chicory has been previously found to have superior heat and drought tolerant characters (Langworthy *et al.* 2018). Chapter 6 also confirmed this idea and this superior heat and drought tolerance was found to be related to its viable green leaf area and ability to produce new biomass (photosynthetically active) under stress from those leaf area (higher Fv/Fm). However, further research is needed to reveal the root zone characteristics of chicory to survive under severe heat and drought and the nutritious quality of the herbage yield under stresses.

Do leaf temperatures better simulate the heat stress effects of pasture plants in mechanistic biophysical plant growth models than air temperatures (using DairyMod as a case study)?

Most crop models do not fully capture the impacts of climate extremes such as heat and drought stresses even though the knowledge in plant stress physiology has been advanced. This is mainly because the knowledge gained from detailed experiments under extremes has not been incorporated to process descriptions of the models (Barlow et al. 2015; Rezaei et al. 2015). The work reported in Chapter 7 demonstrates how to link experimentation (Chapter 6) and simulation modelling to improve the simulated responses of pasture species to heat and drought stresses. Canopy temperature depression data under well-watered and water stressed conditions showed significant differences, with well-watered plants showing cooler canopies and water stressed plants showing warmer canopies than air temperature. This feature was incorporated into the DairyMod biophysical model using the leaf energy budget calculation. The energy budget is a process based approach that represent interaction between soil moisture content and air temperature via leaf temperature and the feedback effect of stomatal closure on transpiration is incorporated through the leaf temperature (Campbell and Norman 2012). The results showed that the simulated reduction of photosynthesis to moderate heat stresses is closer to the actual photosynthesis reduction when using leaf temperature for simulation. In contrast, the effects were overestimated when the air temperature was used in simulations. Therefore, leaf temperature realistically simulates heat stress responses in pasture plants.

Chapter 7 also used experimental data (Chapter 6) to parameterize the high temperature stress recovery function (T sum recovery) of DairyMod for perennial ryegrass. In this way, Chapter 7 gives an example of how to design controlled experiments to extract important information required to address knowledge gaps in crop simulation models particularly related to climate extremes. This is an area that needs further development because both magnitude and frequency of climate extremes are increasing. In future, long term field studies should aim to address specific uncertainties of crop simulation models and improve simulations which is important to assess the climate change impacts on agriculture accurately.

Most crop simulation models do not have a true energy budget component to account for the feedback effects of stomatal behavior on the leaf/canopy temperature in a mechanistic way (Boote *et al.* 2013). This is a major limitation in crop models which needs to be addressed in order to accurately simulate heat stress impacts. Webber *et al.* (2017) conducted a multi-model comparison using nine wheat models and found that the use of canopy temperature calculated using energy budget improved heat stress responses compared with the simulations conducted using air temperature. The results reported in Chapter 7 introduced a novel method of incorporating an energy budget to crop models by modifying the environment at which plants are growing and showed that heat stress simulations can be improved. This was done by replacing the maximum daily temperatures of the climate file by the calculated leaf temperatures using the leaf energy budget approach.

Canopy temperature data reported in Chapter 6 was used for this study. All pasture plants used in this study showed limited homeothermy nature which means that pasture plants can buffer the temperature variation in the environment within the optimum temperature range for photosynthesis. This was modelled using the energy budget equation reported by Campbell and Norman (2012) and validated using the leaf temperatures measured using infrared images (in Chapter 6). Photosynthesis was simulated using both leaf and air temperatures using DairyMod and compared with the measured data for perennial ryegrass using the response ratio (effect size compared to the well-watered control treatment). It was found that the simulation conducted with leaf temperature accurately estimated the observed photosynthesis response to moderate heat stress (30 °C/20 °C day/night) while the simulation that used air temperature overestimated the impacts. This was mainly due to the feedback effects of stomata on leaf temperature. Perennial ryegrass plants sense heat stress at 30 °C and the model was parameterized to respond to heat stress when the maximum daily temperature reached that level. When the air temperature was used, temperatures reach the heat stress onset (30 °C) and started to simulate the heat stress response in the model. However, the calculated leaf temperature was cooler than the air and didn't reach the high temperature stress threshold. Therefore, use of calculated leaf temperature (cooler leaves) simulated the measured pattern of leaf temperature

accurately by maintaining below 30 °C. Improving the heat stress function in the DairyMod pasture model is increasingly important for areas like SE Australia because in the late spring and early summer, temperature could reach the high temperature stress threshold (30 °C) while there is still enough moisture in the soil to keep stomata open. In such situations, transpirational cooling may reduce the heat stress effects. In conclusion, plant growth models need to consider explicitly modelling leaf temperatures, to model heat stress and the impacts if extreme climate events.

The heat stress recovery function in DairyMod was also parameterized using the experimental data in Chapter 7. The model previously used the default value of Tsum=100 for perennial ryegrass to fully recover after heat stress and this was observed as too long. Chapter 6 data showed that perennial ryegrass could recover from a 7-day severe heat stress (35 °C/ 25 °C, day/night) after 7 days. Two T-sum recovery functions were tested in this study; 50 and 20 and observed that T sum-20 closely simulated the days to recover from severe heat stress.

Chapter 7 is a good example on how to design controlled experiments to address critical aspects of crop modelling. This research not only improved heat stress functions using leaf temperature incorporating leaf energy budget, but also parameterized the heat stress recovery function using the measured data. However, long term field studies over different seasons are needed to validate the findings under field conditions.

8.2. Future research directions

CSSSMD has been previously used as an indicator of tiller mortality in temperate and Mediterranean pasture species (*Festuca arundinacea* Schreb. and *Dactylis glomerata* L.) under European conditions (Poirier *et al.* 2012). In that study, temperate and Mediterranean populations of these species decreased tiller numbers when the CSSSMD levels exceed beyond 450 mm and 550 mm respectively. Chapter 3 adopted CSSSMD as a potential indicator that might limit persistence of pasture species commonly grown in SE Australia and found that CSSSMD exceeded the threshold of 550 mm, particularly at medium RF warm temperate climates at Wagga Wagga and Dookie sites, where phalaris is the main pasture species. Further, at Hamilton, where perennial ryegrass is the

major pasture species, CSSSMD reached 450 mm level in 2002-2015 compared with 350 mm in the earlier time periods. These results highlight the potential threat of increasing abiotic stresses and tiller mortality in common pasture species grown in SE Australia. However, lack of good quality tiller count data sets, more relevant to Australian grown pasture species (perennial ryegrass, phalaris, tall fescue and cocksfoot), is a limitation to validate these thresholds to Australian conditions. Therefore, future research should focus on threshold soil moisture levels that trigger tiller mortality under field conditions at different localities in Australia. This information will be very important for planning adaptation measures for hot and dry climates particularly for areas experiencing intense spring and summer droughts (Cullen *et al.* 2014a).

Chapter 7 demonstrated the importance of using leaf temperature instead of air temperature in simulating high temperature stress responses and in turn reducing the uncertainty in broad scale pasture simulations. Simulations conducted with leaf temperatures reliably simulated the effect size of moderate heat stress (30 °C) on photosynthesis, compared to the simulations conducted using air temperatures. However, this approach could be further improved by calculating canopy temperature rather than leaf temperature. In this research, the data collected from the experiment (Chapter 6) were insufficient to calculate canopy temperature using a canopy energy budget approach. Therefore, further research is recommended to collect crucial data such as canopy conductance and heat storage in soil to use them in canopy energy budget estimation (using the equation 14.8) (Campbell and Norman 2012), which is the most relevant variable than leaf temperature when simulating pasture production. Over prediction of leaf temperature observed in chicory would be able to correct when the canopy temperature is calculated, because the leaf energy budget equation does not account for the mutual shading effect due to the surrounding leaves of the canopy.

Repetition of this controlled experiment was not done in this research due to time and resource limitations. Therefore, it is recommended to conduct the similar experiment with repeated heat and drought stress under field conditions to validate the results reported in this study.

The modelling approach used in this research has some limitations. The key limitation of the DairyMod biophysical model is that the model does not simulate pasture plant death under extreme

climate conditions. Among many factors governing pasture persistence such as pasture species composition (Tozer *et al.* 2011), grazing frequency and intensity (Cousins *et al.* 2003), pest and diseases (Popay and Hume 2011) and weed infestation (Tozer *et al.* 2011), climate has been identified as a key factor (Culvenor and Simpson 2014). Due to the complex interaction between these factors, it is hard to model pasture persistence in a biophysical model. However, tiller mortality of temperate pastures has been modelled in a previous study by Ruget *et al.* (2009) using the STICS model considering cessation of leaf growth, leaf senescence, tiller mortality during drought and leaf and tiller regrowth after the first rains in autumn. Tiller mortality was driven by the ratio of actual to potential evapotranspiration in STICS. By this way the drought induced production loss and decreased persistence has been modelled by that study. However, DairyMod pasture model does not have a tiller density module as in STICS model but has the potential to incorporate a separate module to simulate tiller counts. This is another future research direction which has the potential in improving the simulations under extreme climate events. Apart from this limitation, heat stress thresholds need to be correctly identified using controlled environmental studies and recovery functions need to be parameterized for a range of pasture species commonly grown in Australia. This will improve the model confidence in predicting pasture production under increased climate variability and extremes.

8.3. Conclusions

The historical modelling of pasture growth rates showed that pasture growth patterns have changed in SE Australia with increased winter production, decreased spring pasture growth rates and increased year to year pasture yield variability in the autumn and spring seasons in the most recent period (2002-2015). These changes are clearly linked to the changes observed in the climate such as increased heat and drought stresses. Extreme climate events seem to be increasingly important as well as the average climate change in explaining the year to year pasture yield variability, highlighting the importance of forecasting these extremes before the start of the growing season to make the proactive management decisions. Adaptation measures such as breeding deep rooted and heat tolerant pastures need to be prioritized as climate change is occurring faster than expected.

A plant physiological experiment and biophysical modelling was used to better understand the impacts of heat and drought stresses on temperate pastures in south-eastern Australia. Physiological measurements were used to parameterize the heat stress responses of temperate grasses in the DairyMod model using leaf instead of air temperatures and found that use of leaf temperatures can improve modelling of the plant responses to heat stress compared with air temperature. This research highlight the importance of considering climate variability and extreme climate events in any climate change impact studies in the future because these extremes are increasing both frequency and magnitude and cause much harmful impacts than average climate change alone.

CHAPTER 9. References

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Appendix

Response to the reviewers' comments – Chapter 5.

Reviewer	Reviewers' comment	Response to the reviewers
1	"Length is 3600 words, including References. Without references, still 2600 words".	Word count is 2293 without references.
1	"In the topic maybe just put **"synoptic climate oscillations"** instead of El-Niño Southern Oscillation and Indian Ocean Dipole Phases"	This study addressed only ENSO and IOD phases and not all synoptic climate oscillations. Therefore, this title is specific for this research.
	General comment about the statistical approach used: "The main weakness of the method is the use of Null Hypothesis Significance Testing (NHST) methods to analyse the data with p-values. This approach is not really suited to simulation studies. A small p-value essentially says, "it is probable that there is a non-random difference". However the p-value is mainly a function of the number of data points, 65 in this case. With a longer simulation, every treatment will be significantly different, but this is not very enlightening. It is more appropriate to	This is a valid comment in a statistical context and acknowledged. The comment was addressed in the abstract and results section by emphasizing more on the bio-physical production aspects during each climate driver phases rather than highlighting the statistical significance between those phases. However, the statistical approach remained in the analysis (in the bar graphs) to clearly identify the effect of each phase on pasture production figures because this approach has been previously accepted and used in a similar analysis.

	focus on the size of the effect and whether these are practically meaningful. The bar charts do a reasonable job of this, although the error bars should perhaps be e.g. 90% quantiles rather than 1 standard deviation." **Specific comment:** In bar graphs; Are they a single standard deviation? Then the variation is huge! Using significance (p-values) is a bit invalid for simulation studies, because it mainly reflects the number of data points (years simulated). You could just simulate more years until ALL the differences were significant. I think you'd be better looking at average differences and don't worry about significant.	See the reference: Jarvis, C., Darbyshire, R., Eckard, R., Goodwin, I. & Barlow, E. 2018. Influence of El Niño-Southern Oscillation and the Indian Ocean Dipole on winegrape maturity in Australia. *Agricultural and forest meteorology*, 248**,** 502-510. The changes can be found in the abstract and paragraph 1 of the results section.
1	Abstract: In this study, multivariate ENSO index bimonthly ranks (MEI) and dipole mode index data from the winter-spring period were used to classify ENSO and IOD phases during the period 1950-2015	Two indices were used to classify ENSO and IOD into three phases each in winter-spring period during 1950-2015. The changes can be found in the Abstract.

	"This is quite dense and technical. I wonder if you should make the abstract more accessible for laymen to understand."	
1	Nicholls (1985) found that wheat yields were related to rainfall changes during El-Niño and La-Niña events with varying spatial impacts What does this mean?	This was explained in the introduction section-paragraph 3.
1	If the 95% confidence interval of the mean yield differences were not zero, those differences were identified as significantly different. "This doesn't make sense; how can a confidence interval be zero?"	Yield differences were tested in those phases using 0.05 significance level. Can be found in the materials and methods section-statistical analysis-paragraph 2.
1	I think you should include a map showing site locations.	A map was not included as the paper becomes bulky. Authors have provided the location of each site with the latitude and longitude coordinates in the Table 2.
2	Rainfed pasture production, which responds more strongly to rainfall variation, will benefit more if these event phases can be predicted before the key adapted management decisions are implemented (Ash *et al.* 2007).	1. "Management decisions to adapt to climate variability may involve planning for increased fodder conservation, early destocking or forward

	Comment: 1. What types of decisions could be informed by this information? 2. What criterion would farmers apply before trusting the information? *Requirement: include reference to farmer decision-making frameworks, e.g. Austen et al 2002, Aust J Exp Agric . 42, 173-183.*	contracting of supplementary feed" (Austen *et al.* 2002). Discussion - paragraph 2 2. "A survey showed that farmers expected at least 70% forecast accuracy in order to use them in their decisions" (Austen *et al.* 2002). discussion – paragraph 2 Also, the authors discuss that the climate driver phases can be predicted with >70 accuracy, at the end of winter, but this is not a sufficient lead time to be used in farm decision making. Therefore, this limitation has been identified as an area of further research. *"Detailed analysis of each of the phases further revealed that 70% of the ENSO and 85% of the IOD phases recognised in the March-*

		August period remained unchanged for the rest of the year while the probability that any phase may reverse in direction after this window was very low or zero." Discussion - paragraph 2