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Crop Evapotranspirative Cooling Across Spatio-temporal Scales

by

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Declaration of authorship

The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

The content of the publication Deva, C., M. Urban, A. Challinor, P. Falloon and L. Svitáková, 2020: Enhanced Leaf Cooling Is a Pathway to Heat Tolerance In Common Bean. *Frontiers in Plant Science*, **11**,
doi: https://doi.org/10.3389/fpls.2020.00019 is included in chapters 2 and 3 of this thesis. The candidate is the first author of the above mentioned publication, which was jointly authored with Milan Urban, Andrew Challinor, Pete Falloon and Lenka Svitáková. A description of the authors contributions is included below.

Chetan Deva conceived the study, performed the analysis and wrote the paper. Milan Urban performed the experiments and provided guidance on using the observations. Milan Urban also provided feedback as the paper took form and commented on draft versions of the paper. Andrew Challinor provided regular feedback as the paper took form and provided discussion and feedback on draft versions of the paper. Pete Falloon provided regular feedback as the paper took form and provided discussion and feedback on draft versions of the paper. Lenka Svitáková conducted the specific leaf area measurements for experiment D2, explained the protocols and instrumentation used and provided guidance on using and interpreting these measurements. Lenka Svitáková also provided discussion and feedback on draft versions of the paper.

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Abstract

Plants experience heat stress when exposed to high temperatures. High temperature events have caused shocks to food production in some of the world's most important growing regions, and global heating is expected to increase the frequency and magnitude of such events. Evapotranspirative cooling is a mechanism of heat avoidance at plant, farm and regional scale. In this thesis, the importance of evapotranspirative cooling is explored at all three of these scales.

At the plant scale, thousands of observations of leaf temperature are used to explore the magnitude of heat avoidance from transpirational cooling and its connection to heat tolerance. At the farm scale, the ORYZA crop model is used to test the importance of transpirational cooling in modelling the trade-off between saving water and heat avoidance in irrigated rice. At the regional scale, large spatial data sets of irrigated rice area are used in combination with observed temperature data to examine the impact of landscape wide irrigation on heatwaves in India over the historical period.

The results of this thesis show that evapotranspirative cooling is an important heat avoidance mechanism in common bean. The first empirical evidence demonstrating a connection between transpirational cooling and heat tolerance in common bean is presented. At the farm scale, evapotranspirative cooling is shown to explain a far greater share of variability in yield than changes in irrigation strategy. Modelling of evapotranspirative cooling is shown to be a key uncertainty in efforts to understand the trade-off between saving water and resilience to heat stress in a warming climate. Finally, region-wide irrigation is shown to reduce the frequency and duration of heatwaves in India.

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Abbreviations

ATP Adenosine Triphosphate

BCMNV Bean Common Mosaic Necrosis Virus

CF continuously flooded

CIAT The International Centre for Tropical Agriculture

CLM Community Land Surface Model

$\mathbf{CO_2}$ Carbon Dioxide

CTD Canopy Temperature Depression

DAP days after planting

EBN energy balance models

EBSC energy balance models corrected for stability

EHF Excess Heat Factor

EMP empirical models

ET Evapotranspiration

FAO Food and Agriculture Organisation

GCMs Global Climate Models

GxExM Genotype × Environment × Management

HWD heatwave duration

HWN heatwave number

IGP Indo-Gangetic Plains

IMD Indian Meteorological Department

IPCC Intergovernmental Panel on Climate Change

IR infrared

IRRI The International Rice Research Institute

LA leaf area

LAI Leaf Area Index

LTD Leaf Temperature Depression

MOST Monin-Obukhov Similarity Theory

NCAR National Center for Atmospheric Research

OLS Ordinary Least Squares

PAR Photosynthetically Active Radiation

Phi2 steady state efficiency of photosystem II

phiNO non-regulatory energy dissipation

phiNPQ quantum yields of non-photochemical exciton quenching

QTL Quantitative Trait Loci

RMSE Root Mean Squared Error

Rubisco Rubilose-1.5-biphosphate

SLA Specific Leaf Area

TPE Target Population of Environments

VPD Vapour pressure deficit

Chapter 1

Introduction

1.1 Motivation

Global heating is expected to increase the frequency and magnitude of temperature extremes (IPCC 2013), presenting a risk to food production. Most of the crops that we eat experience heat stress when exposed to temperatures above the range they are adapted to (Barnabás et al. 2008). Heat stress reduces crop yields and, when particularly severe, can also result in failed harvests (Lesk et al. 2016). Extreme heat and drought events causing region-wide reductions of crop production have been documented in some of the world's most important crop growing regions (Vogel et al. 2019; Bastos et al. 2014). As the risk of extreme heat increases, adaptation of agricultural systems will play a vital role in ensuring food security in some of the world's most vulnerable places (Rippke et al. 2016).

Understanding and responding to the scale of this challenge will require an integrated approach to adaptation. The concept of Genotype × Environment × Management (GxExM) provides a useful conceptual framework through which such integration can take place. A change in mean temperature and the frequency of extreme heat represents a change to the environmental conditions experienced by the plant. The impact of this change in temperature depends on how tolerant the plant is to heat (genetics) and the way in which the plant is managed.

This thesis aims to further understanding of two applied science problems in which interactions between genetics, environment and management must be understood to cope with rising temperatures. The first of these problems is the need to enhance heat tolerance in common bean (Phaseolus vulgaris). Common bean is the most consumed legume in the world (Araujo et al. 2015), and an important source of protein in tropical Latin America , eastern and southern Africa (Beebe et al. 2011). Common bean is grown in a variety of environments with mean air temperatures between 14°C and 35°C (Araujo et al. 2015). It has evolved in mid-high latitudes and is more sensitive to high temperatures than other legumes (Beebe et al. 2011). This makes breeding for heat tolerance an urgent priority as the climate continues to warm (Beebe et al. 2011).

The second challenge addressed in this thesis is the need to produce food, save water and remain resilient to high temperatures in one of the world's most important rice growing regions. Long known as the breadbasket of India, today Punjab faces plummeting water tables that threaten the sustainability of crucial agricultural systems for regional food security (Tiwari et al. 2009; Perveen et al. 2012). As groundwater retreats, it becomes more energy intensive to pump water, creating an ever-increasing burden on the electricity grid. This dependency between irrigated agriculture, groundwater and electricity consumption can be described as a water-energy-food nexus (Bazilian et al. 2011; FAO 2014). As policy makers grapple with this challenge, they must also contend with the way in which adaptations to groundwater decline interact with a warming climate.

The first strand of work in this thesis was designed to help breeders to produce more heat tolerant common bean varieties, and is focused on GxE interactions. Despite being a globally important source of protein, much less is known about heat tolerance in common bean than in major cereal crops such as rice and wheat. In particular, there is a gap in understanding the role of heat avoidance as a strategy to prevent damaging tissue temperatures. The first strand of work in this thesis provides the first test of the theory that heat tolerance in common bean is linked to the ability to avoid high tissue temperatures through an enhanced ability to cool via transpiration.

The second strand of work in this thesis was designed to explore potential trade-offs between the introduction of water saving technologies in Punjab's rice growing regions and exposure to damaging temperatures. This strand of work is focused on MxE interactions, and attempts to characterize the interactions between reducing irrigation and keeping the rice crop cool in a hot climate. The third and final strand of work in this thesis is also focused on MxE interactions at a larger spatial scale. This strand of work moves from field to regional scale to explore the historical relationships between region-wide irrigation and the occurrence of damaging heatwaves in India.

These three strands of work move from plant–field–regional scale and cover different areas of GxExM interactions with heat stress. They are unified by the common theme of interactions between water and heat stress. The first strand of work considers how enhanced transpiration relates to heat avoidance and how this can be utilised by the bean breeding community. The second strand of work considers the interaction between the provision of water and heat stress at field scale. This relationship hinges on the importance of interactions between transpirational cooling and water limiting conditions. Finally, the relationship between landscape scale irrigation and the occurrence of extreme heat is governed by the extent to which evaporative cooling from widespread irrigation modifies energy fluxes in rice growing regions.

This thesis is an exploration of the interaction between evapotranspirative cooling and heat avoidance across spatio-temporal scales and the space explored is summarized in the next section - thesis aim and structure.

1.2 Thesis aim and structure

The aim of this thesis is to explore the contribution of evapotranspirative cooling to heat avoidance across scales.

Within this broader area, three research questions were chosen to address the pressing applied science questions at plant, field and regional scales described in the previous section. Each of the questions chosen addresses knowledge gaps identified in the literature review section.

- Is transpirational cooling important to heat avoidance and heat tolerance in common bean?
- Is transpirational cooling important in modelling the trade-off between saving water and resilience to heat stress?
- Has evapotranspirative cooling from irrigation had an impact on heatwaves?

The remainder of chapter 1 is split into a key concepts section and a literature review section. The key concepts section describes the core scientific concepts that need to be understood in order to answer the research questions above. The literature review section demonstrates that these question address knowledge gaps identified from a review of the scientific literature. Chapter 2 of this thesis describes the methods used to address these research questions, including instrumentation and process-based modelling. Chapters 3, 4 and 5 address the research questions listed above respectively, and chapter 6 synthesises the knowledge gained from the results chapters in light of the thesis aim.

1.3 Key concepts

1.3.1 Evapotranspiration

Evapotranspiration is the sum of two processes, evaporation from the soil and transpiration from plants (Allen et al. 1998). Evaporation refers to the vaporization of water from liquid to gaseous form, while transpiration refers specifically to vaporization of water from plant tissues to the surrounding atmosphere (Allen et al. 1998). Both evaporation and transpiration share common atmospheric drivers. Energy is required to break the bonds in liquid water, therefore both evaporation and transpiration depend on the supply of energy from solar radiation and heat from the surrounding air (Allen et al. 1998). The rate of both evaporation and transpiration depends on the difference in the vapour pressure between soil, plant and atmosphere - often called the Vapour pressure deficit (VPD). Since the difference in vapour pressure is influenced by the rate at which moist air is replaced with drier air, both evaporation and transpiration are also strongly influenced by windspeeds (Allen et al. 1998).

1.3.2 Heat Stress and heat tolerance

Heat stress can be defined as the negative impacts of high temperatures on the growth and development of a plant (Rezaei et al. 2015; Porch and Hall 2013). Heat stress can impact the plant directly through mechanisms connected with tissue temperature, or indirectly through the impact of increased evaporative demand on water availability (Porch and Hall 2013). Plants are sensitive to high temperatures throughout the growing season and there is general agreement that field crops are most sensitive to high temperatures during the reproductive period (Prasad et al. 2017).

Plants experience heat stress when temperatures exceed optimal or critical temperature thresholds (Porch and Hall 2013). The impact of heat stress is a function of the intensity and duration of the temperature event (Porch and Hall 2013) and the time the plant has to acclimatise to higher temperatures (Porch and Hall 2013). The field of heat stress and heat tolerance is vast, as different types of plants experience heat stress differently and have evolved different coping mechanisms. The purpose of this first section is to provide a high level introduction to important concepts regarding heat stress and heat tolerance. There is therefore an emphasis on the impacts of heat stress that field crops have in common and shared mechanims for heat tolerance. Examples for rice and bean are provided, since these two crops are central to this thesis.

1.3.2.1 Temperature and crop development

Crop development can be split into three stages, the vegetative stage, the reproductive stage and the ripening stage. Different varieties of a crop can exhibit faster or slower progress through these stages. Figure 1.1 shows a common way of expressing differences in varietal duration for transplanted rice. Temperature is an important control on the rate of crop development (Atkinson and Porter 1996). Between a low temperature (often called the base temperature) and a peak temperature (often called the optimum temperature), the rate of crop development increases. Above this optimal temperature, developmental rates decrease (Atkinson and Porter 1996). An increase in temperature to levels which do not cause stress can still reduce yield by accelerating crop development. A shorter growing season reduces the time available for biomass accumulation, which limits end of season yield (Atkinson and Porter 1996). The impact of a shortening of duration is larger if high temperatures occur during grain filling. Lower yields from a shorter life cycle is an important pathway through which global heating is expected to impact Indian agriculture (Mall et al. 2006).

1.3.2.2 Impacts of high temperatures on photosynthesis

Net accumulation of dry matter during the growing season also depends on the difference between photosynthesis and respiration. In this subsection, the most important impacts of high temperatures on photosynthesis are reviewed. Photosynthesis increases between a minimum and optimum temperature above which it declines (Rezaei et al. 2015). These minima and optima differ by plant type (Galmes et al. 2015) and are systematically different in C3 and C4 plants (Rezaei et al. 2015). C3 plants tend to exhibit an optima between 20 °C and 35 °C, while the optima is thought to be higher in C4 plants (Sage et al. 2008). Since this thesis focuses on rice and bean crops, the impact of heat stress on C3 crops is discussed here.

The temperature response curve is largely driven by the kinetic properties of Rubilose-1.5-biphosphate (Rubisco), the enzyme responsible for carbon fixation in plant cells (Galmes et al. 2015). Rubisco provides the active site for photo-

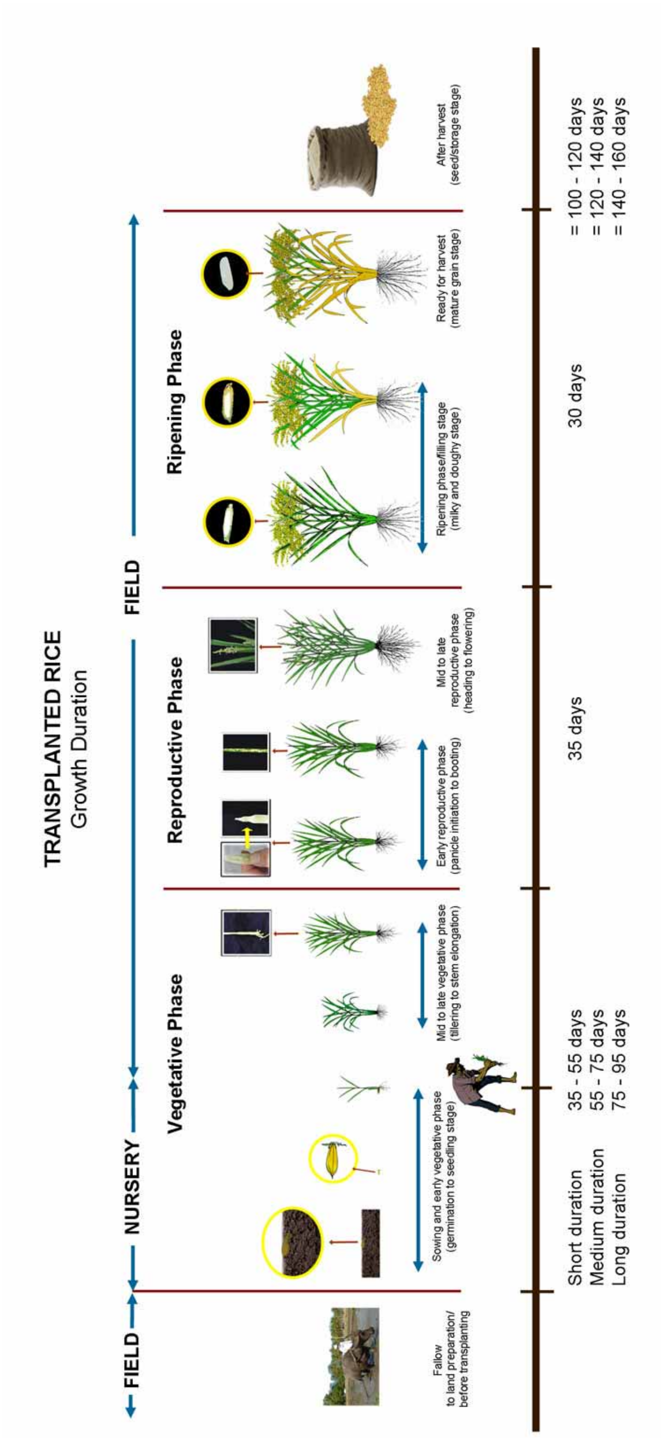


Figure 1.1: Crop calendar for rice varieties with different durations (IRRI 2020). This image was published by IRRI under a CC BY-NC-SA 3.0 license.

synthesis to take place. As temperature increases, so too does the rate at which Rubisco fixes carbon (Galmes et al. 2015). However, as temperatures rise, the affinity of Rubisco for Carbon Dioxide (CO_2) declines relative to its affinity for oxygen (Salvucci and Crafts-Brandner 2004). As a result, the efficiency of carbon fixation becomes increasingly limited by the availability of CO_2 at higher temperatures (Salvucci and Crafts-Brandner 2004).

1.3.2.3 Impacts of high temperatures on respiration

Respiration is the process through which the building blocks of cells are produced (Millar et al. 2011). These building blocks are called Adenosine Triphosphate (ATP). ATP is used by plants for both cell maintenance and growth (Millar et al. 2011). Up to approximately 40-50 °C, an increase in temperature also increases respiration (Taiz and Zeiger 2010). In rice plants, respiration occurs at night, and high nighttime temperatures have been shown to increase respiration and reduce yields (Mohammed and Tarpley 2009; Peng et al. 2004). The products of photosynthesis can be used in growth or maintenance respiration. At higher temperatures, more photosynthates are consumed in maintenance respiration, reducing the assimilated carbon available for growth (Shi et al. 2013). Projections for south Asia suggest an increase in nighttime temperatures (IPCC 2013), which are expected to reduce yields through increases in maintenance respiration (Jagadish et al. 2015).

1.3.2.4 Impacts of high temperatures on reproduction

Crop yields are most sensitive to high temperatures during flowering, because this is when seeds and fruits are developed (Hedhly 2011). Field crops are most vulnerable to heat stress when reproductive cells are formed (gametogenesis) and during flowering (anthesis) (Prasad et al. 2017). The duration of sensitivity differs by crop. Most field crops are sensitive to high temperatures for between 14 and 21 days (Prasad et al. 2017), and are extremely sensitive in the 9 to 5 days prior to anthesis (Prasad et al. 2017). When flowers are open, high temperature events lasting only a few hours can result in heat stress (Prasad et al. 2017). The impact of high temperatures on crops during the reproductive period can be split into three distinct periods; sexual organ development, pollination and embryo development (Hedhly 2011).

The two main mechanisms by which high temperatures impact rice during the flowering period are through spikelet sterility and anther indehiscence (Prasad et al. 2006). The spikelet forms at the end of the panicle, and provides the location for floret development. A spikelet is referred to as being sterile if it does not produce any seed. Anther dehiscence describes the process by which the anther splits open to release pollen. Failure to do so prevents pollen from reaching the stigma and embryos being fertilized.

Jagadish et al. (2007) show that spikelets can become sterile very quickly. In an experiment using both Indica and Japonica rice varieties, they found that temperatures greater than 34 °C resulted in sterility in less than an hour. Further, they found that spikelets which opened one hour on either side of the imposition of high temperatures were also affected. In an experiment with 14 rice cultivars, including some heat tolerant cultivars, Prasad et al. (2006) found that imposing temperatures 5 °C hotter than ambient temperatures resulted in decreased fertility in all 14 cultivars. They found spikelet sterility was associated with lower pollen production and reduced pollination.

During anthesis, rice florets open allowing pollen grains to absorb moisture and swell. This provides a source of pressure, which subsequently ruptures the anther and releases the pollen (Matsui et al. 1999). High temperatures interrupt this process in two ways; if experienced before floret opening, high temperatures change the structure of the cell wall, inhibiting dehiscence (Matsui et al. 2000). If high temperatures occur on the day of flowering, pollen grain swelling is reduced, weakening the force which drives the anther to split open (Matsui et al. 2000).

Beans are also sensitive to high temperatures during the reproductive period. There is strong evidence that elevated temperatures around flowering reduces pod set, seed set and subsequently grain yield (CIAT 2015). There are a number of proposed mechanisms for these reductions, which can claim empirical support. As is the case for most legumes, high temperatures during the flowering period can increase abscission of reproductive organs. In some experiments, seed set reductions are associated with changes in pollen viability (Dickson and Boettger 1984; Gross and Kigel 1994; CIAT 2015), while in others they are associated with structural damage to pollen wall architecture and anther dehiscence (Porch and Jahn 2001). It has also been shown that high temperatures can impact grain filling. This suggests that reduced photosynthate re-mobilization (from leaves to pod walls and then to grain) may be a further mechanism by which crop yield is affected (Soltani et al. 2019; CIAT 2015).

1.3.2.5 Heat Stress Thresholds

The term heat stress threshold is not used uniformly throughout the literature. Studies focusing specifically on heat stress thresholds tend to define them in terms of the cardinal temperatures. They refer to a base temperature (the minimum temperature required for a physiological process to occur), an optimum temperature (the temperature at which a physiological process is maximized) and a maximum temperature, above which the process stops (Porter and Gawith 1999; Sánchez et al. 2014; Luo 2011). These studies also define a lethal temperature, above which the plant dies. Cardinal temperatures have been shown to vary widely for different crops and across growth stages for the same crop (Porter and Gawith 1999; Sánchez et al. 2014; Luo 2011). An accurate estimate of these heat stress thresholds is important for understanding heat tolerance across and within species. Understanding how global heating will impact crop yields requires heat stress to be modelled, which in turn requires an accurate estimate of threshold exceedence.

Sánchez et al. (2014) conducted a literature review of the cardinal temperatures for rice. The optimum and maximum thresholds are summarised in figures 1.2 and 1.3. The maximum temperature threshold is highest during germination and lowest during grain filling. There is a clear difference between the temperature thresholds for panicle initiation and anthesis - the two most sensitive parts of the growing season. The standard error of the maximum temperature threshold is highest for panicle initiation and lowest for grain filling, which appears to be well constrained. There is some overlap between the standard errors of maxi-

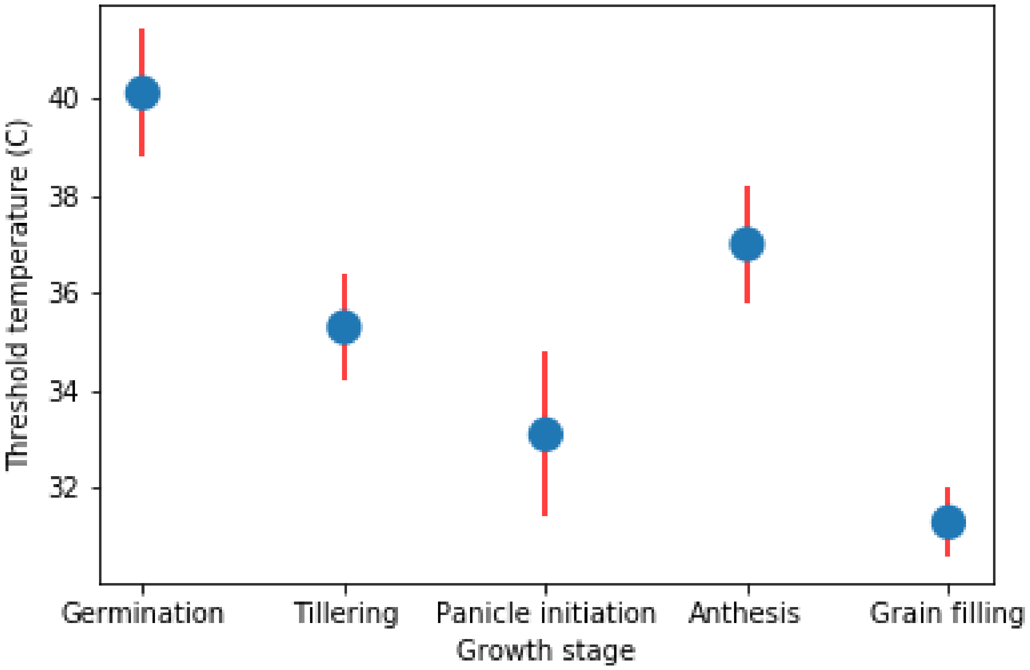


Figure 1.2: Maximum temperature thresholds for each stage of the rice growing season. Data taken from a literature review of cardinal temperatures for rice Sánchez et al. (2014) composed of 124 studies. Red lines represent the standard error for each growth stage

mum temperatures for tillering and panicle intiation and grain filling and panicle initiation. In general, however, Figure 1.2 suggests that maximum temperature thresholds do differ for different growth stages.

The picture is less clear for optimum temperatures. Figure 1.3 shows that there is considerable overlap between optimum temperatures for most stages of the growth cycle. Sensitivity to temperature is once again highest during grain filling, but lowest during tillering rather than germination. The optimum temperature threshold is higher for panicle initiation than for anthesis. As was the case for maximum temperature thresholds, the standard error is largest during panicle initiation and lowest for grain filling, which once again appears to be well constrained.

Sánchez et al. (2014) discuss a number of limitations to defining the cardinal

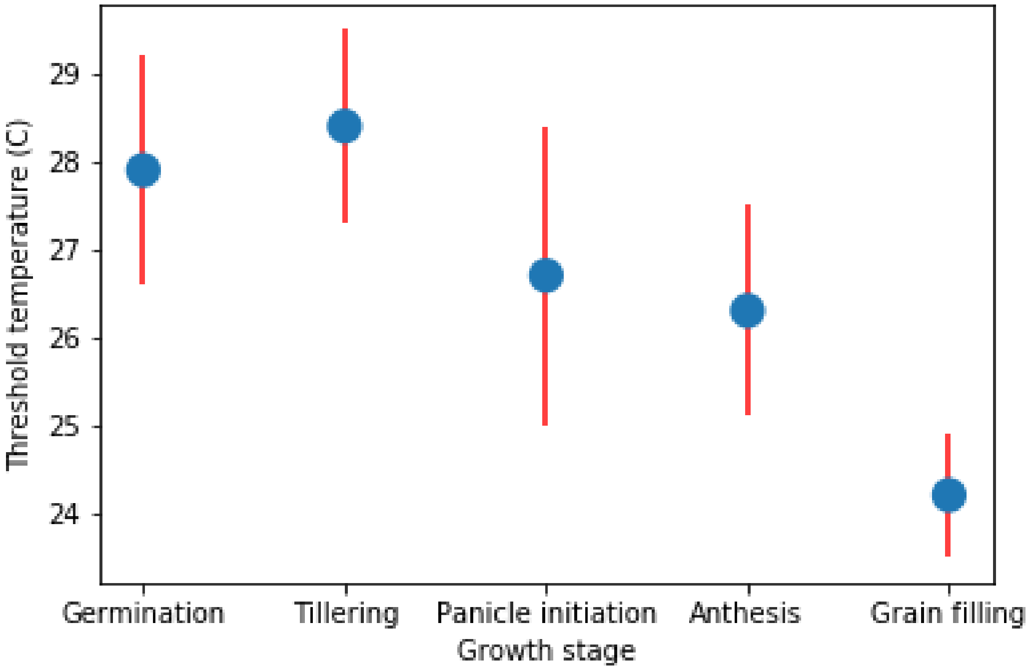


Figure 1.3: Optimum temperature thresholds for each stage of the rice growing season. Data taken from a literature review of cardinal temperatures for rice Sánchez et al. (2014) composed of 124 studies Red lines represent the standard error for each growth stage

temperatures using a literature review approach. First, the experiments sampled varied in treatment, management conditions and variety (Sánchez et al. 2014) and it is not clear to what extent the standard error of estimates reflects each of these differences. Second, it is not always clear whether these thresholds refer to air or canopy temperatures (Sánchez et al. 2014). As will be discussed in detail in the literature review, differences in air and canopy temperatures can be very large - much larger than the standard error of the estimates presented by Sánchez et al. (2014).

Despite these uncertainties, the literature reviews conducted by (Sánchez et al. 2014) and (Porter and Gawith 1999) represent advances in quantifying uncertainty in the cardinal temperature thresholds for rice and wheat. Studies of this nature have not yet been conducted for common bean. Rainey and Griffiths (2005a) exposed plants to four temperature treatments 7 days prior to anthesis. They found that both heat sensitive and heat tolerant genotypes displayed reductions in seed set at temperatures starting from daytime temperatures of 30 °C and nighttime temperatures of 27 °C, which is in keeping with earlier studies. (Rainey and Griffiths 2005b) exposed plants to daytime temperatures of 32 °C and nighttime temperatures of 28 °C nine days before anthesis and found that increased abscission of reproductive organs occurred at these temperatures. Porch and Jahn (2001) applied daytime temperatures of 32 °C and nighttime temperatures of 27°C prior to anthesis. They found that imposing these temperatures during microsporogenesis retarded anther and pollen development. In two studies of the impact of high temperature on photosynthesis, Pastenes and Horton (1996) imposed temperatures of 30-35 °C on two bean varieties. They found changes in the structure of the thylakoid and postulate an increase in cyclic electron transport may be a pathway to changes in photosynthesis between these temperatures. However, Traub et al. (2018) found that very high daytime temperatures of 45 °C and nighttime temperatures of 35 °C were required before changes in gas exchange, photorespiration and chlorophyll fluorescence were significantly changed.

Even for globally important staple crops like rice and wheat, uncertainty in heat stress thresholds represents a key gap in understanding heat stress. This gap stems in large part from a lack of coordinated experiments testing optimum and maximum temperatures while systematically varying GxExM. Further, knowledge of how these thresholds vary by leaf and air temperature increases the uncertainty of estimates that have already been made. These uncertainties pose a challenge to both targeted breeding programs and heat stress assessments using crop models. For common bean, the size of this uncertainty is far greater. There seems to be limited support for a daytime maximum temperature threshold of between 30 °C and 35 °C during the reproductive period, although since many experiments imposed increases in both day and night time temperatures simultaneously, it is difficult to untangle daytime and nighttime effects.

1.3.2.6 Heat tolerance

Plants are described as heat tolerant if they are able to grow, develop and produce yield when exposed to high temperatures (Wahid et al. 2007). Heat tolerance is associated with the ability to maintain photosynthesis in all plant species (Bita and Gerats 2013). It is useful to subdivide heat tolerance into 3 main categories; true heat tolerance, heat tolerance through avoidance and heat tolerance through escape (Jagadish et al. 2007). A plant that has acquired true heat tolerance is able to better mitigate the impacts of a given tissue temperature, while a plant that acquires heat tolerance through avoidance is able to prevent damaging tissue temperatures from being experienced. Finally, a plant that achieved heat tolerance through escape mechanisms is able to avoid experiencing damaging air temperatures in the first place.

There are many physiological mechanisms through which plants achieve heat tolerance. Studies examining differences in cell membrane structure have found that some heat tolerant plants store more saturated fatty acids in membrane lipids. This increases their melting point, allowing them to maintain greater membrane fluidity when exposed to high temperatures (Bita and Gerats 2013). Some studies have found that heat tolerant plants are better able to maintain leaf osmotic potential, through the production of more osmoprotectants. These substances sustain membrane integrity and lower osmotic potential in the leaf (Ashraf and Foolad 2007), thereby helping to maintain water uptake (Bita and Gerats 2013). Heat tolerant plants have also been found to exhibit higher levels of carbohydrate availability during episodes of heat stress. This allows them to maintain sink capacity and pollen grain carbohydrate content (Bita and Gerats 2013). Finally, there is empirical support for an association between the presence of growth regulators during high temperature episodes and heat tolerance (Bita and Gerats 2013). Some studies suggest that heat tolerant plants are better able to synthesize growth regulators when experiencing heat stress (Bita and Gerats 2013).

Evidence of potential escape mechanisms have been identified in rice. Julia and Dingkuhn (2012) show that rice plants adapt the time of flowering to the prevailing temperature and relative humidity. Ishimaru et al. (2010) showed that the early morning flowering trait was able to improve heat tolerance, by ensuring that flowers opened under cooler conditions. Bheemanahalli et al. (2017) have shown that wild growing rice can flower much earlier than cultivated varieties. Hirabayashi et al. (2014) succeeded in breeding wild rice with the early morning flowering trait into popularly grown varieties and found that this provided greater tolerance.

Heat avoidance has also been documented in rice plants. Julia and Dingkuhn (2013) and Weerakoon et al. (2008) have shown that transpirational cooling keeps panicle temperatures well below air temperatures in hot and dry conditions, helping to explain how rice is able to be grown in hot environments such as Australia and north western India (Jagadish et al. 2015). Matsui et al. (2007) showed that rice varieties growing in hot and dry conditions in Australia exhibit strong transpirational cooling, and that this is instrumental to their survival.

In a review of the challenges to field crops from heat stress in a warming climate, Prasad et al. (2017) note that the heat avoidance mechanism is not characterized in many crops and suggests that future research addresses this knowledge gap. Transpiration cools by changing the energy balance of the plant. The next section introduces the fundamentals of this energy balance in preparation for more detailed study of transpirational cooling in the results chapters of this thesis.

1.3.3 Energy Balance

1.3.3.1 The energy balance at canopy scale

This section describes the physical framework for understanding differences in canopy and air temperatures. It draws extensively from the chapter entitled Steady State Heat Balance (i) Water surfaces, Soil and Vegetation in Principles of Environmental Physics (Monteith and Unsworth 2013). The following paragraph is a short summary of the energy balance, following the structure and notation in Monteith and Unsworth (2013).

In its simplest form, the energy balance can be described as a dynamic budget of incoming and outgoing energy (Monteith and Unsworth 2013).

$$\overline{R}_{\mathrm{n}} + \overline{M} = \overline{C} + \lambda\overline{E} + \overline{G} \tag{1.1}$$

Equation 1.1 describes this balance for an organism, where $\mathrm{R_n}$ is the net heat gained from radiation, M is the net heat generated from metabolic activity, C is the heat transferred to the atmosphere through convection, the E term is the heat used up in the process of evaporation (latent heat loss) and G is heat transferred to the atmosphere through conduction (Monteith and Unsworth 2013). According to the first law of thermodynamics, both sides of equation 1.1 must always balance, because energy is conserved (Young and Freedman 2012). For example, an increase in solar radiation must be balanced by either sensible heat exchanges (convection + conduction) or latent heat exchanges. The change in canopy surface temperature from an increase in solar radiation depends on how the additional energy received is divided between these terms.

Equation 1.1 can be simplified further by assuming that the metabolism term is negligible. Nobel et al. (1999) argue that this has been shown to the case for the leaf energy balance. Equation 1, can then be simplified to:

$$\overline{R}_{\mathrm{n}} = \overline{C} + \lambda\overline{E} + \overline{G} \tag{1.2}$$

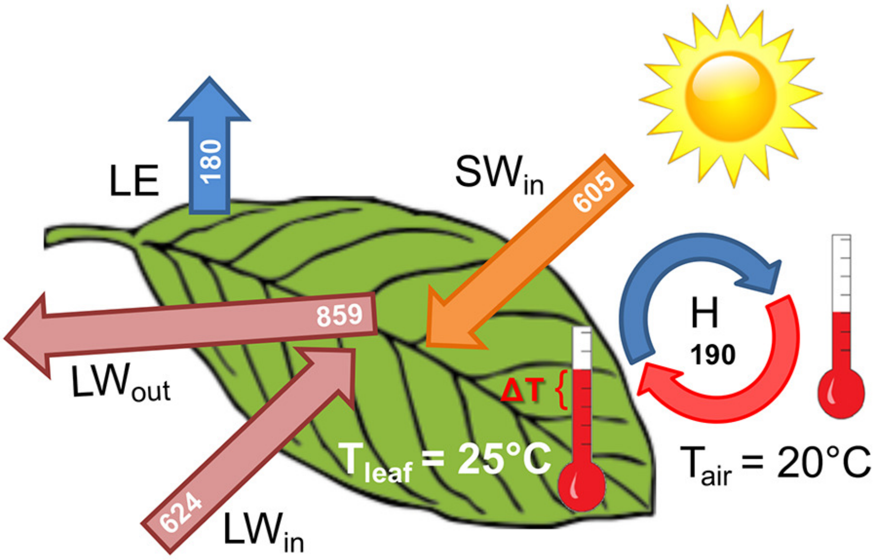
The sensible heat exchange can be simplified further when considering the energy balance of the leaf. Conduction (the molecular exchange of kinetic energy) is an important means of heat exchange in solids, but is less important when considering sensible heating from the leaf to the atmosphere (Monteith and Unsworth 2013). Sensible heat exchange between the leaf and the atmosphere is dominated by the convection term (Monteith and Unsworth 2013). For the purposes of a conceptual overview of the dominant terms in the leaf energy balance, it is therefore possible to simplify equation 1.2 further to equation 1.3.

$$\overline{R}_{\mathrm{n}} = \overline{C} + \lambda\overline{E} \tag{1.3}$$

The convection term in equation 1.3 can be broken down into two parts, free and forced convection (Monteith and Unsworth 2013). Forced convection refers to heat transfer between two regions with different temperatures through a boundary layer (Monteith and Unsworth 2013). In this case, heat is transferred from the leaf through a boundary layer to the surrounding atmosphere. Free convection refers to heat transfer through circulation. In this case, differences in temperature drive pressure gradients, which in turn create differences in buoyancy (Monteith and Unsworth 2013). In the vertical dimension, the pressure gradient force is the difference between the force derived from the pressure gradient and the force of gravity. If the pressure gradient force is positive then buoyancy is positive and air will rise (Markowski and Richardson 2011).

Figure 1.4 is a representation of the simplified energy balance of a warming leaf taken from Still et al. (2019). The net gain from radiation ($\mathrm{R_{in}}$) is represented by $\mathrm{SW_{in}}$, $\mathrm{LW_{in}}$ and $\mathrm{LW_{out}}$. This refers to the solar radiation received by the plant ($\mathrm{SW_{in}}$), the amount of incoming solar radiation that is re-emitted by the plant ($\mathrm{LW_{out}}$) and the longwave radiation absorbed from the surrounding environment ($\mathrm{LW_{in}}$) (Still et al. 2019). The sum of convection and conduction are represented by the H term, and the latent heat exchange is represented by LE (Still et al. 2019).

This thesis contributes to understanding of the impacts of the E term at two scales. The first scale considers the importance of E on the heat stress expe-



$$R_{net} = \alpha SW_{in} + \varepsilon_{IR}(LW_{in}) - 2\varepsilon_{IR}\sigma\left(T_{leaf}\right)^{4}$$

Figure 1.4: A visual representation of the energy balance of a leaf. Source: Still et al. (2019), published by John Wiley and Sons under a CC-BY 3.0 license

rienced by the plant. The second scale considers the importance of E on the surrounding atmosphere at landscape scale. The next section provides a more detailed discussion of the determinants of the E term.

1.3.3.2 Latent heat exchange

When heat is transferred to an object without increasing the temperature of that object, it is described as latent heat (Monteith and Unsworth 2013). The latent heat exchange term can be broken down into heat transfer from transpiration, evaporation and condensation (Monteith and Unsworth 2013). Both transpiration and evaporation are cooling, because energy is required to evaporate water (Young and Freedman 2012). Condensation on the other hand is warming, because energy is released when water condenses (Young and Freedman 2012).

Water which evaporates from the leaf is commonly known as transpiration (Taiz and Zeiger 2010). The rate at which water evaporates from the leaf is controlled by the concentration gradient between the leaf and the air, and the resistance encountered to diffusion of water across this gradient (Taiz and Zeiger 2010). Resistance to diffusion comes from two main sources - stomatal and boundary layer, which are also influenced by the weather (Taiz and Zeiger 2010).

Water diffuses from the leaf to the air through stomatal pores. Plants regulate the conductance of these pores depending on water availability (Taiz and Zeiger 2010). When water is available and demand for CO_2 is high, stomatal resistance is low (Taiz and Zeiger 2010). This facilitates transpiration when there is a sufficient vapour pressure gradient between the leaves and the atmosphere (Taiz and Zeiger 2010). However, when water availability is low, stomatal resistance increases to conserve the supply of water. This reduces transpiration for a given vapour pressure gradient (Taiz and Zeiger 2010).

The boundary layer between the leaf and the atmosphere provides a second source of resistance (Taiz and Zeiger 2010). The boundary layer refers to a thin film of still air, which surrounds the leaf and lies between the surface of the leaf and the atmosphere (Taiz and Zeiger 2010). Boundary layer resistance can vary with the thickness of the boundary layer (Taiz and Zeiger 2010). Wind speed is an important determinant of boundary layer resistance. In windy conditions, the boundary layer is thinner than in low wind conditions (Taiz and Zeiger 2010). The boundary layer is also influenced by the surface properties of the leaf, which will be discussed in more detail in the literature review section.

1.4 Literature Review

The literature review is split into five parts, each representing a body of knowledge relevant to the three strands of research discussed in the motivation section of this thesis. Since one of the primary goals of this thesis is to test the importance of heat avoidance to heat tolerance in common bean, the first section of the literature review outlines what is known about heat tolerance in beans to date.

The second section of the literature review examines heat avoidance through transpirational cooling in plants. Here, the evidence base describing the mechanisms for transpirational cooling and how it relates to heat tolerance is discussed.

The section finishes by describing the knowledge gaps in the relationship between transpirational cooling and heat tolerance for common bean.

The third section of the literature review is shorter. It explores current methods of modelling the difference between canopy and air temperatures in crop models and their performance. The purpose of this section is to examine the ways in which energy balance theory has been translated into models aiming to simulate heat avoidance. An understanding of model performance in this regard provides a benchmark for the model developed in this thesis.

Section four provides the background knowledge required to understand the water-food-energy nexus in Punjab, India. Literature on the history through which this nexus emerged is discussed and modelling studies aiming to assess the impact of climate change on the rice-wheat cropping system in this region are reviewed. Knowledge gaps in this modelling literature are then highlighted.

Finally, section five discusses the contribution of irrigation to heat avoidance at regional scale. Evidence for an impact on temperature extremes and heatwaves from large scale irrigation are explored and knowledge gaps in the Indian context are highlighted.

1.4.1 Heat tolerance in Common Bean

Genetic diversity in heat tolerance has been identified in bean genotypes. These include elite common bean lines and crosses with Tepary bean (*P.acutifolius*), a species found in arid parts of northwestern Mexico (CIAT 2015). Tepary bean exhibits yield stability at elevated temperature and expresses stomatal control, dehydration avoidance and deep rooting behaviour, all of which may contribute to heat tolerance in suitable environments (Kole 2013). This section explores some of the different pathways to heat tolerance found in both common bean and Tepary crosses.

There is evidence to suggest that heat tolerant genotypes experience reduced abscission of reproductive organs at elevated temperatures. In a study of 24 genotypes grown in a variety of day and night temperature regimes, heat tolerant genotypes produced more seeds and pods and maintained a higher pod harvest index (Rainey and Griffiths 2005a; Porch et al. 2010). Lower pod numbers in heat sensitive genotypes was linked to greater abscission of reproductive organs (Rainey and Griffiths 2005a). The authors conducted a follow on study, in which they compared abscission rates of 3 generations of a heat sensitive genotype and 3 generations of a heat tolerant genotype. Using generation means analysis, they found evidence to suggest that abscission of reproductive organs during heat stress may be controlled by a single recessive gene (Rainey and Griffiths 2005b).

In addition to maintaining pods under elevated temperatures, heat tolerant genotypes also maintain higher levels of pollen viability. In a study of 1000 lines grown in field conditions in Armero, Colombia (average maximum temperature of 35 °C), 40 genotypes from the Mesoamerican gene pool and 7 genotypes from the Andean gene pool were identified as heat tolerant. Tolerant genotypes were more likely to form pods, suggesting viable pollen and successful pollination (CIAT 2015). A further field study was conducted in the same location, accompanied by smaller studies in Caribia, an even hotter region on the Carribean coast of Colombia. In a comparison of 36 elite Tepary crosses and 25 inter-specific crosses, heat tolerant varieties maintained higher levels of pollen viability. Against a backdrop of 80 percent in control breeding sites, heat tolerant genotypes maintained greater than 64 percent pollen viability, compared with less than 20 percent in heat sensitive varieties.

Resilient microsporogensis may be a further pathway to heat tolerance. Porch and Jahn (2001) examined one heat tolerant and one heat sensitive genotype under both field and greenhouse conditions. Experiments were conducted exposing the genotypes to 32/27 °C during sporogenesis, pollen and embryo sac development and anthesis. High temperature stress induced reductions in pollen viability, damage to pollen wall architecture and anther indehiscence in the heat sensitive genotype when exposed to high temperatures during sporogenesis (Porch and Jahn 2001). Interestingly, differential impacts on anther architecture were not observed in a previous study assessing the impacts of heat stress during sporogenesis on common bean. This may have been the result of different duration of heating, or may simply reflect different pathways to tolerance.

Different pathways to heat tolerance of the photosynthetic apparatus have also been observed. Traub et al. (2018) grew 15 bean genotypes in a greenhouse before exposing them to 2 days of high temperature in a growth chamber 1 month after the third trifoliate leaf had fully expanded. Two separate treatments at 40 °C and 35 °C and 45 °C and 40 °C day and night time temperatures were conducted. They found two heat tolerant genotypes, TB1 (a Tepary cross) and SB776 were least affected by exposure to very high temperatures (Traub et al. 2018). TB1 retained the highest efficiency of photosystem 2 during exposure to high temperatures, while SB776 experienced lower values of electrolyte leakage. This clearly reveals different pathways to heat tolerance in two heat tolerant genotypes. The authors suggest that ability to maintain efficiency of photosystem 2 during elevated temperatures, may explain why Tepary beans experience smaller reductions in biomass than common bean lines when exposed to heat stress (Lin and Markhart 1996).

1.4.2 Plant thermal regulation

1.4.2.1 Differences between plant and air temperatures

As early as 1964, a literature review by Linacre (1964) explored the differences in leaf and air temperatures for more than 41 plants in well-watered conditions. The plants reviewed covered a wide range of vegetation from fruit trees to field crops. Linacre (1964) found a large range of differences in temperature across plants and environments, ranging from 11.5 °C cooler to 13 °C warmer.

In extreme climates, the difference between leaf and air temperature can be even larger. Smith (1978) found that the leaf temperature of a large leafed desert species with high transpiration rates dropped to 18.1 °C below the temperature of the air, while the temperature of cactus stems rose to 22 °C above the temperature of the air. In a study of alpine vegetation in Colorado, Salisbury and Spomer (1964) found that leaf temperatures could rise to 22 °above the temperature of the air in full sunlight, but remained closer to air temperatures in shaded conditions.

Evidence from remote sensing and satellite observations supports the existence of plant thermal regulation at canopy and ecosystem scales. For example, Good (2016) found that vegetation growth at ecosystem scale had a cooling effect on land surface temperatures. This finding is supported by Mildrexler et al. (2011), who found that at high temperatures, evapotranspirative cooling allowed forest ecosystems to avoid temperature increases exhibited by other land surface types.

1.4.2.2 Transpirational cooling and water availability

In the key concepts section, the energy balance framework for transpirational cooling was discussed. It was suggested from theory that stomatal conductance increases in response to a reduction in water availability, and that this provides a control on transpirational cooling. This theory is supported by high correlations between canopy temperature and stomatal conductance (Roche 2015). There is a large body of empirical evidence suggesting that transpirational cooling is connected with water availability. Indices based on canopy temperature have been shown to be associated with soil moisture or crop water stress for: cotton and sorghum (Mahan et al. 2012; Idso and Ehrler 1976; Idso et al. 1982), chickpea (Sivakumar 1986), ryegrass (Jiang et al. 2009), sugarcane (Khera and Sandhu 1986), potato (Erdem et al. 2006a), winter wheat (Howell et al. 1986), wheat (Jackson et al. 1981), grapevine (Möller et al. 2006), castor bean (Vijaya Kumar et al. 2005) and common bean (Erdem et al. 2006b).

Although it has been shown that the relationship between canopy temperature and water availability also depends on atmospheric conditions (Stockle and Dugas 1992; Keener and Kircher 1983), it is clear that classical theory for the relationship between transpirational cooling and water availability holds across a wide range of plant types. This suggests a trade-off between saving water and cooling the plant and points to the possibility of a dual role for stomatal conductance. It has been suggested, that in addition to its role in conserving water, stomatal control also provides a means of thermal regulation (Jones 1998).

Recent theoretical work suggests that at damaging high temperatures, stomatal function may switch from water conservation to thermal regulation in order to ensure leaf survival (Blonder and Michaletz 2018). Blonder and Michaletz (2018) propose that a dual role for stomata is more likely to have evolved in wet environments with ample supplies of water. They note that in water scarce environments (for example deserts), spending water to reduce temperatures may be less advantageous, and water saving behaviour is more likely to dominate.

1.4.2.3 Leaf temperature and leaf morphology

Desert leaves are often noticeably smaller than the leaves of plants growing in cooler and wetter environments (Smith 1978). The theoretical explanation for this is that since the depth of the boundary layer between the leaf and the atmosphere increases with leaf size, smaller leaves are more easily able to exchange heat through convection (Leigh et al. 2017). Further, smaller leaves transpire less and are therefore more water efficient (Smith 1978). The combination of these two lines of reasoning are commonly used to explain the small leaves observed in many desert plant species.

However, in a study of desert perennials, Smith (1978) found that the coolest plants had larger leaves, and were able to remain cool at high temperatures through enhanced transpirational cooling. This result brought into question the universality of the small leaves - thin boundary layer theory for the relationship between leaf size and temperature.

Recent work has challenged this theory further. In a study of 7670 species worldwide, Wright et al. (2017) found that leaf size increased with temperature and noted that this was consistent with the work of early ecologists who observed that leaves were often bigger in tropical regions. Wright et al. (2017) argue that the small leaf - thin boundary layer theory for leaves in deserts only applies in hot and dry conditions. They further contend that when water is available for transpirational cooling, there is no longer an evolutionary advantage to having small leaves. They show that the geographical distribution of leaf size can be better explained by a simple energy balance model utilizing the existing knowledge of the relationships between boundary layer conductance and size (Wright et al. 2017).

It has also been suggested that thicker leaves may confer an advantage when plants are exposed to extreme temperatures. Observations from many hundreds of species suggest that thicker leaves are found in hot environments (Leigh et al. 2012). Thicker leaves have greater thermal mass, which increases thermal stability (Leigh et al. 2012). It also provides more space for storing water, a feature that is common to succulent plants (Griffiths and Males 2017) and has been shown to help them regulate leaf temperature (Monteiro et al. 2016).

1.4.2.4 Plant cooling and heat tolerance

In a review of heat tolerance in plants, Porch and Hall (2013) propose that higher transpirational cooling in heat tolerant plants reflects higher stomatal conductance and photosynthesis in hot conditions. In addition, they suggest that transpirational cooling may be an important heat avoidance mechanism, which ensures that tissue temperatures do not exceed stress inducing thresholds.

Majority of evidence supporting this view has come from studies of wheat, which are brought together in (Reynolds and Langridge 2016; Reynolds et al. 2009, 2007). Reynolds and Langridge (2016) describes Canopy Temperature Depression (CTD) - the difference between the temperature of the canopy and the temperature of the air as an integrative trait, because it is the result of complex interactions between simpler traits. Reynolds and Langridge (2016) argue that there is sufficient variation in CTD in modern cultivars to make it an attractive target for rapid phenotyping techniques to improve stress tolerance. Interestingly, the relationship between enhanced CTD and yield is not restricted to hot environments. In a summary of breeding progress made by the International Maize and Wheat Improvement Centre, Aisawi et al. (2015) found that CTD post anthesis was strongly associated with grain yields in potential conditions.

Evidence for the theory that enhanced CTD increases heat tolerance through a stomatal conductance and photosynthesis pathway also has support from studies of other crops. For example, Takai et al. (2010) found that higher yielding rice varieties had cooler canopies, higher stomatal conductance and higher rates of photosynthesis on days with both high and low solar radiation. Purushothaman and Krishnamurthy (2014) also found support for this pathway in chickpea.

Although the evidence for this pathway is compelling, it is not necessarily universal to heat tolerance in all crops and under all conditions. In a recent study of heat tolerance in cotton, Karademir et al. (2018) found a positive correlation between leaf temperature and yields, which suggests that in the hot and arid conditions in which they conducted their experiments, stomatal closure reduced transpiration to conserve water, with corresponding implications for yield. It should be noted that the authors mentioned that this finding was unusual, and that majority of studies had found the opposite to be true.

It is difficult to disentangle the effects of higher CTD on photosynthesis and advantages that may be gained from heat avoidance (Porch and Hall 2013). Porch and Hall (2013) note that studies of the relationship between CTD and kernel number in wheat grown in hot conditions could support two hypothesis. First, that enhanced CTD allowed kernels to avoid high temperatures, or, that photosynthesis was unaffected by high temperatures. Evidence from studies examining the relationship between the temperature of reproductive organs and fertility provides qualified support for a heat avoidance pathway. Chuan et al. (2008) found that varietal differences in CTD were associated with spikelet fertility and that these differences were stronger in drier compared with more humid conditions. This finding was also supported in similar experiments conducted by Yan et al. (2010). Since transpirational cooling would be expected to be higher in drier conditions, taken together, these studies suggest the possibility of a heat avoidance pathway in rice.

For enhanced CTD to confer heat tolerance, a supply of water to feed transpirational cooling is required. Pinto and Reynolds (2015) found that enhanced transpirational cooling was maintained through plasticity of root behaviour under stress. Under drought conditions, cooler genotypes exhibited greater rooting depth. Under hot irrigated conditions on the other hand, root mass was concentrated at the surface where water was most readily available. The authors found common Quantitative Trait Loci (QTL) relating to root plasticity in both heat and drought tolerant genotypes. These results are supported by the work of Saxena et al. (2014), who noted the same pattern of adaptive root behaviour.

The prospect that cooler canopies can be explained by root behaviour in both heat and drought tolerant varieties is intriguing, as the link between transpirational cooling and deeper rooting in water limiting conditions is well established. For example, Thapa et al. (2017) and Lopes and Reynolds (2010) support the theory that higher transpirational cooling is accompanied by deeper rooting behaviour in wheat. There is also evidence that cooler rice varieties with higher stomatal conductance and photosynthesis rate also grow deeper roots (Fukuda et al. 2018; Taylaran et al. 2011). A QTL for cooler canopies has been found in rice (Fukuda et al. 2018), but it is not yet known whether this QTL is also associated with heat tolerance.

To date, understanding of the role of transpirational cooling in heat tolerance has focused on wheat and rice. This has provided an understanding of the physiological and genetic basis for cooler canopies under stress conditions that may also be useful for other crops. Many crops exhibit some of the traits described above. For example, slow wilting soybean and mustard crops exhibit cooler canopies and higher yields than drought sensitive varieties (Bai and Purcell 2018; Chaturvedi et al. 1999). Further, this relationship between cooler canopies, leaf water potential and drought tolerance has also been observed in potato (Mahmud et al. 2016).

These findings may be of particular interest to common bean breeders. Varieties with low canopy temperatures have been shown to produce more seed under water limiting conditions (Barrios-Gómez et al. 2008), and maintenance of cooler canopies has been shown to be associated with deeper rooting in drought tolerant varieties (Sponchiado et al. 1989). In recent years, crosses between Common bean and Tepary bean have produced new lines with improved heat tolerance. Tepary bean is known for deeper rooting behaviours (Mhlaba et al. 2018), which suggests that heat tolerant common bean lines may, like wheat, share a common basis for heat and drought tolerance that can be phenotyped through transpirational cooling.

1.4.2.5 Knowledge gaps

To the authors knowledge, no studies have tested whether heat tolerant common bean genotypes cool more than heat sensitive genotypes, or whether transpirational cooling is linked to greater stomatal conductance and photosynthesis rate. Further, there are no comprehensive studies of the magnitude of transpirational cooling, and subsequently little is known about the role of canopy cooling in heat avoidance. Chapter 3 of this thesis aims to fill that knowledge gap.

1.4.3 Modelling the temperature of the plant

1.4.3.1 Modelling canopy temperature

Growing recognition that heat stress depends on canopy rather than air temperature has resulted in efforts to simulate canopy temperature from the crop and land surface modelling communities. Webber et al. (2018) provide a comprehensive comparison of the different modelling approaches that have been used to simulate canopy temperatures of wheat, and their respective performance. Webber et al. (2018) break down the approaches taken in different models into three main groups. The first of these groups is energy balance models (EBN). These models use simple characterizations of the energy balance to solve for canopy temperature. The second group identified by Webber et al. (2018) are energy balance models that also consider the convective stability above the boundary layer. These are called energy balance models corrected for stability (EBSC). The third approach are empirical models (EMP), which use statistical models of the soil-plant-atmosphere continuum to estimate canopy temperature.

The review by Webber et al. (2018) exposes both similarities and differences in the approaches to canopy temperature simulation taken by different modelling groups. In six of the nine models they analysed, canopy temperature was simulated at the daily time scale, while in the remaining three, canopy temperature was simulated at hourly timescale. The models discussed in the Webber et al. (2018) review varied in their complexity, both between and within the different model categories. In the following paragraphs, differences in complexity will be discussed.

The Nwheat model employs the simplest empirical approach. They extracted the maximum difference in the air and canopy temperatures in potential and stressed conditions from the literature, and scaled CTD between these two limits using a water stress index shown to be associated with changes in canopy temperature (Jackson et al. 1981). This contrasts with the more complex empirical approaches, such as the hybrid empirical and simulation model employed by Neukam et al. (2016). Neukam et al. (2016) use a quantile multiple linear regression model to predict canopy temperature. The regression coefficients were obtained with a stepwise approach and include the air temperature, incoming radiation, the natural logarithm of the leaf area index, a dummy variable for development stage, the ratio of actual to potential transpiration, interaction variables between phenology, VPD and water availability. The crop growth elements of this model were obtained by running the HUME model (Neukam et al. 2016).

The models grouped as EBN models in Webber et al. (2018) share a similar approach to deriving the canopy temperature from the standard energy balance equations. In three out of four cases, they follow the method proposed by Jamieson et al. (1995). The following description of the way in which the EBN models solve for canopy temperature follows the way the equations are laid out in Jamieson et al. (1995). The purpose of this is to explain the approach taken by the EBN models in relation to the fundamental energy balance defintions described in section 1.3.3. These models begin with a version of the energy balance equation using the symbol H to represent sensible heating where C has been used in equation 1.3).

$$\overline{R}_{\mathrm{n}} = H + \lambda\overline{E} \tag{1.4}$$

This equation is then re-arranged to solve for the sensible heating term, which means that equation 1.4 becomes equation 1.5. $\mathrm{R_n}$ is calculated from meteorological data and λE is calculated using variants of the Penman-Monteith equation.

$$H = R_{\mathrm{n}} - \lambda\overline{E} \tag{1.5}$$

This gives an estimate of H. These models then use the approximation for H given below to solve for the canopy temperature. Where $\mathrm{c_p}$ is the specific heat capacity of air at a given pressure, $\mathrm{r_a}$ is the aerodynamic resistance, T is the air temperature and $\mathrm{T_{can}}$ is the canopy temperature.

$$H = \rho c_{\mathrm{p}}/r_{\mathrm{a}}(T - T_{\mathrm{can}}) \tag{1.6}$$

The EBN models do not account for the atmospheric stability of the boundary layer. The EBSC models pioneered by Webber et al. (2015) build upon the EBN models by using the Monin-Obukhov Similarity Theory (MOST) to use iteration to calculate the aerodynamic resistance based on whether forced or free convection dominates the sensible heating term (Webber et al. 2015).

Almost all of the approaches taken consider the impact of water availability either directly or indirectly (Webber et al. 2018). In the majority of the models, water stress influenced transpiration, which reduces ET, and subsequently reduces the ET cooling term in the energy balance equation. In the EBSC models water stress also has a direct scaling impact on the canopy temperature, between the upper and lower transpiration limits. Neukam et al. (2016) use the ratio of actual to potential transpiration as an independent variable in their regression model. In the Sirius and SSM models, the effect of water stress is channelled indirectly through the reduction of LAI and biomass and an increase in senescence (Webber et al. 2018).

Of the nine models considered, three models involved a calibration procedure and six did not (Webber et al. 2018). It is worth noting that none of the EBN models considered were calibrated, while both of the EBSC models were calibrated. The EMP model that was described as calibrated by Webber et al. (2018) used half of the available data for generating optimized regression coefficients and half of the

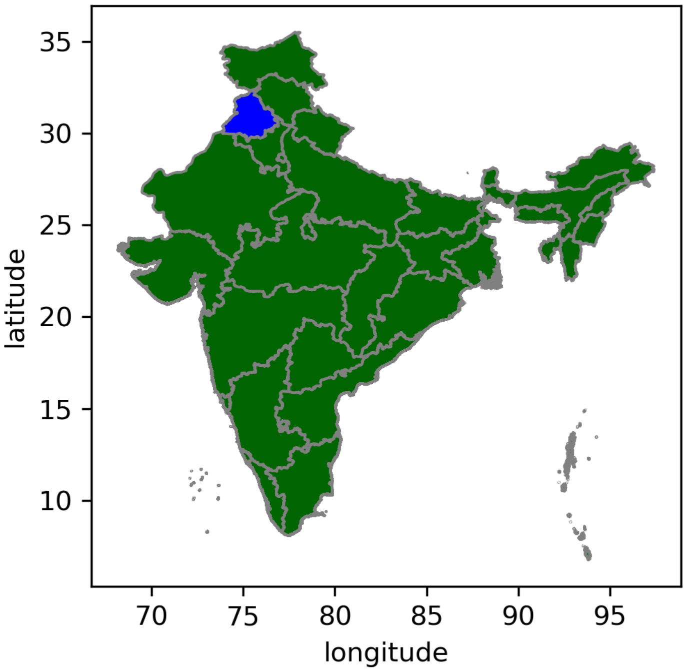


Figure 1.5: Map of India with the state of Punjab highlighted in blue. Shapefile data for this plot was taken from GADM (GADM 2020).

data for testing the model (Neukam et al. 2016). The EBSC models calibrated a canopy resistance term, presumably to account for genotypic differences in canopy structures.

The empirical models, energy balance models and more complex models all obtained low levels of accuracy when tested across a greater number of field experiments and environmental conditions (Webber et al. 2018). Webber et al. (2018) found that site effects explained the largest share of variance between observed and simulated values.

1.4.4 The Food-Water-Energy nexus in India

1.4.4.1 Overview

Over the past 60 years, India has gone from being water abundant to water scarce. In 1951 estimates of usable water were between 3000 and 4000 cubic meters per person (Luthra and Kundu 2013). In 2011 that figure stood at 1000, 700 cubic meters under the threshold at which a nation is considered water stressed (Luthra and Kundu 2013). Part of the reason for this decline is the combination of a rapid rise in irrigation and the replacement of canals with groundwater as the main source of irrigation (Kumar et al. 2005). The number of irrigation wells with pumps increased from 150,000 in 1950 to 19 million in 2000, and the majority of these are run on electricity (Shah 2009). As a result of this shift, groundwater irrigation accounts for between 15 and 20 percent of national electricity consumption (Shah et al. 2003). This dependency between irrigated agriculture, groundwater and electricity consumption has been described as a water-energy-food nexus (FAO 2014; Bazilian et al. 2011).

Although the Green revolution succeeded in transforming India from a food deficit to a food surplus nation, gains in productivity were not uniform across the country. This created a reliance upon relatively small areas for much of the nation's rice and wheat production. The state of Punjab is responsible for 60 percent of the rice production and 40 percent of the wheat production that makes up India's food stocks of these crops, whilst representing only 1.6 percent of land area (Perveen et al. 2012). Dependence on groundwater for irrigation has resulted in over-exploitation of the water table in 80 percent of water blocks in Punjab, (Aggarwal et al. 2009; CGWB 2012) and groundwater pumping accounts for more than 40 percent of state electricity consumption (Perveen et al. 2012).

1.4.4.2 Groundwater Decline in Punjab

Over the period 1973-2006, the cumulative water table has declined by more than 9 meters in total, the majority of which occurred between 1998 and 2005 (Kaur et al. 2011). During this more recent period the water table dropped by

0.5 meters a year on average (Hira 2004), a similar figure was estimated by the GRACE satellite using changes in the earth's gravity field over Northern India between 2002 and 2008 (Tiwari et al. 2009). The depth of the water table and the rate of decline have not been spatially homogeneous. In areas where the quality of groundwater is good, the share of agricultural land under rice-wheat rotation is greatest and the fall in the depth of the water table has been steepest (Ambast et al. 2006). Much of this land is in the central portion of Punjab where water table depths ranged between 15 and 28 meters in 2006 (Hira 2009). At current trends, by the year 2023 the energy requirements of extracting the same amount of groundwater will have increased by 93 percent from 2006. (Hira 2009).

The short-term economic incentives for farmers to irrigate from groundwater remain strong, the flat rate tariff for electricity use means that there is no marginal cost for water use. Guaranteed purchasing prices from central government assures stability of farm income under the rice-wheat rotation (Perveen et al. 2012).

1.4.4.3 Groundwater Management Options

At it's most fundamental level the decline in Punjab's water table is the result of demand for water outweighing supply. Devineni et al. (2013) show that in Punjab, the average annual water demand exceeds potential groundwater recharge from rainfall. Russo et al. (2015) put the magnitude of this shortfall into perspective by noting that the seasonal crop water demand of rice in Punjab is approximately 1800 mm whilst average annual rainfall stands at 650 mm.

The scale of the difference between demand and supply suggests that halting the decline in groundwater must be achieved on the demand side of the equation. One way of doing this would be for farmers to change the crops that they grow. Devineni and Perveen (2014) show that from the perspective of national food security, it is possible to shift rice production in Punjab to areas further east that receive greater rainfall and replace it with dry land crops such as pulses and oilseeds without reducing nutritional consumption or net income.

Another approach to reducing demand is to make existing farming practices more water efficient. In a review of the technologies that could arrest the decline of the water table in north-west India, Humphreys et al. (2010) discuss mature technologies such as alternate wetting and drying (AWD). AWD involves flooding the field and then allowing the ponded water to evaporate before flooding the field again after a pre-determined number of days (Bouman et al. 2007). Humphreys et al. (2010) also discuss more radical alternatives such as switching to shorter duration varieties. The use of shorter duration varieties means that the entire growth cycle of the crop is compressed, subsequently reducing both evaporation and transpiration (Jalota et al. 2009).

The authors argue that true water saving must reduce evapotranspiration, since losses to deep drainage replenish groundwater. They go on to say that understanding water saving from different technologies at regional scale remains a gap in the literature for this region and that crop modelling approaches offer a promising avenue of investigation. Recently, such work has been attempted at field scale in the Indo-Gangetic basin, for example (Subash et al. 2015).

1.4.4.4 Climate Change and the Rice-Wheat Cropping Rotation

The most recent Intergovernmental Panel on Climate Change (IPCC) WGI (2013) report projects an increase in mean temperatures across South Asia (high confidence), with strongest increases in winter (IPCC 2013). Mean temperatures are expected to rise more strongly at night than during the day and the number of extremely hot days and nights are both projected to increase (IPCC 2013). Northern India is singled out as a hotspot likely to experience mean temperature changes above the regional average (IPCC 2013). Mean precipitation is also projected to increase over South Asia, though a greater share of total precipitation is expected to fall during storms (medium confidence) (IPCC 2013).

A review of the literature demonstrates that there are many studies estimating the impact of climate change on the rice-wheat cropping system in Punjab using crop models. Field scale studies constitute 77 percent of the accessible literature and 70 percent of studies used Global Climate Models (GCMs) and IPCC scenarios to assemble future projections. There are 10 studies assessing the impact of climate change on both rice and wheat simultaneously, and 5 of these are focused on the Punjab region or the upper Indo-Gangetic Plains (IGP). (Rao et al. 2016; Subash et al. 2015; Kadiyala et al. 2015; Deb et al. 2015; Abedinpour et al. 2014; Satapathy et al. 2014; Jalota et al. 2014; Vashisht et al. 2013; Soora et al. 2013; Hebbar et al. 2013; Jalota et al. 2013a; Koehler et al. 2013; Mishra et al. 2013b,a; Kumar and Aggarwal 2013; Jalota et al. 2013b; Singh et al. 2012; Kumar et al. 2011; Geethalakshmi et al. 2011; Byjesh et al. 2010; Srivastava et al. 2010; Haris et al. 2010; Boomiraj et al. 2010; Bhatia et al. 2010; Challinor et al. 2009; Kalra et al. 2008; Challinor and Wheeler 2008; Challinor et al. 2007; Sarkar and Kar 2006; Challinor et al. 2005, 2004; Mall et al. 2004; Attri and Rathore 2003; Aggarwal and Mall 2002; Mall and Aggarwal 2002; Priya and Shibasaki 2001; Saseendran et al. 2000; Lal et al. 1999, 1998). None of these studies examine potential trade-offs between irrigation and high temperature stress. Very recently, Zaveri and Lobell (2019) used statistical modelling to explore this trade-off for wheat. They found that irrigation may have alleviated some of the impact of increased temperatures on yields, though in some parts of India, it has been outpaced by the rate of temperature increase.

1.4.4.5 Knowledge Gaps

To the best of my knowledge, there are no crop modelling studies considering the joint impact of adapting to groundwater decline and resilience to heat stress in South Asia's most important rice growing region. A single statistical study attempts to explore this trade-off for wheat. There is therefore a clear need for process based modelling of this trade-off that can explore the fundamental mechanisms involved.

1.5 Irrigation and climate

1.5.1 Irrigation and surface temperatures

Theoretical understanding of the impact of irrigation on surface temperatures is now well established. Irrigation changes the physical proprieties of the land surface by altering the energy balance, albedo and surface roughness (Sacks et al. 2009). Irrigation changes the proportion of latent to sensible heating (the Bowen ratio), cooling the land surface (Sacks et al. 2009).

A cooling effect from irrigation is supported throughout the empirical literature (Roy et al. 2007; Lobell and Bonfils 2008; Lobell et al. 2008; Mahmood et al. 2004; Segal et al. 1989; Barnston and Schickedanz 1984; Lee et al. 2009; Adegoke et al. 2007; Yang et al. 2020). The range of the cooling effect found in the empirical literature is large, Barnston and Schickedanz (1984) found differences of 1-2 °C, while Segal et al. (1989) found differences as large as 10 °C when conducting measurements at midday.

Most empirical studies have taken place in north America, with only a handful of empirical studies having been undertaken elsewhere. These few studies have examined the cooling effect of irrigation in India and in China. Given that irrigation covers 2 percent of the land surface and accounts for 40 percent of global food production (Sacks et al. 2009), it is surprising that there are so few empirical studies looking at its impact on surface temperatures.

This under-sampling of the impacts of irrigation on the climate may reflect inherent difficulties in setting up suitable statistical tests. The most common approach is to consider nearby irrigated and non-irrigated areas that do not obviously differ in climate drivers and to test for differences in the evolution of climate variables (Lobell and Bonfils 2008). Such natural experiments are not easy to find, and good quality time series data on irrigation timing, quantity and method is seldom available (Lobell and Bonfils 2008).

Empirical studies alone cannot provide a comprehensive perspective on the impact of irrigation on surface temperatures. This is because the impacts of irrigation on the atmosphere are likely to be more diverse than simple changes to the surface energy balance. Higher levels of evaporation from irrigated areas are also likely to result in more water vapour in the lower atmosphere (Boucher et al. 2004). Changes in atmospheric vapour content could influence cloud formation and rainfall, with connected impacts on solar radiation intercepted at the land surface (Boucher et al. 2004). These additional changes to the atmosphere may feedback on surface temperatures.

The impacts of irrigation on the hydrological cycle are further complicated by interactions with large scale weather circulation patterns. Tuinenburg et al. (2014) suggest that regional scale irrigation can weaken the temperature gradient between land and ocean, which reduces the sea breeze effect in eastern coastal regions. They found that irrigation reduces rainfall in eastern India and increases rainfall in the north-west of India - a finding supported by a number of other studies (Puma and Cook 2010; Lee et al. 2009; Asharaf et al. 2012).

It has therefore been shown that the impact of irrigation on land surface temperatures depends on complex feedback processes between energy fluxes, changes in the hydrological cycle and interactions with large scale circulation patterns. It follows that a robust understanding of the extent and causes of the impact of irrigation on land surface temperatures requires the integration of empirical and model studies.

Majority of modelling studies that use global climate models to test the impact of irrigation on global temperatures agree that irrigation has a cooling effect, but do not agree on the magnitude of cooling (Thiery et al. 2017). For example, Lobell et al. (2005) find a global impact of -1.3 °C, while Sacks et al. (2009) find a very small impact of 0.02 °C. There is also no consensus on the relative importance of different physical drivers at the global scale. Cook et al. (2015) suggest that changes in heat fluxes are the dominant mechanisms in climate responses, while Sacks et al. (2009) suggest that indirect effects such as changes to cloud cover are more important drivers.

Modelling studies do agree that the effects of irrigation vary strongly by region. Sacks et al. (2009) found that irrigation has a cooling effect on the climate in the northern mid-latitudes, central and south eastern parts of the US, parts of southeastern China, southern and southeastern Asia. On the other hand, they found that irrigation produced a warming effect in northern Canada.

Puma and Cook (2010) conducted century long runs with and without irrigation using the Community Atmosphere Model. They found that the sign of the irrigation effect in some regions varied by season. In the boreal summer, irrigation produced a cooling impact in parts of North America, Europe and Asia. However, in boreal winter, a warming effect was simulated in parts of North America and Asia. The authors argued that increased humidity at the earth's surface led to enhanced downward longwave radiation in these areas during boreal winter.

Cook et al. (2015) conducted ensemble simulations using five GCMs between 1850 to the present using a Food and Agricultural Organization data set for the years 1901-2002. They found that strong cooling was simulated in Western North America, the Mediterranean, the middle east and parts of Asia. In these regions, cooling was accompanied by an increase in cloud formation and a subsequent decrease in solar radiation at the earth's surface. South Asia was the exception to this pattern, as irrigation weakened the monsoon. Here, changes in the Bowen ratio accompanied irrigation induced cooling.

Evidence for regional variation in the impacts of irrigation on temperature is also supported by a multi-model inter comparison project. Twelve atmospheric general circulation models were run with 16 different soil moisture combinations for the whole globe. Koster et al. (2004) found that the models agreed that strong coupling between soil moisture and the atmosphere existed in parts of the Sahel and India, though agreement for other heavily irrigated regions was not found.

Regional modelling studies over heavily irrigated areas tended to find stronger effects. Kueppers et al. (2007) conducted two 20 year runs with and without irrigation over the state of California using the International Center for Theoretical Physics model (RegCM3). They found that in irrigated areas, simulated mean temperatures were approximately 3.7 °C cooler and maximum temperatures were 7.5 °C cooler in the month of August. A much smaller cooling effect (approximately 1 °C) was found for minimum temperatures.

Douglas et al. (2009) studied the impact of irrigation on regional climate on the Indian sub-continent. They used the Regional Atmospheric Modeling System (v4.3) to study the impact of irrigation over a 5 day period between the 16th and 20th of July. They found that heavily irrigated areas in many (though not all) parts of the country showed a reduction in sensible heating and an increase in latent heating as expected. They found that this change to the Bowen ratio resulted in a reduction in temperature. They found cooling of between 1 °C and 2 °C, accompanied by an increase in atmospheric water vapour.

1.5.2 Heatwaves and Irrigation

1.5.2.1 Heatwave Definitions

Heatwaves can be a danger to human beings, plants and infrastructure. For this reason, different meterological aspects of heatwaves are of concern to different communities (Perkins and Alexander 2013). This has led to a vast array of heatwave definitions, many of which are also designed with regionally specific climatology and societal impacts in mind (Perkins and Alexander 2013). For example, heatwave defintions that are focused on human health tend to incorporate elements of meterological extremes that have proven links to morbidity or mortality (Smith et al. 2013).

In view of the fact that temperature extremes are projected to increase in the future, the first two decades of this century has seen growing efforts to create heatwaves metrics that can be compared across the globe (Perkins and Alexander 2013). This effort began in earnest with the work of the joint World Meteorological Organization's Commission for Climatology, which developed a suite of indices for measuring climate extremes (Alexander et al. 2006). These indices consider the magnitude and duration of maximum and minimum temperatures and the diurnal temperature range (Alexander et al. 2006).

Heatwave metrics can be usefully subset into two categories, absolute and relative. Absolute thresholds are more often designed to target specific regional and societal impacts, while relative thresholds allow extremes to be compared with the climatology anywhere in the world (Perkins 2015). Relative heatwaves metrics are therefore more easily comparable across regions (Perkins and Alexander 2013) and allow a specific extreme event to be put in context with the temperatures usually experienced by humans, plants or infrastructure in the location of interest.

1.5.2.2 Heatwaves Drivers

Heatwaves around the globe share common physical drivers. Generally, the existence of high pressure synoptic systems leads to extended periods of clear skies and dry weather, which result in higher levels of incident solar radiation at the land surface (Perkins 2015; Fischer 2014). High temperature increases evaporation from the earth's surface, which in turn reduces soil moisture. This can induce a negative feedback loop between drier soils and increased sensible heating, which further increases surface temperatures (Perkins 2015). Recent work examining the 2003 and 2010 mega-heatwaves over Europe shows that these conditions were accompanied by nighttime heat entrainment and increasing accumulation of heat in the atmospheric boundary layer as the heatwaves progressed (Miralles et al. 2014).

The interaction between drying of the land surface and heatwave development is mediated by ecosystem characteristics. The rate of evapotranspirative decline is controlled by how vegetation (transpiration) and soil moisture (evaporation) respond to heating (Miralles et al. 2019). Evapotranspiration depends on soil moisture content. Seneviratne et al. (2010) breaks down the relationship between soil moisture and evapotranspiration into three regimes. In the first regime, soil moisture content lies above a critical threshold and does not limit evapotranspiration. In the second regime, soil moisture content lies below this critical threshold and above the wilting point. In this regime, evapotranspiration continues, but is limited by the available soil moisture. In the third regime, soil moisture content falls below the wilting point and no more evapotranspiration is possible.

1.5.2.3 Evidence for the impacts of irrigation on heatwaves

Theoretically, irrigation can be expected to reduce both the number and duration of heatwaves. The previous subsection suggests that the positive feedback between surface heating and soil drying is a core element of heatwave generation. Apriori, irrigation can be expected to interrupt this feedback loop by increasing latent heat fluxes and subsequently reducing sensible heating (Perkins 2015).

This first order conclusion remains to be comprehensively proven. The body of literature considering the impacts of irrigation on heatwaves is far smaller than the literature on surface temperature impacts. Further, empirical studies of the impact of irrigation on maximum temperatures suggest that there are counteracting mechanisms of impact that may vary with the conditions studied. Barnston and Schickedanz (1984) found that the impact of irrigation on maximum temperatures was greater than the impact of irrigation on mean temperatures. The size of this difference was larger on hot and dry days than on damper and cooler days, as would be expected. On the contrary, Lobell et al. (2008) found that irrigation cooled mean and maximum temperatures by a similar amount, despite the expectation that increased heating would results in greater evaporative cooling.

Lobell et al. (2008) analysed the impact of irrigation on heatwaves in California and Nebraska for the years 1915-1980 and 1950-1980 respectively. They compared observations of heatwaves for irrigated and non-irrigated areas, defining heatwaves as 6 consecutive days (or more) when maximum temperatures exceed the 90th percentile for a given area. They found a significant reduction in the number of heatwaves in irrigated vs. non-irrigated areas in California, but not in Nebraska. They note that the weather time series included many years with no heatwave occurrences, which lead to a statistical distribution that makes the extraction of trends more difficult.

Kumar et al. (2017) used MODIS satellite observations of the normalized vegetation index to distinguish irrigated agricultural regions from non-irrigated regions. They used land surface temperatures from the same product to estimate the difference in the urban heat island effect in irrigated and non-irrigated areas during the period when heatwaves are most common in India (March-May). They found that cities in irrigated regions exhibited the urban heat island effect, but that this was not the case in cities in non-irrigated areas, many of which exhibited an urban cooling effect. They hypothesised that irrigation plays an important role in maintaining cooler temperatures in agricultural areas, providing a contrast between urban and rural areas.

In a follow up study using similar methods Kumar and Mishra (2019) found that the frequency of hot nights has declined in the Indo Gangetic Plains over the period 1951-2016. They used the Community Land Model to perform climate model runs for this region with non-irrigated and irrigated cropland. They found stronger cooling for the irrigated runs (by approximately a degree) in the Indo Gangetic Plains. Combining the empirical evidence of a decline in nighttime extreme temperatures and the results of their modelling experiment, they hypothesised that irrigation has played a role in the decline of extreme temperatures in the Indo Gangetic Plains.

Meng and Shen (2014) examined the link between soil moisture and heatwaves in East China. They used a standardized precipitation index for the previous 6 months as a proxy for soil moisture and regressed this index against two heatwave indices for June, July and August. These indices were the percentage of hot days (defined as Tmax exceeding the 90th percentile) and the maximum heatwave duration (defined as the maximum number of consecutive days during which Tmax exceeded the 90th percentile). They found a significant negative relationship between soil moisture and both heatwave definitions in all but the eastern region of the country for the highest quantiles of soil moisture. This suggests that only very high levels of soil moisture impeded heatwave generation in the region studied.

Only one comprehensive modelling study of the global impact of irrigation on heatwaves has been conducted to date. Thiery et al. (2017) assessed the impact of irrigation on climate extremes using the Community Earth System Model. This model includes fully coupled interactions between the land and the atmosphere and represents irrigation in C3 crops. Two 5 member ensemble runs were performed for the years 1981-2010. In the first set of runs, irrigation is switched off and in the second it is switched on. Grid cells were considered irrigated if irrigation covers more than 10 percent of the land area. Strong and significant impacts on global temperature extremes were found. These included significant negative impacts on the duration of heatwaves.

Lu and Kueppers (2015) modelled the impact of irrigation on heatwave frequency, duration and intensity in the US using the Community Land Model. Two sets of simulations were performed for the period 2002 and 2011 with irrigation switched on and off. The results were inconclusive. Although a number of heatwave indicators did show significant impacts on heatwaves from turning irrigation on, there was low model agreement and the effect size (and even sign) varied across the indices examined. In general, indices that included humidity were less influenced by irrigation, as irrigation reduced temperature but increased humidity - with counteracting effects on evapotranspiration from the surface.

1.5.2.4 Knowledge Gaps

There are a reasonable number of empirical studies examining the impacts of irrigation on surface temperatures and a large body of modelling studies. However, there are very few empirical studies and only a small number of modelling studies exploring the relationship between irrigation and heatwaves. The studies that do exist often do not include direct observations of irrigation and are centred almost exclusively on the United States. Despite high temperatures and a vast land area irrigated every year, no studies have empirically examined the impact of irrigation on heatwaves in India.

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Chapter 2

Methods

2.1 Overview

This chapter provides a description of the core instrumentation and models used in this thesis. The first section of this chapter introduces the instrument used to take measurements of leaf temperature. The second section introduces the crop model used to analyse the trade-off between saving water and resilience to heat stress. The remainder of this methods overview section discusses the reasons why these methods were chosen for use in this thesis.

The leaf temperature observations used in this thesis were collected using the MultispeQ v1 phenotyping instrument. The MultispeQ v1 is capable of taking a combination of micro-meteorological and photosynthetic measurements of a leaf in less than 15 seconds. This has facilitated the collection of large samples of leaf temperature measurements spanning different crops, genotypes, seasons and times of day. The data generated is freely available online and represents a phase change in the volume of leaf temperature observations available to scientists.

ORYZA V3 was selected for use in this thesis because it has a number of capabilities that are useful for exploring research question two. ORYZA V3 includes highly flexible irrigation routines, incorporates spikelet sterility and includes a routine linking water limitation to leaf temperature. This in turn impacts on spikelet sterility.

A second consideration in selecting ORYZA for use in this thesis was that its predecessor (ORYZA 2000) was shown to most closely simulate grain yields in the AgMIP rice inter-comparison project (Li et al. 2015) and ORYZA V3 has been demonstrated to outperform ORYZA 2000 for a range of environmental conditions (Li et al. 2017). Finally, both ORYZA 2000 and ORYZA V3 have been tested on the field experiment used in this study in previous work (Sudhir et al. 2011) (Li et al. 2017). These studies provided a baseline for model performance.

2.2 MultispeQ device

2.2.1 Device description

MultispeQ v1 is a handheld phenotyping instrument, capable of taking a series of measurements relating to leaf productivity, health and micro meteorology in less than 15 seconds. The MultispeQ instrument was designed to take rapid measurements in field conditions, which are instantaneously relayed to an open source online database maintained by PhotosynQ.

Figure 2.1 shows the MultispeQ device in use. An ambient Photosyntheticaly Active Radiation (PAR) sensor sits on top of the leaf clamp. The MultispeQ device uses an off the shelf Red Green Blue White (RBGW) sensor in combination with an algorithm to estimate PAR (Kuhlgert et al. 2016). MultispeQ PAR estimates are highly correlated with PAR measurements taken using the LICOR industry standard ($r^2 = 0.9967$) (Kuhlgert et al. 2016).

An integrated temperature, humidity and pressure sensor is located on the side of the leaf clamp. The MultispeQ v1 uses the Bosch BME280 sensor. In this thesis, temperature and humidity measurements are used. The temperature sensor has an operational range of between -40 °C and 85 °C and a full accuracy operational range of between zero and 65 °C (Bosch 2019). Within this range, the temperature sensor is accurate to within 1°C (Bosch 2019). All measurements used in this thesis fall within the full accuracy temperature range. The humidity sensor outputs relative humidity. Within the full accuracy temperature range, the humidity sensor has an operating range of between 0 and 100 percent (Bosch 2019). The humidity sensor is accurate to within 3 percent between 20 and 80 percent relative humidity (Bosch 2019).

Leaf temperature measurements are made using a contactless infrared (IR) sensor embedded beneath the leaf clamp. The MultispeQ v1 uses the Melexis MLX9065 sensor, which has been calibrated for object temperatures ranging between -40 °C and 115 °C. The sensor is accurate to within 0.5 °C within 0 °C and 50 °C.

2.2.2 Measurement Protocol

Based on the recommended best practices for taking good quality measurements (PhotosynQ 2019b), the following protocol was used for taking leaf temperature measurements using the MultispeQ device. First, the person taking the measurement was positioned to avoid casting a shadow over the leaf or the PAR sensor. The central portion of a fully developed young leaf was then placed within the leaf clamp without altering the angle of the leaf for a period of approximately 15 seconds. This is the time taken for the Photosynthesis RIDES protocol to take a full suite of fluorescence and absorption measurements. During the first second in which the leaf was within the leaf clamp, the contactless IR sensor and the humidity and temperature sensors took measurements of leaf temperature, air temperature and relative humidity. At no point did the IR sensor touch the leaf. Throughout the measurement, two vents in the leaf clamp maintained air exchange. Leaf size was sufficient to ensure that the leaf fully covered the light guide, consistent with measurement best practices (PhotosynQ 2019b). The working device was protocol was called Photosynthesis RIDES no open/close.

2.2.3 Data Quality Control

The device automatically flags measurements, which meet a low quality criteria. The MultispeQ device issues two types of quality warnings for measurements. Red flags strongly suggest a serious measurement error, and PhotosynQ suggest that any measurements with red flags are discarded immediately (PhotosynQ 2019a).

Figure 2.1: The MultispeQ device in use

In addition to red warnings, the device also issues yellow warning flags, which are intended to draw attention to potential low quality measurements (PhotosynQ 2019a). Low quality measurements are often caused by the device shaking during a measurement or the leaf not being held steadily in the clamp (PhotosynQ 2019a). Low quality measurements can also occur if the leaf does not fully cover the light guide. Relative chlorophyll measurements are compared with an expected range and a flag is issued if the value of an observation falls outside of this range. Warning flags can also occur if a leaf is dead or dying and observations fall outside of expected ranges in Phi2, PhiNPQ or PhiNO values (PhotosynQ 2019a). Only measurements of functioning leaves were sampled in the experiments described in this thesis. Measurements with red warning and issues flags were removed from the sample during quality control procedures. Further, any observations with missing values for any of the variables were also discarded. Only complete observations without issues were included in analysis.

2.3 The ORYZA crop model

2.3.1 Model description

ORYZA V3 is the successor of the ORYZA 2000 ecophysical rice model, a detailed description of which can be found in Bouman et al 2001 (Bouman 2001) and (Li et al. 2017). ORYZA V3 simulates rice production under paddy, lowland and upland conditions. ORYZA V3 can be run in potential conditions, where growth is determined by weather and varietal characteristics, or in water and nitrogen limiting conditions. Stresses from weeds, pests and diseases are not simulated by the model (Bouman 2001). In the section that follows, aspects of ORYZA V3 that are relevant to the use of the model in this thesis are described, with a particular emphasis on how spikelet sterility is simulated, as this routine is used extensively in chapter 4. Since all of the simulations conducted in this thesis use optimal nitrogen practices, a discussion of the way in which soil nitrogen is simulated is not included here. However, a full description of is available in (Li et al. 2017).

2.3.1.1 Growth and development

In ORYZA V3, plant growth is determined by CO_2 assimilation. CO_2 assimilation is calculated at leaf level using incoming solar radiation, temperature and leaf area index as inputs. The net CO_2 assimilation is calculated as the difference between the integrated leaf level photosynthesis throughout the canopy and maintenance respiration (Bouman 2001). Net CO_2 is calculated on a daily basis and is allocated between the roots, stems, storage organs and leaves depending on the phenological stage of development.

For most of the season, phenological development is determined by temperature in ORYZA V3. In photoperiod-sensitive varieties, the start of flowering is also influenced by day length. In ORYZA V3, the growing season is split into four phenological stages; emergence, panicle initiation, flowering and physiological maturity. The rate of phenological development is calculated from the accumulation of daily increments in heat units. These units are determined by three temperatures, the base (8 °C), the Optimum (30 °C) and the maximum temperature (42 °C). No daily heat units are accumulated if the daily mean temperature is below the base temperature or above the maximum temperature. When the temperature is between the base and maximum temperature, temperature units are accumulated based on an imposed sine wave distribution (Bouman 2001).

2.3.1.2 Evapotranspiration

ORYZA V3 calculates the potential evaporation from the soil and ponded layer and the potential transpiration from the plant (Bouman 2001). If drought stress is experienced, potential transpiration is scaled by a water stress routine (Bouman 2001). Potential evaporation and transpiration are calculated using the Food and Agriculture Organization's method. This method assumes that the ground is wet and that rice resembles a generic green grass that fully covers the ground (Allen et al. 1998). ORYZA offers a variety of methods for calculation of Evapotranspiration (ET). These include the Penman-Monteith equation, the Priestly Taylor equation and the Makink equation. Where data is available, the developers of ORYZA recommend the use of the Penman-Moneith equation (Bouman 2001).

2.3.1.3 Drought Stress

Water stress is simulated in ORYZA V3 through changes in photosynthesis, assimilate partitioning, phenological development, spikelet sterility and leaf senescence (Bouman 2001). The impact of water stress on these processes is mediated through a drought stress index, which is calculated from the ratio of water uptake to water demand (Li et al. 2017).

In ORYZA V3, the water uptake per soil layer depends the proportion of root mass in the layer and the ratio of extractable water in that layer and extractable water in the entire root zone (Li et al. 2017). Extractable water is defined as the difference between current soil water content and soil water content at wilting point (Li et al. 2017). The drought stress factor is therefore determined by the amount of water available and the ability of the root to absorb the available water in a particular layer.

Root growth in ORYZA V3 is determined by the difference between the assimilated carbon allocated to the roots and root senescence in a time step (Li et al. 2017). This newly available root carbon is then distributed through the different soil layers using a function that assumes that root biomass decreases exponentially with the depth of the soil profile (Li et al. 2017).

Root growth is also modified by soil temperature, as well as the properties of the soil and varietal rooting depth (Li et al. 2017). In particular, the ability of the root to penetrate the soil is modulated by soil moisture, clay content and bulk density (Li et al. 2017). Root growth in ORYZA V3 is itself modified by drought stress through changes to assimilate partitioning. In water limiting conditions, assimilate partitioning to the roots increases, making it possible for the roots to draw water from deeper layers.

The drought stress index modulates simulated photosynthesis through its influence on the ratio between actual and potential transpiration. This ratio is then used to scale simulated photosynthesis (Li et al. 2017). The impact of limitations in soil water availability are mediated by a varietally determined drought tolerance factor. Photosynthesis is also moderated by leaf rolling in the model

(Bouman 2001). Leaf rolling reduces leaf area, subsequently reducing light interception and reducing simulated photosynthesis (Turner et al. 1986). The mechanism for the impact of drought stress on spikelet sterility works through changes to simulated leaf temperature (Bouman 2001).

2.3.1.4 Spikelet sterility

Crop growth between panicle initiation and the appearance of the first flowers determines the number of spikelets produced during the flowering period (Bouman 2001). Empirically, the relationship between the weather experienced by the crop and the number of spikelets formed can be approximated using the amount the crop grows during this period (Bouman 2001). Experiments at The International Rice Research Institute (IRRI) have shown that this relationship holds during different seasons and for different levels of nitrogen and water limitations (Bouman 2001). These experiments were used to derive the following relationship capturing the relationship between growth and spikelet number:

$$S_{\mathrm{i}} = \sum_{i=P}^{F} * G_{\mathrm{i}} * y \tag{2.1}$$

where on a given day (i), P is the date of panicle initiation, F is the date when 50 percent of flowers have emerged, G is growth and y is the spikelet formation factor. If spikelets are not affected by stress, then they will go on to become grain. ORYZA V3 simulates high temperature stress and spikelet sterility through the inclusion of a spikelet fertility variable, which reduces the number of fertile spikelets in line with accumulation of heat over a temperature threshold. Equation 2.2 delineates the calculation of the spikelet sterility factor, where TFERT is the average daily maximum temperature when the development stage of the crop is between 0.96 and 1.2 and CTSTER is the genetic threshold at which spikelet sterility occurs (Bouman 2001).

$$SF2 = 1/(1 + e^{(0.853 * TFERT - CTSTER)}) \tag{2.2}$$

This equation for spikelet sterility was taken from an experiment in which Akihikari rice was grown in temperature gradient tunnels in Tokyo. One of these experiments was conducted using potted plants and the other in field conditions with similar results. After incorporating this equation into the SIMRIW model (Horie et al. 1995), the model was shown to closely estimate yearly variations in yield between 1979 and 1990 in three prefectures representing the different climates in Japan (Horie 1993). In the absence of stress from cold temperatures, the total spikelet sterility factor (SPFERT) is equal to SF2.

The impact of water limitations on spikelet sterility is captured through an increase in temperature mediated by leaf rolling,

$$T_i = 5(1 - S_{rl})1.6 \tag{2.3}$$

where T is the change in temperature and S_{rl} is the leaf rolling factor. If there is no water stress, then the leaf rolling factor is equal to one and the whole equation is subsequently equal to zero. Otherwise, the increase in temperature resulting from leaf rolling is added to TFERT, which then increases SF2 and subsequently spikelet sterility. The linear relationship between leaf rolling and leaf temperature is taken from a study by Turner et al. (1986), in which canopy temperature was measured in seven diverse cultivars during the imposition of 10 days of gradated limitations in water availability.

The spikelet sterility factor is subsequently used to reduce the rate at which the grain number increases (GNGR) by constraining the growth rate of the number of spikelets (NSP). It is through this impact on the growth of grains that spikelet sterility impacts end of season yield.

$$GNGR = NSP * SPFERT \tag{2.4}$$

2.3.1.5 Important model assumptions in the context of this thesis

The ORYZA V3. crop model is used in chapter 4 of this thesis to explore the impact of including the impacts of transpirational cooling on spikelet sterility under continuous flooding and alternate wetting and drying treatments in the Indian Punjab. It therefore follows that an important assumption of chapter 4 is that the routine for simulating spikelet sterility works well. As discussed above, the routine used in ORYZA V3 is taken from the work of Horie (1993) in Japan. This routine was shown to perform well in field treatments and to improve the simulation of their rice model (SIMRIW) in three prefectures representing different environmental conditions.

There is therefore a solid rationale for the inclusion of this routine in ORYZA V3. It should be noted however, that (although widely used), to the authors knowledge, this routine has not been systematically tested across the range of genotypic and environmental variation. There is therefore an element of genotypic uncertainty in the use of this routine. A degree of GxE uncertainty is unavoidable, since there is currently a lack of high quality data sets examining the the impact of high temperatures on spikelet sterility and seed setting in rice plants (Sun et al. 2018).

Since the link between water limitation and leaf temperature in ORYZA exists through the leaf rolling mechanism discussed above, a second important assumption is that this pathway is well simulated. This assumption requires that soil water limitations are simulated well by ORYZA V3 and that the mechanism through which leaf rolling changes leaf temperature is well simulated. Li et al. (2017) tested ORYZA V3 under the AWD conditions simulated in chapter 4 and demonstrated high r-squared and model efficiency scores. As discussed above, the equation linking leaf rolling to leaf temperature spans a reasonable range of genetic material, however, it does not encompass a large number of environments. This suggests that there is also a degree of GxE uncertainty in the representation between leaf rolling and leaf temperature. Once again, this uncertainty reflects the lack of high quality data sets on the relationship between leaf rolling and leaf temperature across a range of environments.

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Chapter 3

Enhanced leaf cooling is a pathway to heat tolerance in common bean

Chapter 3 addresses the first question identified in the thesis aims and structure section: Is transpirational cooling important to heat avoidance and heat tolerance in common bean? The chapter begins with a description of why breeding for heat tolerance in common bean is an important goal, before moving on to give a short description of what is known about transpirational cooling in other food crops. The mechansisms through which transpirational cooling has been found to differ within a particular species are then addressed. The aims and objectives of the chapter are then stated.

3.1 Introduction

Common bean (Phaseolus vulgaris) is the most consumed legume in the world (Araujo et al. 2015), and an important source of protein in tropical Latin America and eastern and southern Africa (Beebe et al. 2011). Common bean is grown in a variety of environments with mean air temperatures of between 14°C and 35°C (Araujo et al. 2015). There are two major gene pools, Andean and Mesoamerican. Beans from the Andean gene pool are adapted to mid-higher altitudes (1400-2800 masl) and cooler temperatures, while beans from the Mesoamerican gene pool are adapted to low-mid altitudes (400-2000 masl) (Araujo et al. 2015). Common bean is more sensitive to high temperatures than other legumes (Beebe et al. 2011), making breeding for heat tolerance an urgent priority as the climate continues to warm (Beebe et al. 2011).

Plants are described as being heat tolerant if they are able to maintain the capacity to grow and produce economic yields at high temperatures (Wahid et al. 2007). Some heat tolerant crops maintain photosynthesis under elevated temperatures by maintaining stomatal conductance (Porch and Hall 2013). Keeping the stomata open at elevated temperatures sustains diffusion of CO_2 into the leaves and enhances transpirational cooling (Porch and Hall 2013). Plants that are able to maintain stomatal conductance at high temperatures are therefore better able to regulate their temperature (Porch and Hall 2013; Prasad et al. 2017). It has been suggested that enhanced transpirational cooling may be a useful trait in identifying bean genotypes with the thermal plasticity to adapt to climate change (McClean et al. 2011). The magnitude of transpirational cooling has been used by plant breeders to screen for heat tolerance in spring wheat cultivars (Porch and Hall 2013). The next section turns to the evidence on the contribution of leaf and canopy cooling to heat avoidance in important food crops and the links between heat tolerance and leaf cooling.

3.1.1 Transpirational cooling in food crops

Plants that have evolved in extreme environments are able to strongly regulate the temperature of their leaves, decoupling leaf and air temperatures. In cool alpine environments and humid tropical conditions, leaf temperature can exceed air temperature by as much as 20 °C. In hot and dry desert conditions on the other hand, leaf temperature can be 20 °C cooler than air temperature (Blonder and Michaletz 2018). A recent review of the challenges facing field crops from rising temperatures identifies further research into the physiology of canopy cooling as a key priority (Prasad et al. 2017).

From an energy balance perspective, leaf thermoregulation is controlled by net radiation and evaporative cooling. The relationship between these variables is mediated by leaf thermal traits, including stomatal conductance, size, shape, absorptivity and emissivity (Michaletz et al. 2016). Stomatal conductance responds to many internal and external factors that influence the rate of carbon assimilation and transpiration. In a simplified model of photosynthesis, when RubP carboxylase/oxygenase is unsaturated, stomata respond to the gradient between inter-cellular and ambient levels of carbon dioxide to maximize assimilation. Similarly, stomatal conductance is sensitive to the hydraulic gradient between the soil, stem, leaf and atmosphere. When there is a lack of water, stomatal conductance decreases, reducing transpiration and conserving water (Farquhar and Sharkey 1982). Since high temperatures and drought often occur simultaneously, stomatal behaviour points towards a potential trade-off between leaf cooling and water conservation in hot non-irrigated conditions.

Successful breeding of food crops able to avoid high temperatures through enhanced cooling, requires an understanding of the magnitude and inter-species variation in transpirational cooling. There has been significant progress in understanding the role of transpirational cooling in temperature regulation of rice and wheat plants. Controlled experiments have shown that the difference between the temperature of the air and the reproductive organs of a rice plant is mediated by relative humidity (Weerakoon et al. 2008). This finding has been supported by experiments in field conditions. In hot and dry rice growing conditions in Senegal, the temperature of reproductive organs was found to be up to 9.5 °C cooler than the air temperature, while in cooler and more humid conditions in the Philippines, reproductive organs were at times hotter than the air by 2 °C (Julia and Dingkuhn 2013). A large range in canopy temperature depression (CTD) has also been found in wheat plants. Under varying soil moisture conditions, the canopy temperature ranged from between 6°C cooler and 7 °C warmer than the temperature of the air (Siebert et al. 2014). Though less well established, there is also a smaller body of evidence suggesting that transpirational cooling is an important mechanism for avoiding stress at high temperatures in potato, maize and a variety of legumes (Kumar et al. 2017a).

Transpirational cooling also varies within species. In rice and wheat, there is robust evidence of within species variation, which has been linked to both drought and heat tolerance. Here again, the evidence base is larger and clearer for the major cereal crops than it is for legumes. A study of 56 varieties of chickpea found a difference in CTD between heat tolerant and heat sensitive varieties (Kumar et al. 2017b). On the other hand, a study extending analysis to chickpeas, lentils and faba beans found that although heat tolerant varieties exhibited lower mean canopy temperatures, differences between heat tolerant and heat sensitive varieties were not statistically significant (Ibrahim 2011). A single study exists in which leaf temperature is compared between common bean genotypes at high temperatures. No significant difference was reported (Traub et al. 2018).

There are mechanisms underlying inter-species variation in transpirational cooling that are common across crops. Recent work has shown that heat tolerance in wheat is associated with root architecture. Under drought stress, genotypes that were better at canopy cooling had deeper roots, whilst under heat stress, the same genotypes displayed greater concentration of shallow roots, maximising access to water (Pinto and Reynolds 2015). Pinto and Reynolds (2015) were subsequently able to identify Quantitative Trait Loci (QTL) for root behaviour, providing a common genetic basis for canopy cooling in wheat genotypes. QTL for canopy cooling have also been identified in rice plants. Here, the genetic control for cooler canopies operates through deeper rooting and increased stomatal conductance. Interestingly, this QTL did not significantly correlate with QTLs for drought tolerance, indicating that improvements in yield from canopy cooling can also be conferred directly through stomatal conductance and photosynthesis (Fukuda et al. 2018). In chickpea, molecular markers were able to explain a significant share of variance in CTD and were linked to drought tolerance. Four out of five drought tolerant varieties shared these molecular markers, suggesting that high throughput phenotyping of deeper rooting varieties with cooler canopies may be viable (Purushothaman et al. 2015). Connections between CTD, deeper rooting behaviour and drought tolerance have also been found in common bean (Polania et al. 2016). Associated QTLs have not yet been discovered, and it is not known if deeper rooting behaviour is associated with heat tolerance in common bean.

Crops also share a second mechanism connecting intra-species variation in CTD . Intra-species variation in stomatal response to Vapour pressure deficit (VPD) has been found across crops in both controlled and field conditions (Sinclair et al.

2017). Water saving genotypes respond to high temperature and high VPD by decreasing stomatal conductance and conserving water for later in the season. These drought tolerant varieties therefore exhibit a lower transpiration rate in high temperature and high VPD conditions. Water saving genotypes are often more drought tolerant than their water spending counterparts. Transpiration limiting behaviour is temperature sensitive (Sinclair et al. 2017). At higher temperatures, some varieties lose their transpiration limiting response to changes in VPD. This modulation of stomatal conductance by environmental conditions suggests that there may be a dynamic trade-off between drought tolerance and heat tolerance, where transpiration limiting traits control inter-species variation in CTD (Tardieu 2011). Breeding for heat tolerance via enhanced cooling therefore requires careful analysis of Target Population of Environments (TPE) (Tardieu 2011).

The literature demonstrates that transpirational cooling is an important mechanism for heat avoidance in food crops. It also shows that there is robust evidence for both inter and intra species variation in transpirational cooling, and that there are common mechanisms across crops that determine genotypic variation in this trait. Further, it is not yet known if transpirational cooling is an important mechanism for heat avoidance in common bean nor whether this trait is linked to heat tolerance.

3.1.2 Aim and Objectives

The first objective of this chapter is to test whether i) The magnitude and range of transpirational cooling is sufficient to reduce heat stress. The second objective will be to test whether ii) Transpirational cooling varies with heat tolerance. Answering this question will help breeders determine whether it is worth breeding for cooler beans. The third objective will test whether iii) The association between leaf cooling and VPD varies with heat tolerance. A larger association between leaf cooling and VPD would be indicative of a greater transpirational response to the atmospheric demand for water. Finally, assessing the value of enhanced leaf cooling requires genotype specific modelling of leaf temperature under a range of environments. A model for estimating leaf temperature from meteorology is therefore developed. The fourth and fifth objectives will be to test whether; iv) Leaf temperature can be modelled using meteorology under well-watered conditions and v) If leaf temperature - meteorology interactions are genotype dependent. Genotype specific modelling of leaf temperature will allow breeders to assess the value of greater leaf cooling as a criterion for selection. It will help crop modellers to assess the need/feasibility of genotype specific modelling of leaf temperature in heat stress assessments.

3.2 Material and Methods

3.2.1 Study Site

The experiments used in this study took place at the headquarters of The International Centre for Tropical Agriculture (CIAT) in Cali, Colombia - 965 m above sea level (3 °29" N, 76 °21" W). Figure 3.1 provides a monthly climatology of temperature and precipitation for the CIAT HQ between the years 1978 and 2018. The mean monthly maximum temperature remains close to 30 °C and the mean monthly minimum temperature remains close to 18 °C over the course of the year. These temperatures are just below the thresholds at which bean crops are expected to experience some daytime and night time heat stress (Porch et al. 2010). There are two rainy seasons during the year, which correspond to the two main bean growing seasons. The main rainy season takes place in March, April and May and a second rainy season takes place in October, November and December. The soil is a Mollisol (fine-silty mixed, isohyperthermic Aquic Hapludoll) as described by the USDA classification system, with no major fertility problems (pH = 7.7). For a more detailed description of the experimental site, see Beebe et al. (2008) and Rao et al. (2017).

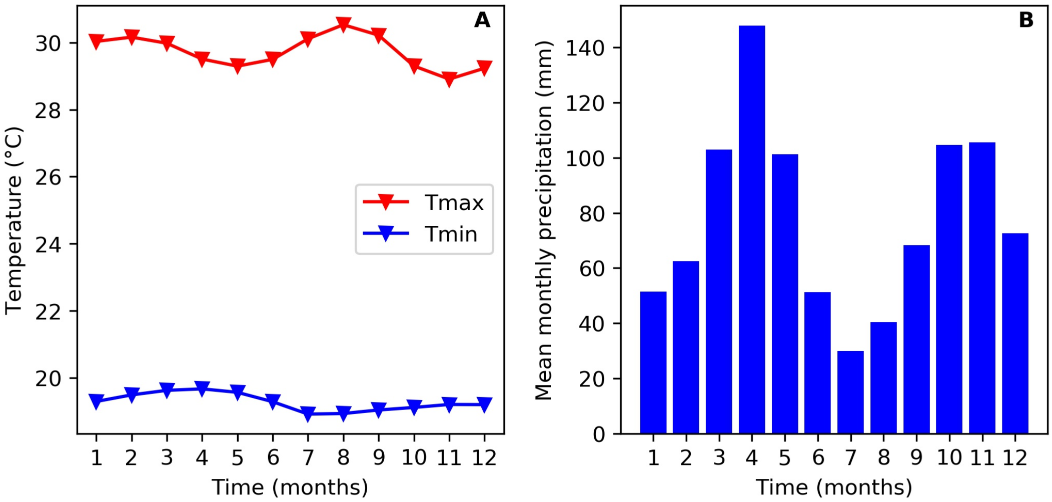

Figure 3.1: Mean monthly climatology at the experimental site (CIAT HQ) between 1978 and 2018 for (A) Temperature (B) Rainfall

3.2.2 The Experiments

The data used in this paper is taken from 6 experiments, each organized in randomized complete block design. H1 (Urban and Ricaurte 2018a) and H3 (Urban et al. 2018b; Urban and van Dam 2018) consisted of three treatments; an ambient treatment undertaken in field conditions (AMB), a greenhouse control experiment with nighttime temperatures kept at 20 °C (GH1) and a greenhouse night heat experiment with nighttime temperatures raised to 24 °C (GH2). Throughout this paper ambient is defined as grown under field conditions and not subjected to stress treatments. For experiment H3, only observations of plants grown in the soil are included, so that observations are fully comparable with the other experiments. H2 (del mar Angel 2017) consisted of an ambient treatment undertaken in field conditions (AMB) and a greenhouse night heat experiment with nighttime temperatures kept at 25 °C (GH). H2 included measurements of fully developed old leaves (base), fully developed young leaves (upper – if not otherwise specified, this is the stage normally taken for all measurements) and young leaves that were not yet fully developed (top). In each of the greenhouse experiments, there was some evidence to suggest that the bean plants may also have experienced stress from above optimal soil pH (pH = 8.1). All of these treatments were kept well-watered. The drought stress experiment (D1) (Urban et al. 2018a) involved 3 treatments; an ambient treatment undertaken in well-watered field conditions using drip irrigation, and two water limited treatments grown under a rain shelter using sprinkler irrigation. In the first of these treatments (the early drought treatment), watering ceased 27 days after sowing for a period of 15 days, after which it was kept at 80 percent of field capacity. In the second treatment, watering ceased 30 days after flowering. The rain shelter remained open when it was not raining. The soil experiment (S1) (Urban and Ricaurte 2018b) consisted of a single treatment. Six genotypes were cultivated on compacted soils following a recent rice growing season. Plants were kept fully irrigated throughout the season. A second drought stress experiment (D2) was used to compare Specific Leaf Area (SLA). This was part of a bigger experiment called BASE 100 (Bean FOR Abiotic Stress Evaluation, 100 genotypes). The experiment consisted of two treatments, control (9 irrigations) and drought (4 irrigations), with the final irrigation 30 days after sowing. Both treatments were conducted in experimental fields at CIAT. SLA was measured 38/39 days after planting (DAP) and 58/60 DAP in both treatments. For each of these days, measurements contained 15 leaves per genotype (3 repetitions of 5 leaves). For each repetition, the trifoliar leaf was cut off so that the central and side leaves could be measured separately. After the leaf area was measured, each repetition was dried at 70 °C for 3-4 days until constant weight was achieved. The 5 central leaves were weighed together and the 10 side leaves were weighed together.

3.2.3 Instrumentation

Observations of air temperature, leaf temperature, relative humidity, leaf thickness and leaf angle were collected using the MultispeQ v1 device made by PhotosynQ. MultispeQ v1 is a handheld device with a Photosynthetically Active Radiation (PAR) sensor on top of the device and temperature and humidity sensors on the right of the leaf clamp. A small infrared (IR) sensor is housed in the bottom of the device. The device uses photodiodes placed above and below the leaf clamp to measure absorbance at 450, 535, 605, 650, 730, 850 and 940 nanometres. These measurements are used to derive a variety of absorbance and fluorescence-based indicators of photosynthetic activity and leaf health (Kuhlgert et al. 2016). A lengthy description of this device and protocols for its use are described in chapter 2 of this thesis.

Measurements of stomatal conductance were taken during experiment H2 using the SC-1 Leaf Porometer from METER group. The central axial part of the leaf was measured, where most stomata in bean are located. Measurements of the youngest fully developed leaf (upper) and the youngest not fully developed leaf (top) were taken. Instrument preparation, calibration and measurements were performed as recommended by the manufacturer (metergroup 2019). The device has a range of 1-1000 mmol/m^{2}s, a resolution of 0.1 mmol/m^{2}s and an accuracy of 10 percent from 0-500 mmol/m^{2}s. Beyond this range, the device is able to measure relative change in stomatal conductance, but the manufacturers are not able to verify the absolute accuracy of the device. The operating temperature of the device is 5-40°C and the operating relative humidity is 1-100 percent. 182 measurements were taken within this range over 5 days, 92 measurements from the ambient treatment and 90 from the greenhouse treatment. In total, 95 successful measurements for the heat sensitive genotype and 87 for the heat tolerant genotype were recorded. Measurements were taken over the course of the day at 8 am, 10 am, 1pm and 3pm.

During experiment D2, leaf area measurements were made using the Licor LI-3100C meter for the harvest taken 38/39 DAP from the control experiment. Leaf area measurements made from all other harvests were made with the LI-3000C LA meter connected to an LI-3050 transparent conveyor accessory from the same manufacturer. The resolution of all leaf area (LA) measurements was 1mm squared, with an accuracy of 2 percent (LICOR 2019).

3.2.4 Data Selection

Objective i) was tested using the aggregated data from the 5 experiments (called the whole sample from here onwards) and for a subset containing only observations taken under ambient conditions (called the ambient subset from here onwards). Table 3.1 shows that the mean air temperature is similar in the whole sample and the ambient subset. The standard deviation and range of temperatures is 0.5 °C and 3.6 °C larger in the whole sample. The difference between samples is larger for relative humidity than for air temperature. The mean, standard deviation and range of relative humidity is lower in the ambient subset than in the whole sample.

The remaining objectives required a comparison of heat sensitive and heat tolerant genotypes. They were therefore tested on the H1 and H2 experiments, because the same heat sensitive and heat tolerant genotypes were used in both experiments and the number of measurements taken were sufficient for statistical analysis. Figure 3.2 compares the MultispeQ measurements taken in the H1 and the H2 experiments. Figure 3.2 demonstrates that the measured temperatures in the H2 experiment were hotter than the measured temperatures in the H1 experiment. In both of the H2 treatments, the median sampled temperature was above 37 °C and the upper quartile of temperatures would be expected to impose heat stress on common bean plants. Figure 3.2 also shows that relative humidity was lower in the H2 measurements than in the H1 measurements.

Table 3.3 gives a detailed comparison of air temperature, relative humidity and PAR during the daytime in each of the three H1 treatments. The mean air temperature was similar in all of the treatments. The standard deviation was higher in the ambient treatment than in either of the two greenhouse treatments, meaning that plants experienced more variable daytime air temperatures in the ambient treatment. The minimum and maximum temperatures were lowest in the ambient treatment and highest in the night heat treatment. Mean relative humidity was lowest in the ambient treatment and similar in both greenhouse treatments. Relative humidity was more variable in the ambient treatment and similar in both of the greenhouse treatments. Mean photosynthetically active radiation (PAR) was much larger in the ambient treatment than in the two greenhouse treatments. The standard deviation and maximum of PAR was also higher in the ambient treatment, as expected.

In the H1 experiment, plants were sampled between 8:30 am and 10:45 am in the morning and 1:30 pm and 3:15 pm in the afternoon. In the H2 experiment,

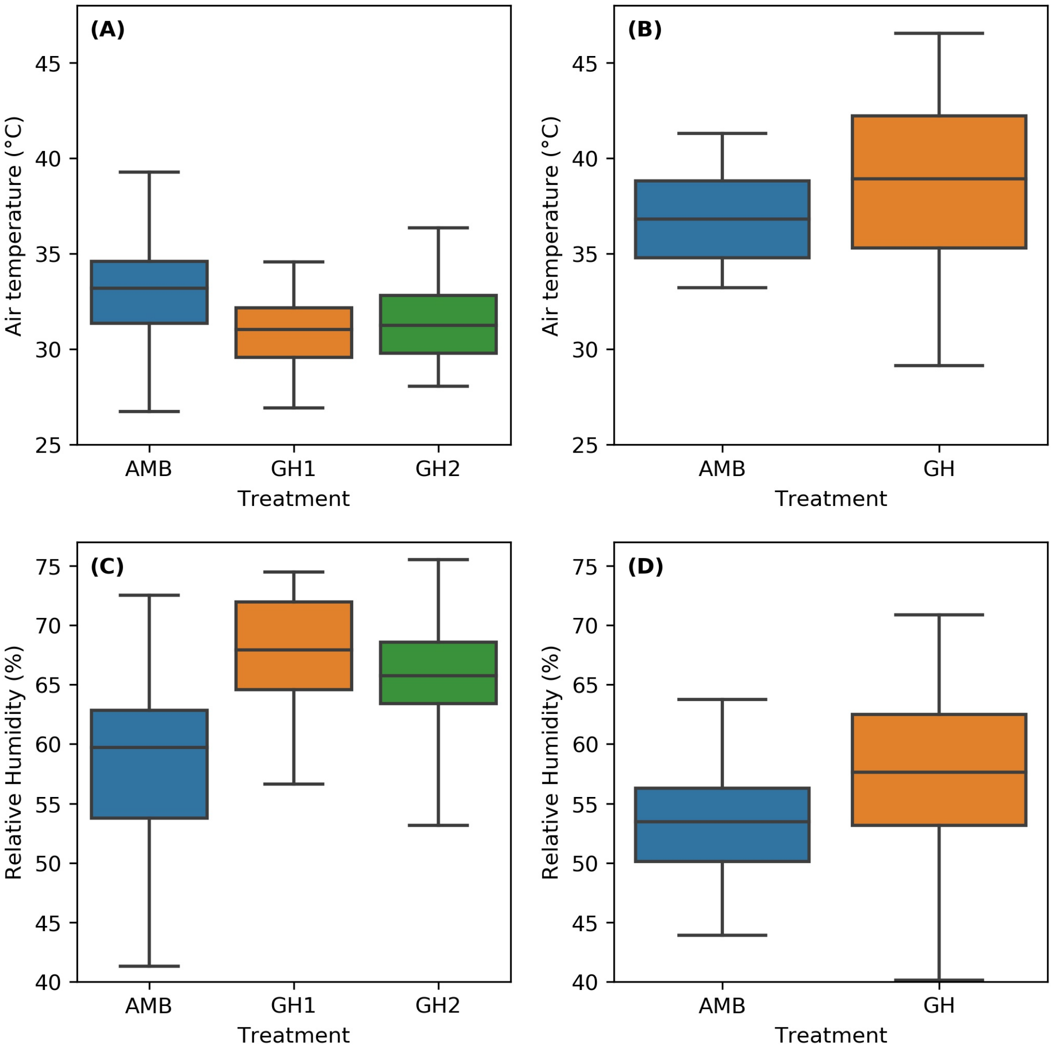

Figure 3.2: Comparison of sampled air temperature and relative humidity in the H1 and H2 experiments (A) Temperature in the H1 experiment (B) Temperature in the H2 Experiment (C) Relative humidity in the H1 experiment (D) Relative humidity in the H2 experiment

plants were sampled between 8 am and 9 am, between 10 am and 11 am, between 1 pm and 2 pm and between 3 pm and 4 pm. This work is therefore only able to capture the impacts of high daytime temperatures as night time temperatures were not sampled. It is therefore possible to capture the impact of high daytime temperatures on leaf temperature depression, but not those of high night time temperatures.

3.2.5 Data Preparation

The MultispeQ device automatically flags potentially unreliable measurements by including a binary issues variable. The device automatically flags measurements during which it was not held steady or if the leaf did not fully cover the light guide. It can also issue a warning flag if measurements of the realized steady state efficiency of photosystem II (Phi2), the quantum yields of non-photochemical exciton quenching (phiNPQ) and non-regulatory energy dissipation (phiNO) values are outside of the expected range. In the data set used in this chapter, flagged measurements largely referred to instances where the device was not held steadily. In this analysis, all measurements with an issues flag were removed and all measurements which contained missing data for any of the variables. This analysis therefore only contains complete measurements for all variables without potential issues. Employing this protocol results in the loss of approximately 3.7 percent of the total samples taken. For genotype comparisons, in which variables with a higher propensity of measurement error were used, measurements that were more than three times the interquartile range above the third quartile and below the first quartile were also removed.

The arithmetic mean of technical replicates for each genotype are treated as independent random samples for the purposes of testing differences between genotypes. Only sampling days when both genotypes are tested during the same time periods are included in the analysis. Three replicates were taken in the H1 experiment. Post data preparation and averaging of replicates, the H1 experiment consisted of 821 independent observations, 258 observations from the ambient experiment, 271 observations from the greenhouse control experiment and 292 observations from the greenhouse night heat experiment. Three replicates were taken in the H2 experiment. Post data preparation and averaging of replicates, the H2 experiment consists of 318 independent observations, 96 from the ambient experiment and 222 from the greenhouse night heat experiment.

3.2.6 Plant Material

Three contrasting genotypes were grown in the H1 experiment. Calima is a heat/drought sensitive check variety, grown throughout Colombia, SAB 686 is a heat/drought tolerant variety and SEF 60 is a heat tolerant variety. Both Calima and SAB 686 are common bean varieties from the Andean gene pool. Calima produces medium sized seeds with a red mottled colour and SAB 686 produces medium sized seeds of a cream mottled colour. Both genotypes are growth types 1; strong and erect systems. SEF 60 is a triple inter-specific cross with Tepary bean (*P. acutifolius*) and Runner bean (*P. coccineus*). Tepary bean originated in arid and semi-arid conditions (Mhlaba et al. 2018) and has been shown to enhance heat tolerance when crossed with common bean varieties (CIAT 2015). SEF 60 produces medium sized red seeds and is resistant to Bean Common Mosaic Necrosis Virus (BCMNV). SEF 60 is from the Mesoamerican gene pool, with growth type 2A; indeterminate erect systems without guidance. Calima and SAB 686 were also grown in the H2 experiment. For the remainder of this chapter, Calima will be referred to as HS-A, reflecting its heat sensitive nature and its Andean origins. SAB 686 will be referred to as HT-A, reflecting its heat tolerant nature and its Andean origins. SEF 60 will be referred to as HT-T, reflecting its heat tolerant nature and that it is a Tepary cross.

3.2.7 Variable Definitions

The term canopy temperature depression is often used inter-changeably to describe the difference between canopy and air temperature and the difference between leaf and air temperature. In this chapter the term leaf temperature depression is used to make clear that it is the difference between air and leaf temperatures that are being analysed. The leaf temperature depression is a good indicator of the canopy temperature depression at the top of canopy. Leaf Temperature Depression (LTD) was calculated from the air temperature and the leaf temperature measured by the MultispeQ device.

$$LTD = Leaf\ temperature - Air\ temperature \tag{3.1}$$

Vapour pressure deficit (VPD) was calculated by subtracting the actual vapour pressure (ea) from the saturated vapour pressure (es). The Magnus method (Andersson-Sköld et al. 2008) was employed for calculating the saturated vapour pressure.

$$es = 0.61094 * e^{(17.625T/T+243.04)} \tag{3.2}$$

The actual vapour pressure was then calculated using the relative humidity (RH) as follows.

$$ea = RH/(100es) \tag{3.3}$$

The vapour pressure deficit (VPD) is then given by:

$$VPD = es - ea \tag{3.4}$$

3.2.8 Statistical methods and inference

In this chapter hypothesis tests that rely on statistical comparison of group means were conducted. The hypothesis that heat tolerant genotypes are cooler than heat sensitive genotypes was tested. This equates to the following hypothesis test:

Ho: The mean LTD of the heat sensitive genotype is identical to the mean LTD of the heat tolerant genotypes.

Ha: The mean LTD of the heat sensitive genotype is greater than the mean LTD of the heat tolerant genotypes.

A one-sided permutations test (Ludbrook and Dudley 1998) was used to conduct the above hypothesis test. A permutations test was chosen instead of a non-parametric Mann-Whitney U test, as there is no theoretical justification for assuming that the distribution of LTD is the same shape for each genotype. If this assumption were violated, then the Mann-Whitney test would not be a comparison of the averages of the two groups of data.

Permutation testing for equal means between two observed samples begins by concatenating these samples. The concatenated array is then randomly shuffled. This shuffled array (known as a permuted sample) is split into two separate arrays of the same length as the two input samples. The difference in means between these two arrays is then calculated. This process was repeated 10,000 times, resulting in 10,000 permuted samples and mean differences. The p-value was then computed by calculating the proportion of permuted samples in which the mean difference was greater than the mean difference in the observed samples. This provided an estimate of the probability of the difference in means being larger than the observed difference in means by chance.

In addition to testing for differences in the mean LTD between heat tolerant and heat sensitive genotypes, how cooling responds across the temperature distribution is also of interest. Since there is no theoretical reason to suppose a linear relationship between LTD and temperature over the whole temperature distribution, a local regression is used to examine this assumption. Local regression fits a linear or quadratic function to a moving window of the input data set (Cleveland and Devlin 1979). This window is the locality described in the name 'local regression'. The size of the locality (the proportion of the data set used in each window) is user defined and determines how smooth the fit produced is (Cleveland and Devlin 1979). Two thirds of the data was used in each moving window. Observations used in the regression were weighted by their distance from the observation being fitted. A bi-square function of the residuals was used for this purpose, and each observation was weighted 3 times. The lowess regeression was performed and plotted using Python's Seaborn library. The smoothed results of this locally weighted regression are presented on a scatter plot, which is described as a lowess regression in the results section. The purpose of this exercise was to visually examine the form of LTD across the temperature distribution.

Objective 3 (that the relationship between LTD and VPD varies with the tolerance of the genotype) was tested using Spearman rank correlation (Zwillinger and Kokoska 1990) from Python's SciPy library. The relationship between LTD and VPD is noisy and non-linear, since as discussed in the introduction, LTD is also controlled by leaf traits and other environmental variables. This is the reason for using a rank correlation instead of a Pearson correlation.

Objective 4 requires the development of a model to predict leaf temperature using meteorological conditions. Data was combined from the H1 and H2 experiments to ensure that the model performs well in a range of temperatures and relative humidity. The H2 data was subset to only include samples taken from the upper leaf in the canopy to ensure comparability between the two data sets. Since the model may later be used in process based crop models, only variables that are available to crop modellers are used. This approach builds on success in predicting rice canopy temperatures using air temperature and relative humidity (Van Oort et al. 2014). Since the impact of air temperature on leaf temperature is expected to vary at different levels of relative humidity, an interaction term between temperature and relative humidity was included. Finally, a dummy genotype variable was included to test for impact on model performance.

Environmental variables are often highly correlated with each other and strong correlation between temperature and relative humidity introduces a multicollinearity problem for Ordinary Least Squares (OLS) regression. A variation of OLS called Ridge regression that increases the stability of the regression coefficients by renegotiating the bias vs. variance trade-off in favour of reducing variance was therefore used. Ridge regression is an effective way of reducing the impacts of multicollinearity on regression coefficients and is applied to scaled independent variables (Sen and Srivastava 1990). Scaling was performed by subtracting the mean and dividing by the standard deviation to ensure that the mean of each input variable is equal to 0 and the standard deviation is equal to 1.

$$Scaled(X_i) = (X_i - mean(X))/standarddeviation(X) \tag{3.5}$$

The form of the regression is presented below;

$$\hat{y} = \beta_0 + \beta_1 sctair + \beta_2 scrh + \beta_3 sc(tair * rh) + \beta_4 gen + \epsilon \tag{3.6}$$

sctair = scaled air temperature, scrh = scaled relative humidity, sc(tair*rh) = scaled temperature and relative humidity interaction term and gen = binary genotype variable, which is equal to 1 for HS-A and 0 for HT-A.

Ridge regression selects the regression coefficients based upon a variation of the OLS loss function. An additional term is added to the loss function comprising the squared value of the regression coefficients. This effectively penalizes the selection of large coefficients. The formal description of selection of coefficients in a ridge regression is given below in equation 3.7.

$$\hat{\beta}_{(k)} = (X'X + kI)^{-1}X'Y \tag{3.7}$$

where Y is the observations, X is the independent variables and I is the Identity matrix (Ryan 1997). Note that when k = 0, the ridge regression collapses to an OLS regression.

Before applying the ridge regression, the data was randomly split into 70 percent training data and 30 percent testing data. The Train-Test-Split function in Python's sklearn library with seed = 1 was used to perform this random split, employing stratification by experiment, treatment and genotype to ensure a balanced sample. The training data was used to fit the regression and the testing data was used to evaluate the regression. Measures of model performance reported in this chapter are based on the performance of the regression on the testing data alone. The selection of k in equation 3.7 was performed using a grid search of values between 0 and 1 with a search resolution of 0.1. The criterion for selection of k was maximizing r-squared and each value of k in the grid was tested using 5-fold cross-validation on the training data set. A Scikit learn pipeline was used to perform both regression training and grid search operations.

3.3 Results

3.3.1 LTD is an important heat avoidance mechanism

Leaf temperature depression was large in this study, demonstrating that leaf cooling strongly regulated leaf temperature (Table 3.2). On average, the temperature of the leaf was 5.2 °C cooler than the temperature of the air and varied between 13 °C cooler and 2.1 °C warmer.

Figure 3.3 shows that leaf cooling played an important role in keeping leaf temperatures within the range required to maintain their physiological function. This was the case for both the whole sample and the ambient subset. In both the whole sample and the subset of ambient observations, the peak of the leaf temperature distribution was within 25-30 °C.

3.3.2 LTD varies with heat tolerance

The heat tolerant varieties cooled by more than the heat sensitive variety in all three treatments of the H1 experiment (Figure 3.4). In the ambient treatment (A), the heat tolerant varieties (HT-A and HT-T) cooled 0.77 °C and 0.82 °C more than the heat sensitive variety (HS-A). These differences are statistically significant at the 95 percent confidence level (p-values of 0.00 and 0.00 respectively). In the Greenhouse control treatment (B) HT-A cooled 0.2 °C more than HS-A, this difference is not statistically significant at the 95 percent confidence level (p-value = 0.11). HT-T cooled 0.5 °C more than HS-A, this difference is statistically significant at the 95 percent confidence level (p-value = 0.00). In the Greenhouse night heat treatment (C) HT-A cooled 0.2 °C more than HS-A

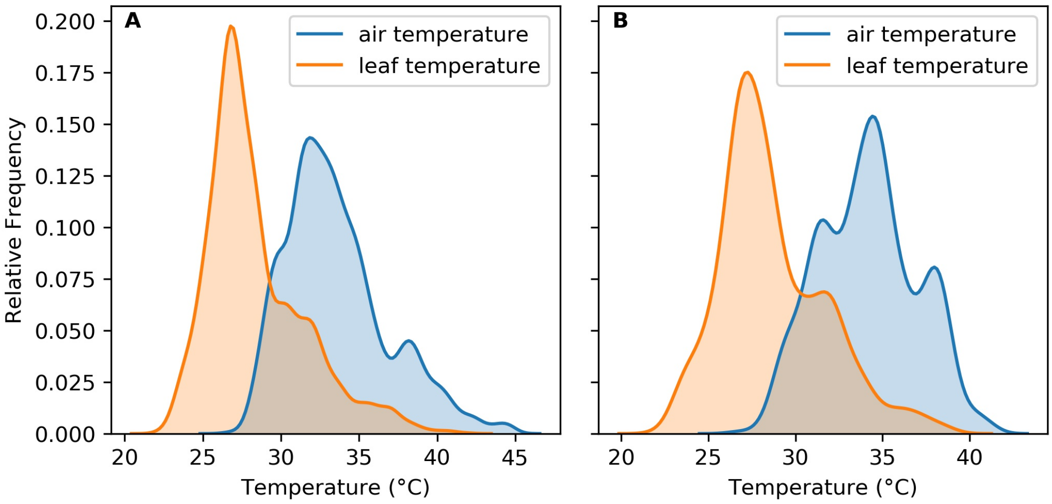

Figure 3.3: Air and leaf temperature distributions for (A) Aggregated observations from the 5 experiments (B) Aggregated observations from the 5 experiments in ambient treatments only

and HT-T cooled 0.1 °C more than HS-A. Neither of these differences are statistically significant at the 95 percent confidence level (p-values of 0.10 and 0.25 respectively).

The H2 experiment supports the hypothesis that HT-A cools more than HS-A. In the ambient treatment (D), HT-A cooled 2 °C more than HS-A and this difference is statistically significant at the 95 percent confidence level (p-value = 0.00). In the GH night heat experiment (E), HT-A cooled 1.3 °C more than HS-A and this difference is also statistically significant at the 95 percent confidence level (p-value = 0.00). In addition to greater mean cooling, HT-A also exhibited greater variability and a larger range of leaf cooling. Table 3.4 summarises these results.

The lowess regression on the pooled H1, H2 data for HS-A and HT-A (Figure 3.5) shows that the relationship between air and leaf temperatures was non-linear for both genotypes. At lower temperatures, the relationship between air and leaf temperatures is similar for both genotypes, however, at higher temperatures, HT-A cooled more than HS-A leading to a gap in leaf temperatures between the two contrasting genotypes.

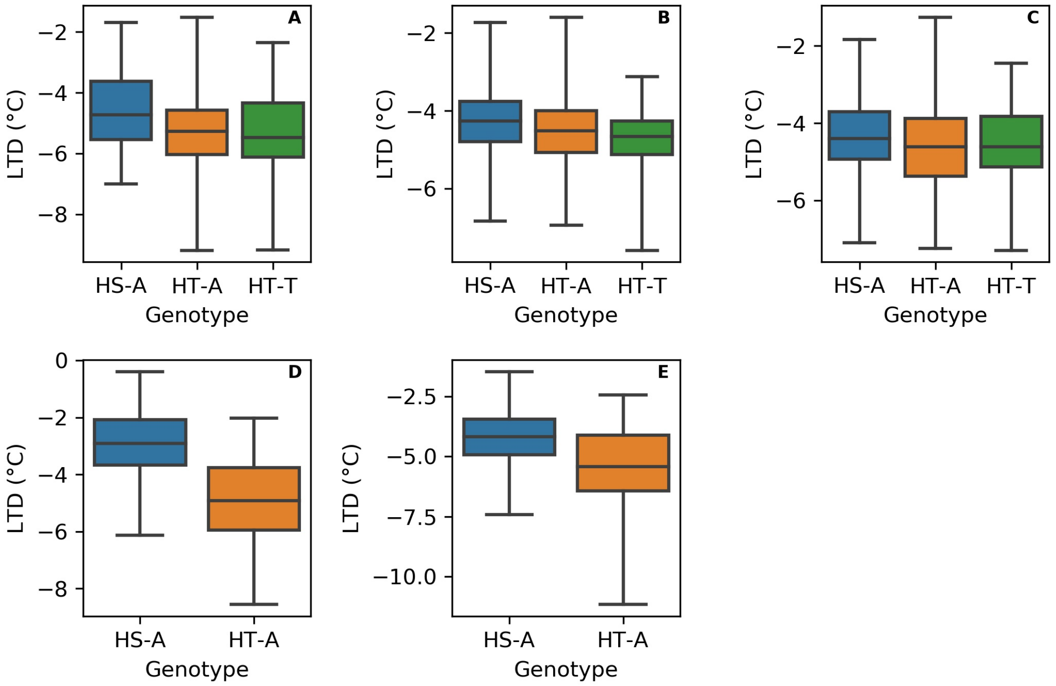

Figure 3.4: Distribution of LTD observations by treatment and genotype for the H1 and H2 experiments (A) H1 experiment - ambient treatment (B) H1 experiment - GH control treatment (C) H1 experiment - GH night heat treatment (D) H2 experiment - ambient treatment (E) H2 experiment - GH night heat treatment

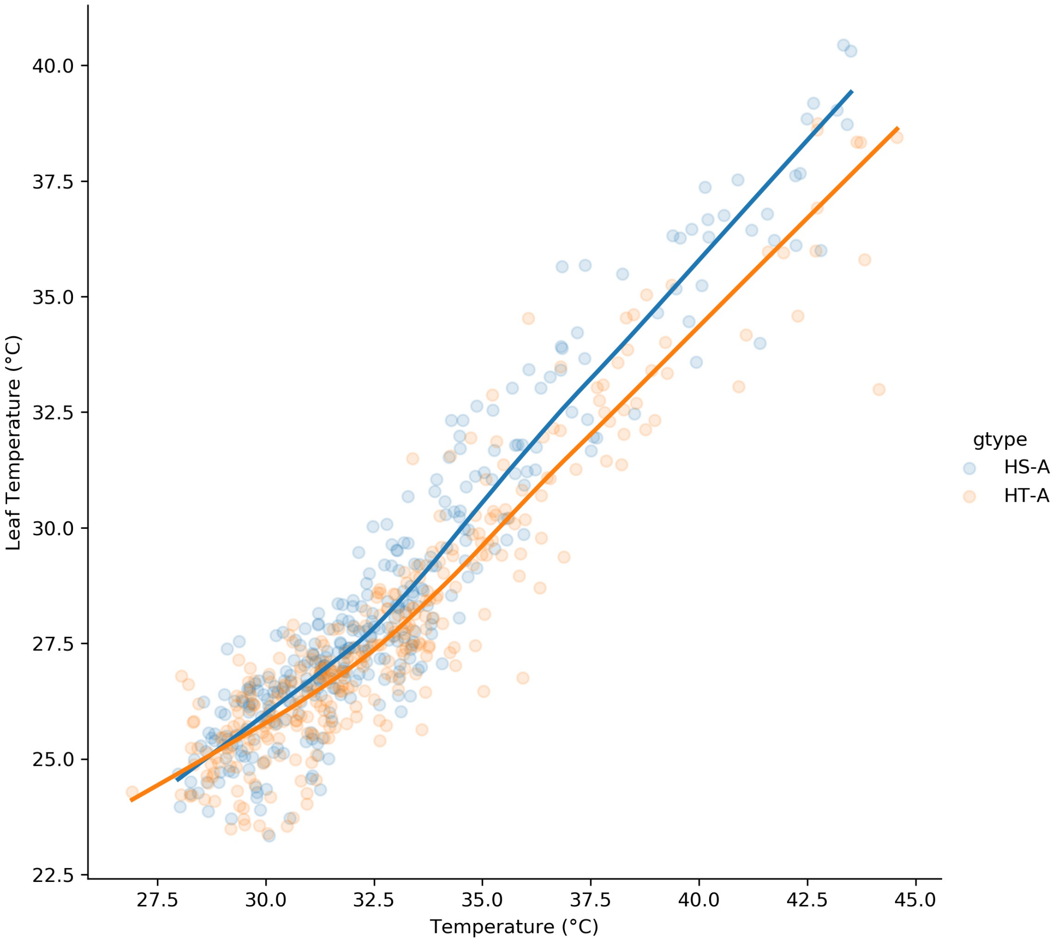

Figure 3.5: Lowess regression on the pooled data for HS-A and HT-A from the H1 and H2 experiments

3.3.3 Thermal gradient within the canopy varies by genotype

For all positions within the canopy and for all treatments of the H2 experiment, HT-A cooled more than HS-A (Figure 3.6). The gradient in leaf cooling through the canopy differed between the two genotypes (Figure 3.6). In both treatments HT-A cooled most at the top of the canopy and least at the bottom of the canopy. Interestingly, this thermal gradient in leaf cooling did not exist for HS-A. The difference in the magnitude of leaf cooling between HT-A and HS-A was greatest at the top of the canopy and smallest at the bottom of the canopy. The last row of Figure 3.6 shows that in ambient conditions, HT-A cooled 2.8 °C more than HS-A at the top of the canopy compared with 1.2 °C more at the bottom of the canopy.

3.3.4 There is genotypic variation in the relationship between LTD and VPD

The relationship between LTD and VPD varied by genotype. Figure 3.7 shows scatter plots of the joint LTD-VPD distribution for each of the genotypes. The first row takes observations from the H1 experiment and compares all 3 genotypes and the second row takes observations from the H2 experiment and compares HS-A and HT-A .

Beginning with the H1 experiment (first row of Figure 3.7), there was a clearer association between VPD and LTD for HT-A (B) and HT-T (C) than for HS-A (A). This is shown by Spearman correlations of -0.46 and -0.46 respectively compared with -0.26. The association between VPD and LTD remained greater for HT-A (E) than HS-A (D) in the hotter and dryer H2 Experiment. The Spearman correlation coefficients for the H2 experiment are -0.46 for HT-A and -0.32 for HS-A. All correlation coefficients discussed in this section are significant at the 99 percent confidence level.

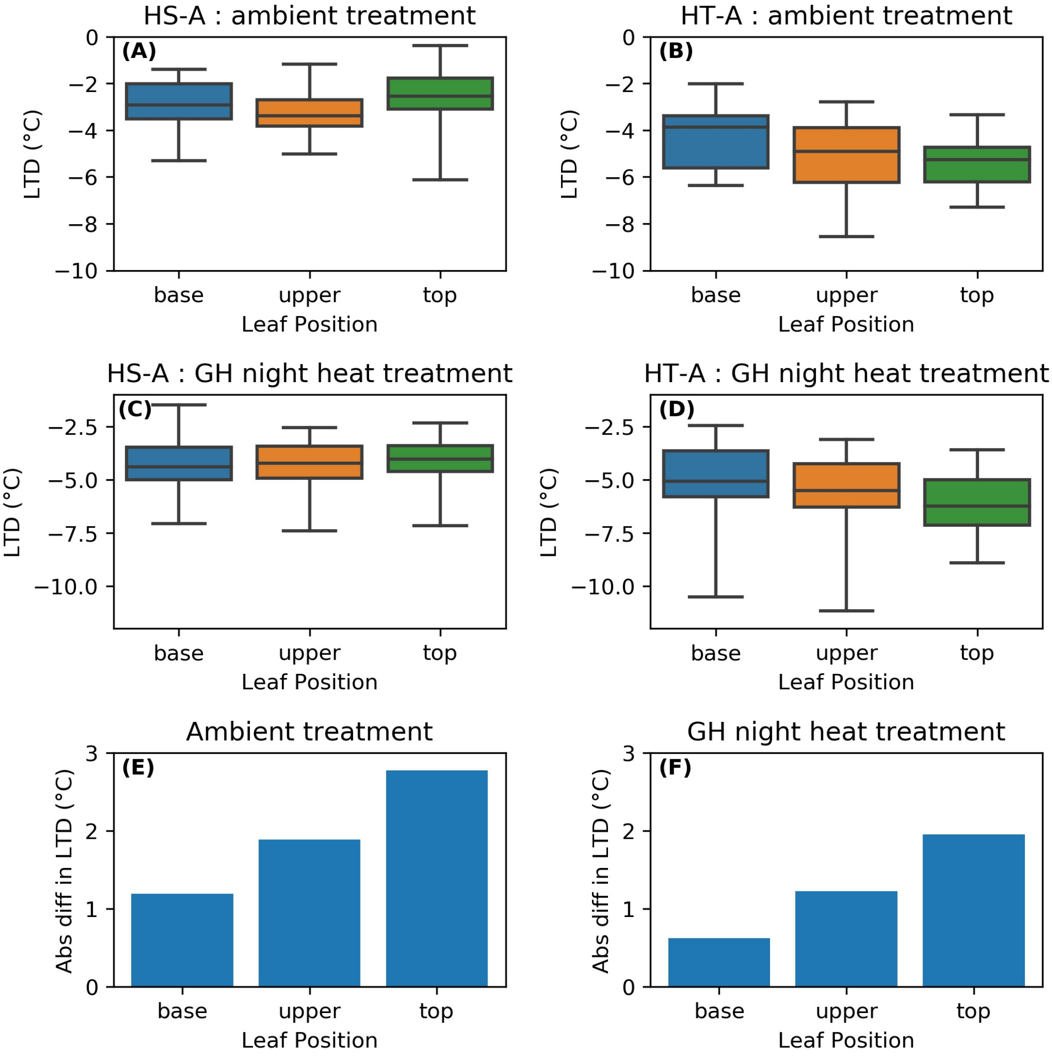

Figure 3.6: Leaf temperature depression at different positions within the canopy by treatment and genotype in the H2 experiment (A) HS-A in ambient conditions (B) HT-A in ambient conditions (C) HS-A in night heat conditions (D) HT-A in night heat conditions (E) The absolute difference in LTD between HT-A and HS-A in ambient conditions (F) The absolute difference in LTD between HT-A and HS-A in night heat conditions

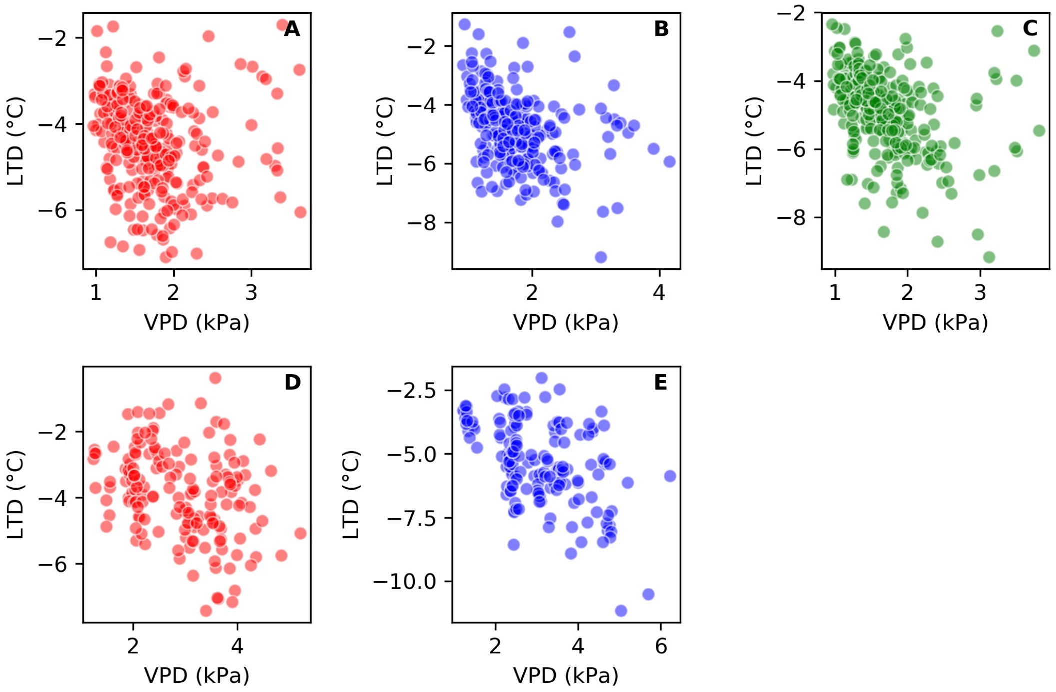

Figure 3.7: Scatter plots for VPD and LTD by genotype for the H1 experiment and the H2 experiment. (A) H1 experiment : HS-A (B) H1 experiment : HT-A (C) H1 experiment : HT-T (D) H2 experiment : HS-A (E) H2 experiment : HT-A

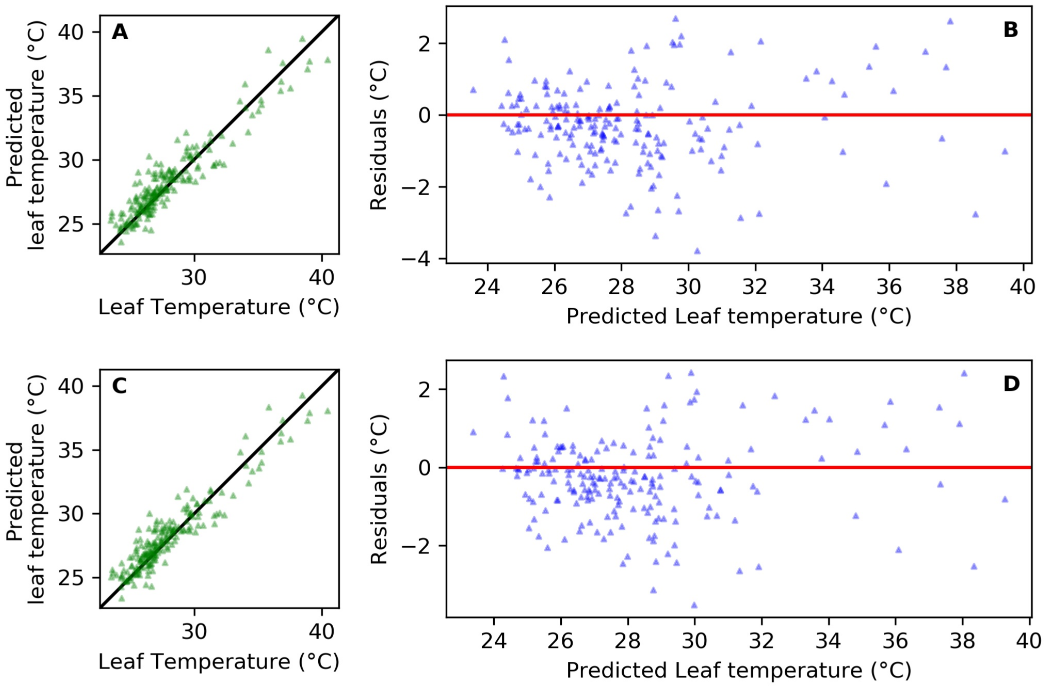

Figure 3.8: Regression output for equations 3.8 and 3.9 applied to the pooled data for HS-A and HT-A from experiments H1 and H2 (A) Leaf temperature vs. predicted leaf temperature - Equation 3.8 (B) Predicted leaf temperature vs. residuals - Equation 3.8 (C) Leaf temperature vs. predicted leaf temperature - Equation 3.9 (D) Predicted leaf temperature vs. residuals - Equation 3.9. In (A) and (C), the solid (identity) line represents perfect agreement

3.3.5 Leaf temperature is explained by air temperature and relative humidity

Figure 3.8 shows that accuracy in predicting leaf temperature was high using only temperature, relative humidity and an interaction term between the variables (Equation 3.8) . The ridge regression is able to explain 87 percent of the variance in leaf temperature (R^2 value = 0.87) with a Root Mean Squared Error (RMSE) of 1.16 °C. When including a dummy variable for genotype, the R^2 value increased to 0.88 and the RMSE decreased to 1.11 °C (Equation 3.9).

Figure 3.8 plots the predicted leaf temperatures against the error term of the ridge regression. A key assumption required for accurate prediction of regression performance is constant variance of the error term (homoscedasticity). In Figure 3.8, the residuals appear randomly spread around the zero line, which suggests that the homoscedasticity assumption is satisfied.

In both equations 3.8 and 3.9, air temperature is the dominant driver of leaf temperature. However, coefficients for relative humidity and the interaction between temperature and relative humidity are also non-zero. This suggests that the impact of temperature on leaf temperature depends on the relative humidity. In Equation 3.9, the coefficient for the genotype dummy is 0.54. This implies that if the heat sensitive variety HS-A (gen = 1) were being modelled, then the leaf temperature would be (on average) slightly over half a degree warmer than when modelling the heat tolerant variety HT-A.

$$L\hat{T} = 28.3 + 3.92(sctair) + 1.14(scrh) - 0.75(sc(tair * rh)) + \epsilon \tag{3.8}$$

$$L\hat{T} = 28.0 + 4.05(sctair) + 1.31(scrh) - 0.89(sc(tair * rh)) + 0.54(gen) + \epsilon \tag{3.9}$$

3.4 Discussion

3.4.1 Heat avoidance through transpirational cooling

Section 3.3.1 showed that leaf cooling shifts the temperature distribution experienced by the upper leaves of the plant to a range in which physiological function is maintained. A second way in which transpirational cooling contributes towards heat tolerance is through maintaining temperatures below damaging biochemical thresholds (Porch and Hall 2013).

A number of studies have been conducted illustrating the impacts of heat stress on common bean during the reproductive period. Although many pathways to impact have been established by thorough experimental work, different studies have imposed different combinations of day and night time temperatures (Araujo et al. 2015). This makes it hard to pinpoint exactly what daytime temperature threshold results in heat stress. For this reason, the impact of transpirational cooling on a threshold grounded in the biochemistry of photosynthesis is examined.

In C3 plants, photosynthesis declines above a threshold of 35 °C as a result of a reduction in the activation state of Rubisco (Sage et al. 2008; Salvucci and Crafts-Brandner 2004). This limits carbon fixation and subsequently, net photosynthesis. In the whole sample, 27 percent of air temperature observations were greater than 35 °C, while only 4.8 percent of leaf temperatures were above 35 °C. It follows that leaf thermal regulation plays an important role in maintaining photosynthesis at high temperatures in common bean.

3.4.2 Genotypic variability in leaf cooling

To date, there are many theories seeking to explain the physiological mechanisms through which heat tolerance is conferred in common bean. This chapter asked if heat tolerance could be linked to enhanced leaf cooling. Section 3.3.2 showed that heat tolerant genotypes cool more than heat sensitive genotypes in 4 out of the 5 treatments studied. Unlike, Traub et al. (2018) significant differences between heat tolerant and heat sensitive genotypes were found. The size of these differences ranged from 2 °C to 0.1 °C depending on the environmental conditions.

A difference of 1-2 °C matters in the context of adaptation to a warming climate. A difference of 1-2 °C in leaf thermal regulation could conceivably reduce heat damage by reducing heat stress threshold exceedance during extreme temperature events. Differences in leaf cooling of this magnitude could also contribute to heat tolerance by reducing the time the plants spend at sub-optimally high temperatures over the course of the growing season. For example, the plant may cumulatively experience less photorespiration.

Section 3.3.3 showed that the difference in the strength of leaf cooling between the heat tolerant variety and the heat sensitive variety is largest at the top of the canopy. Since both genotypes are determinate bush beans and flower from the top to the bottom of the canopy, this result suggests that enhanced cooling in heat tolerant varieties is largest where sensitivity to temperature during the reproductive process is greatest. The combination of the magnitude of enhanced cooling and the place where this enhanced cooling is greatest, suggests an important role for leaf cooling in heat tolerance in common bean. The magnitude of the impact of greater cooling on heat tolerance may also be influenced by the extent of leaf acclimation to heat. Future work should seek to test for interactions between leaf cooling and leaf acclimation.

The results show that the connection between heat tolerant genotypes and greater cooling varies under different combined temperature and relative humidity regimes. The difference in mean cooling between heat tolerant and heat sensitive genotypes was much larger in the H2 experiment, in which mean temperature was higher and mean relative humidity was lower. It was also shown that the difference in leaf cooling between heat tolerant and heat sensitive genotypes widened at higher temperatures. This suggests that the effectiveness of enhanced cooling as a pathway to heat tolerance may increase as the climate continues to warm.

The evidence suggests that enhanced leaf cooling will be most effective in aiding adaptation in hot and dry conditions. However, given that transpirational cooling relies on water availability, this method of heat avoidance may not be effective in water scarce conditions. Greater transpirational cooling could make these varieties more sensitive to drought if irrigation is not available during dry spells and net transpiration is increased.

3.4.3 Vapour pressure deficit and leaf cooling

Section 3.3.4 showed that the association between VPD and LTD does vary with heat tolerance. In both experiments, the heat tolerant varieties cooled more in response to changes in VPD than the heat sensitive genotype. This supports the hypothesis that heat tolerant genotypes exhibit greater transpirational cooling.

A stronger association between VPD and leaf cooling may also confer tolerance by helping to maintain leaf water content. In a series of experiments, Omae et al. (2012) showed that heat tolerant snap bean genotypes maintain a higher leaf water content than heat sensitive genotypes under both heat and drought stress conditions. They showed that leaf water content is associated with the number of pods per plant and final yield (Omae et al. 2012). In addition, they find that heat tolerant genotypes exhibit a smaller drop in leaf water content at midday and that this difference was associated with a higher pod setting ratio. They propose that an enhanced water potential gradient between the soil and the leaves allows heat tolerant genotypes to absorb more water, preventing dehydration under hot and dry conditions (Omae et al. 2012). These results support this hypothesis, as a stronger response to VPD in heat tolerant genotypes allows for a stronger water potential gradient.

A stronger cooling response to VPD in heat tolerant genotypes may be the result of higher stomatal conductance. Measurements of stomatal conductance made during experiment H2 (the hotter and dryer experiment) show that the heat tolerant genotype exhibited far higher stomatal conductance during both the hot and dry treatment and the hot and more humid treatment (Figure 3.9). These results are in agreement with Tsukaguchi et al. (2003), who also found that heat tolerant snap bean cultivars maintain greater stomatal conductance under high temperature conditions than heat sensitive cultivars (Tsukaguchi et al. 2003). This suggests that stomatal conductance is greater in heat tolerant genotypes, which allows for a greater transpirational response to VPD and enhanced transpirational cooling.

It should be noted that greater stomatal conductance leading to greater transpirational cooling will only lead to enhanced leaf water content if water remains available. These characteristics would therefore only contribute to heat tolerance in the presence of a third trait enhancing access to water in heat tolerant genotypes. Candidate traits include deeper root systems (discussed in the introduction), lower root radial hydraulic resistance (higher root conductivity) and greater leaf osmotic adjustment resulting in more stable cell tugor. These are promising avenues of enquiry for future work. If one or more of these hypothesise are true, it would suggest that heat avoidance through transpirational cooling has co-evolved with traits for drought resistance. Given that both of the heat

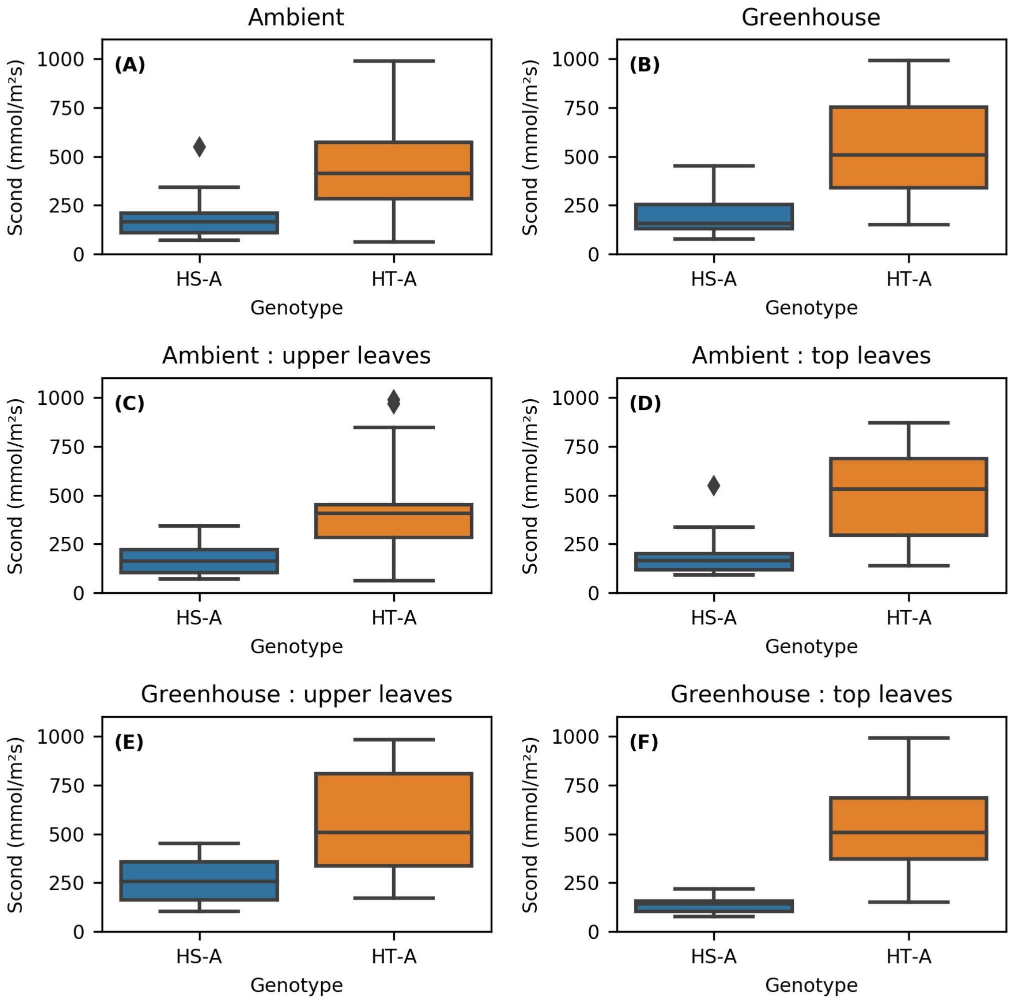

Figure 3.9: The distribution of stomatal conductance for HS-A and HT-A for experiment H2 (A) Ambient conditions (B) Greenhouse conditions (C) Ambient upper leaves (D) Ambient top leaves (E) Greenhouse upper leaves (F) Greenhouse top leaves

tolerant genotypes used in the experiments in this chapter were derived from lines originating in semi/arid environments, co-evolution of traits conferring heat and drought tolerance seems plausible.

Since response to VPD was not reduced in the very hot and dry conditions of H2, this supports the hypothesis put forward by Sinclair et al. (2017) that transpiration limiting traits are modulated by the plants' environment rather than being attached to absolute transpiration breakpoints (Sinclair et al. 2017). The experiments discussed in this chapter are currently in the process of being repeated under varying soil moisture conditions. Future work will explore transpirational cooling and stomatal control in water limiting conditions.

3.4.4 Leaf Morphology

Differences in LTD are not the result of differences in leaf angle and accompanying differences in incident radiation. In all treatments of experiments H1 and H2, no significant differences in leaf angle between the heat sensitive and heat tolerant genotypes were found (Table 3.5 and Figure 3.10).

In all three treatments of experiment H1, the heat tolerant genotypes exhibited lower SLA than the heat sensitive genotype. Figure (3.11) shows that in two out of three treatments the difference in mean SLA between the heat tolerant and the heat sensitive varieties was significant at the 95 percent confidence level. The same pattern was observed in experiment D2 for both ambient and drought conditions (Figure 3.12). Evidence for differences in leaf area were more mixed. HT-A had a larger leaf area in ambient conditions, but there was no clear difference in the drought treatment (Figure 3.13).

A lack of clear distinction in leaf area suggests that differences in SLA was the result of thicker leaves. This is partially supported by Figure 3.14, which shows MultispeQ measurements of leaf thickness from experiments H1 and H2. In four out of five treatments, the heat tolerant genotypes had thicker leaves than the heat sensitive genotype on average. However, differences were statistically significant at the 95 percent confidence level in only one out of the five treatments

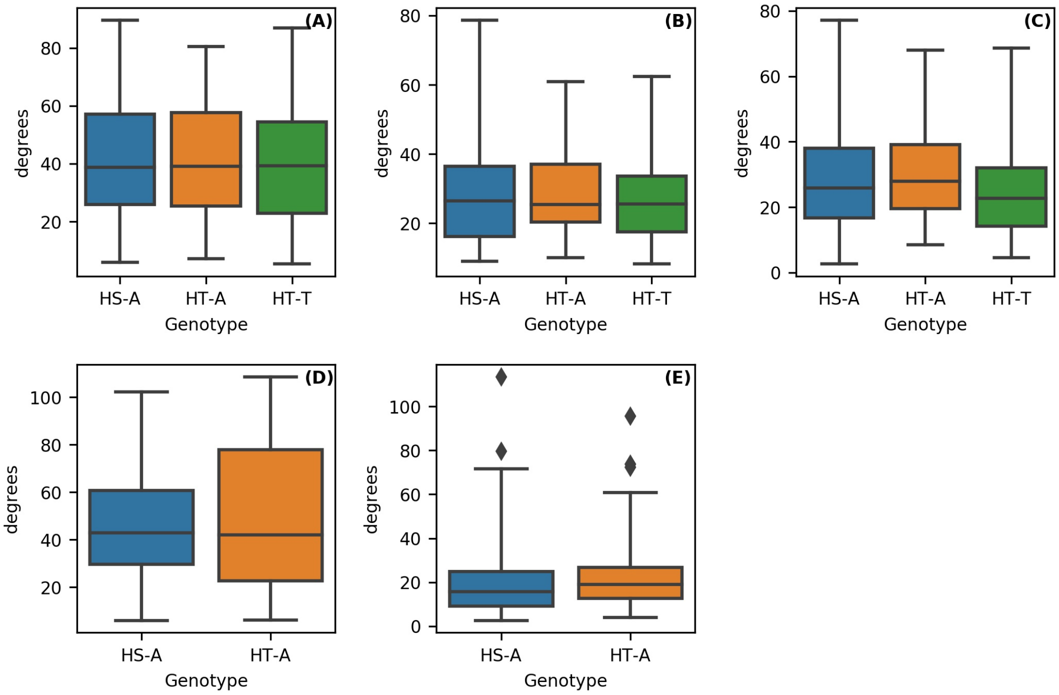

Figure 3.10: The distribution of leaf angle by genotype in experiments H1 and H2 (A) H1-ambient treatment (B) H1-greenhouse treatment (C) H1-greenhouse night heat treatment (D) H2-ambient treatment (E) H2-greenhouse night heat treatment

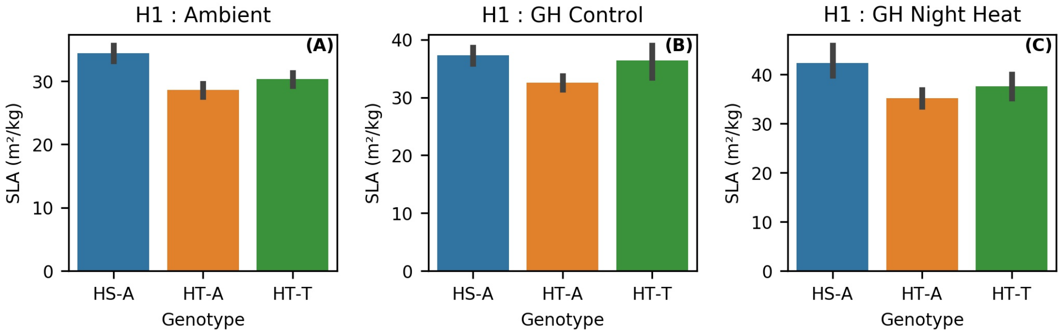

Figure 3.11: Mean Specific Leaf Area by genotype in experiment H1 (A) Ambient Treatment (B) Greenhouse treatment (C) Greenhouse night heat treatment. Error bars represent the 95th confidence interval

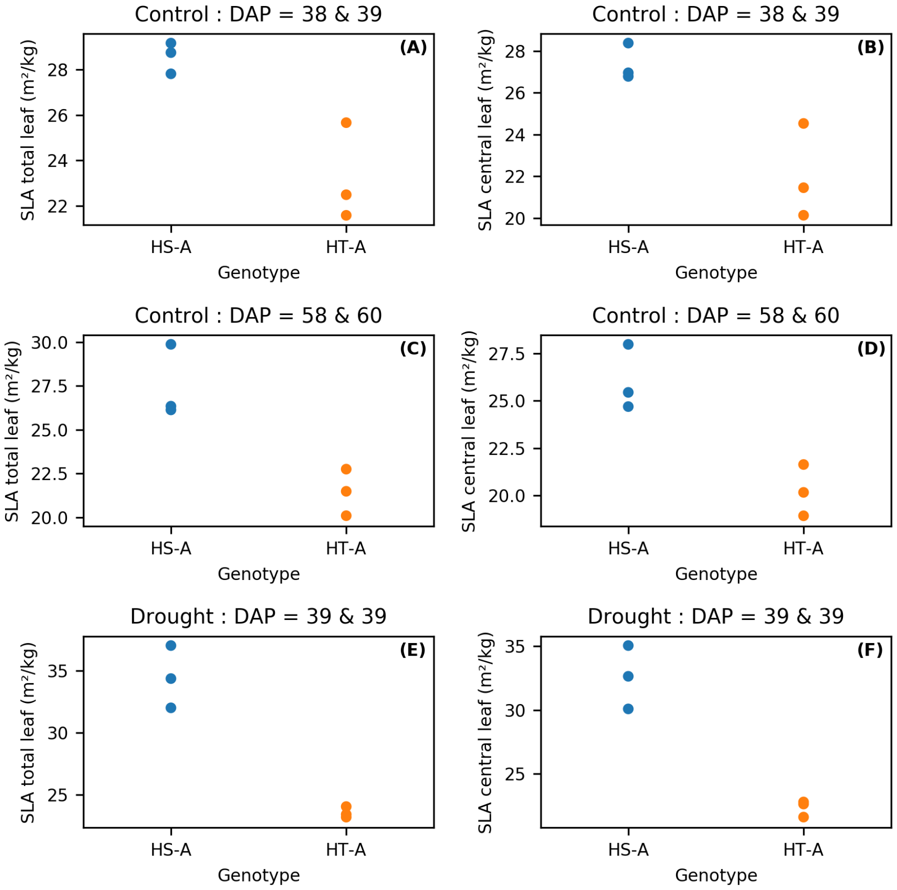

Figure 3.12: Specific Leaf Area by genotype in experiment D2 for the whole trifoliate leaf and the central trifoliate leaf (A), (C) and (E) gives the SLA of the whole trifoliate leaf during snapshots of the control and drought treatments. (B), (D) and (F) gives the SLA of the central trifoliate leaf during snapshots of the control and drought treatments. DAP is short for days after planting. Each dot represents the average of 5 replications

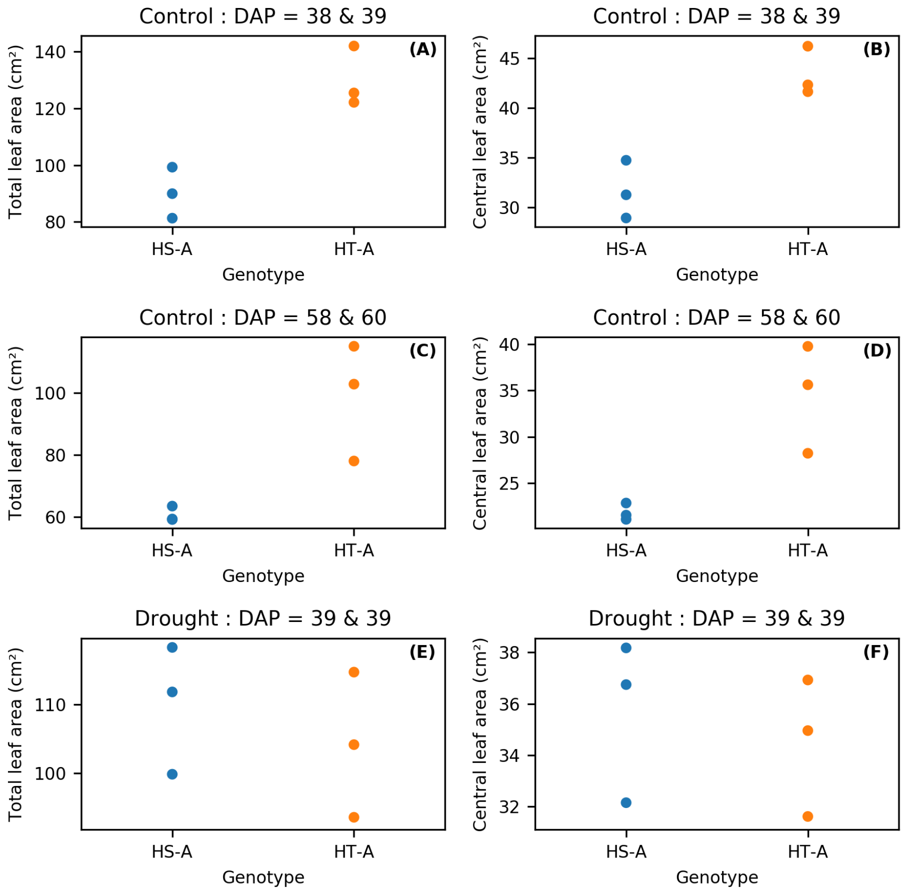

Figure 3.13: Leaf Area by genotype in experiment D2 for the whole trifoliate leaf and the central trifoliate leaf (A), (C) and (E) gives the LA of the whole trifoliate leaf during snapshots of the control and drought treatments. (B), (D) and (F) gives the LA of the central trifoliate leaf during snapshots of the control and drought treatments. DAP is short for days after planting. Each dot represents the average of 5 replications

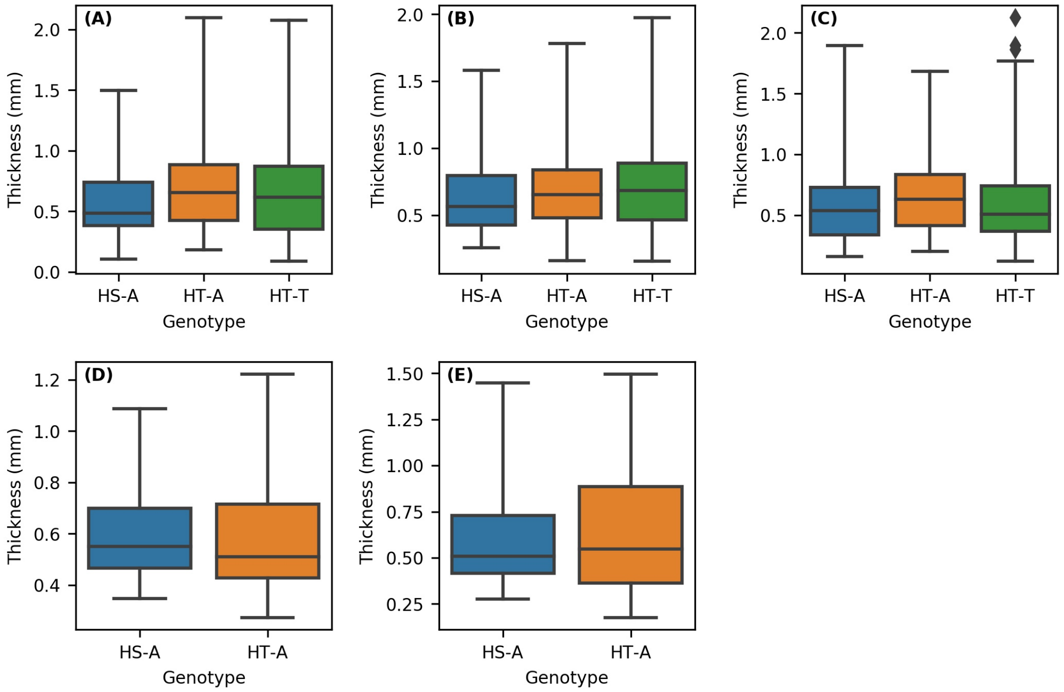

Figure 3.14: Distribution of leaf thickness by genotype in experiments H1 and H2 (A) H1-ambient treatment (B) H1-greenhouse treatment (C) H1-greenhouse night heat treatment (D) H2-ambient treatment (E) H2-greenhouse night heat treatment

(Table 3.6). The sample size was limited in control, drought and high temperature environments. It is therefore not possible to exclude individual adaptive differentiation processes or plastic responses as reasons for differences in thickness between the two genotypes.

Thicker leaves means a greater thermal mass, which increases thermal stability. Increased thickness can therefore reduce the time spent above damaging temperature thresholds, which explains why leaves are often thicker in hot and dry environments (Leigh et al. 2012). Thicker leaves also provide greater storage space for the accumulation of water within the leaves (the succulent effect), which (very likely) increases thermal stability as well. Leigh et al. (2012) found that small increases in thickness in hot desert conditions with low wind speeds can have a large dampening effect on leaf temperatures. They used a leaf temperature model to demonstrate that this effect is particularly important when hot and dry conditions lead to stomatal closure and transpirational cooling is reduced. The results in this chapter suggest that in addition to potential differences in transpirational cooling, the heat tolerant genotypes may have cooled more than the heat sensitive genotype because they had thicker leaves. Differences in leaf thickness were not large enough to prove this, but not weak enough to rule it out. Lower SLA could also be associated with other traits that can increase the thermal resistance of the leaf. For example, leaves with lower SLA may have less permeable leaf cuticles or vary in leaf resistance (glabrous/pubescent leaves may be linked to less/more trichomes and a thin/firm boundary layer).

3.4.5 Modelling Leaf Temperature

Section 3.3.1 showed that leaves are consistently cooler than the air and that this difference is large enough to be an important heat avoidance mechanism. It was also shown that there is a G x E interaction in the processes governing leaf temperature. The importance of modelling leaf temperature for assessing genotype value is therefore clear. Section 3.3.5 showed that it is possible to predict upwards of 85 percent of variation in leaf temperature by genotype in the range of air temperatures covered by these experiments (27-45 °C).

There are a number of simple ways in which breeders can use the model developed in this chapter to assess the value of enhanced leaf cooling as a criterion for selection in a warming climate. Using growing season weather data, breeders can use this model to assess differences in the duration of threshold exceedance between HS-A and HT-A in within sample TPEs. Estimates of threshold exceedence could be focused on micro - and macro-sporogenesis, when the plant is particularly sensitive to high temperatures. Breeders can also use this model to estimate the accumulated impact of differences in leaf cooling over the course of the growing season in within sample TPEs. For example, breeders could use this model in conjunction with growing season weather data to estimate genotypic differences in growing degree days from differences in leaf cooling. Breeders could build similar models for a variety of TPEs to explore the potential benefits of enhanced leaf cooling across bean growing regions.

Breeders could use the methods demonstrated in this chapter to build low input G x E models of leaf temperature in crop growth models. Doing so would allow breeders to assess the emergent impacts of G x E interactions in leaf cooling on complex traits like yield at the system level (Bertin et al. 2010). Theoretically, crop growth models could also be used to study the trade-offs between greater leaf cooling in different TPEs. Integrating genotype specific equations for leaf temperature in crop growth models could help breeders to quantify trade-offs between selecting for enhanced leaf cooling in hot irrigated environments and depletion of available soil water in hot, dry and rainfed environments.

In addition to helping breeders to understand the system-wide implications of genotypic differences in leaf cooling, these results support the argument that simulating the temperature of the leaf/canopy would improve heat stress assessments. An argument that has also been made for other crops (Webber et al. 2016) as well as for land-surface vegetation modelling (Dong et al. 2017). However, the scale of this task should not be underestimated. Crop growth models often use air temperature in growth and phenology functions (Neukam et al. 2016), and these would need to be re-written using leaf/canopy temperatures. Further, in a comprehensive multi-model study testing crop model skill at simulating canopy temperature, Webber et al. (2018) show that the best performing models were able to explain only 30-40 percent of variance in the difference between leaf and air temperatures (Webber et al. 2018).

The success of this endeavour will depend on the availability of sufficient data and further testing of empirical methods across the wide range of environments in which crop models need to perform. The recent uptake of MultispeQ devices with an open source data platform suggests that data availability will be forthcoming. However, findings of a within canopy gradient suggest that future experiments aimed at understanding the impacts of leaf cooling should also consider how temperatures vary within the canopy.

3.4.6 Limitations

Phenotypic differences in leaf cooling during the daytime across three contrasting genotypes were explored. However, beans are also sensitive to high nighttime temperatures. Further research needs to test if heat tolerant genotypes also cool more at night when stomatal conductance is close to zero and overall transpiration is more limited. This will allow the impacts of transpirational cooling to be decoupled from differences in leaf traits and to explore potential differences in the cost of nighttime respiration.

It has been shown that leaf temperature can be accurately and usefully modelled using only temperature and relative humidity in irrigated conditions. However, this does not necessarily imply that the same will be true under varying water-limited scenarios. Ongoing experiments are measuring the same set of environmental variables under varying conditions of water availability. In future work, the results of these ongoing experiments will be used to see if leaf temperature under water limiting conditions can also be simply modelled with high accuracy. A further limitation of the modelling approach used in this chapter is that solar radiation is not included as a variable. This choice was made because solar radiation is often highly correlated with air temperature, so it is not advisable to use both variables in the same model. Temperature was chosen because it is more widely available from weather stations in the TPEs in which breeding work is conducted. The results in this chapter suggest that this formulation works well in environments with very large variation in solar radiation (field vs. greenhouse). However, there are likely to be interaction effects between temperature, relative humidity and solar radiation and new versions of the model may be needed for TPEs with contrasting solar radiation, VPD and soil water availability. This will be explored in future work.

To fully ascertain the importance of variation in leaf cooling between heat tolerant and heat sensitive genotypes, it is necessary to explore the impacts of greater leaf cooling on yield quality and quantity under multiple target population of environments. Tardieu (2011) highlights that traits which confer tolerance in one set of environmental conditions can confer sensitivity under different conditions. For example, genotypes which increase heat avoidance through enhanced cooling, may confer tolerance under hot and irrigated conditions. This same trait could induce sensitivity under hot and dry conditions, through early depletion of available soil water. Future work will need to use models to understand the trade-offs inherent in enhanced leaf cooling in changing target population of environments of the future. This will allow the costs and benefits of breeding for enhanced transpirational cooling to be more realistically assessed.

3.4.7 Summary

This chapter tested the hypothesis that leaf cooling plays an important role in heat avoidance in common bean. This hypothesis was supported by the results, which combined five experiments covering a range of stress and non-stress conditions. Leaf cooling kept tissue temperatures experienced by the plant within a photosynthetically functional range and reduced the number of times thresholds for stress were exceeded.

The second hypothesis tested in this chapter was that heat tolerant genotypes cool their leaves more than heat sensitive genotypes. This hypothesis was supported by the results, which also suggest that this difference increases under hot and dry conditions. Further, the difference in leaf cooling was found to be largest at the top of canopy where determinate bush beans are most sensitive to high temperatures during the flowering period.

The third hypothesis tested in this chapter was that the association between leaf cooling and VPD varies with heat tolerance. It was shown that leaf cooling was more responsive to VPD in the heat tolerant genotypes and that a heat tolerant genotype exhibited higher stomatal conductance. This suggests that the heat tolerant genotype cooled more because of enhanced transpirational cooling. Leaf thickness may also have played a role, but differences in thickness were not large enough to prove this conclusively.

This work suggests that bean breeders can use LTD to screen for beans with enhanced capacity for heat avoidance. Future work will need to test this conclusion with more genotypes and in a wider range of environmental conditions. Heat tolerant common bean genotypes exhibited the same combination of traits as heat tolerant wheat genotypes. At high temperatures, higher stomatal conductance was accompanied by greater transpirational cooling, which suggests a higher rate of photosynthesis.

This chapter showed that it is possible to simulate leaf temperature by genotype accurately. Future work will need to explore the success of the empirical methods used in this chapter with a wide range of genotypes across target population of environments. In particular, it will be important to explore model performance under conditions with contrasting VPD, solar radiation and soil water availability. The results in this chapter suggest that expanding this modelling approach to assess the value of enhanced transpirational cooling across target population of environments has the potential to directly inform bean breeding programs.

3.5 Tables

Data	**Variable**	**Mean**	**Std**	**Min**	**Max**	**Range**
Whole sample	Air temperature	33.6	3.3	26.4	45.0	18.5
Ambient only	Air temperature	34.1	2.8	26.4	41.4	14.9
Whole sample	Relative Humidity	59.2	8.7	32.7	75.8	43.1
Ambient only	Relative Humidity	55.5	7.8	34.4	75.4	41.0

Table 3.1: Summary statistics for MultispeQ samples calculated from the whole sample and ambient observations only.

Variable	**Mean**	**Std**	**Min**	**Max**	**Range**
Air temperature	33.6	3.3	26.4	45.0	18.5
Leaf temperature	28.4	3.1	21.9	42.0	20.1
Leaf temperature depression	-5.2	1.9	-13.0	2.1	15.1

Table 3.2: Summary statistics of MultispeQ observations of air temperature, leaf temperature and leaf temperature depression. Calculated from the whole sample.

Data	**Variable**	**Mean**	**Std**	**Min**	**Max**	**Range**
H1 Ambient	Air temperature	26.6	3.7	17.1	34.7	17.6
H1 GH Control	Air temperature	25.8	3.3	18.4	36.4	18
H1 GH Night Heat	Air temperature	26.3	2.7	19.4	39.9	20.5
H1 Ambient	Relative Humidity	58.1	19.6	19.6	100	80.4
H1 GH Control	Relative Humidity	70.5	13.9	33.3	99.7	66.4
H1 GH Night Heat	Relative Humidity	68.7	13.5	30.3	100	69.7
H1 Ambient	PAR	811.1	624.1	9	2457	2448
H1 GH Control	PAR	449.1	343.3	9	1613	1604
H1 GH Night Heat	PAR	465.0	349.2	9	1610	1601

Table 3.3: Summary statistics for each of the treatments in the H1 experiment. Calculated from daytime observations from an in-situ weather station.

Experiment	**Test**	**Treatment**	**p-value**
H1	Calima vs. SAB 686	Ambient	0.00
H1	Calima vs. SEF 60	Ambient	0.00
H1	Calima vs. SAB 686	Greenhouse control	0.11
H1	Calima vs. SEF 60	Greenhouse control	0.00
H1	Calima vs. SAB 686	Greenhouse night heat	0.10
H1	Calima vs. SEF 60	Greenhouse night heat	0.25
H2	Calima vs. SAB 686	Ambient	0.00
H2	Calima vs. SAB 686	Greenhouse night heat	0.00

Table 3.4: Permutation tests for a comparison of LTD group means between genotypes for each treatment of the H1 and H2 experiments.

Experiment	**Test**	**Treatment**	**p-value**
H1	Calima vs. SAB 686	Ambient	0.980
H1	Calima vs. SEF 60	Ambient	0.576
H1	Calima vs. SAB 686	Greenhouse control	0.608
H1	Calima vs. SEF 60	Greenhouse control	0.431
H1	Calima vs. SAB 686	Greenhouse night heat	0.205
H1	Calima vs. SEF 60	Greenhouse night heat	0.062
H2	Calima vs. SAB 686	Ambient	0.836
H2	Calima vs. SAB 686	Greenhouse night heat	0.398

Table 3.5: Two sided permutation tests for a comparison of leaf angle group means between genotypes for each treatment of the H1 and H2 experiments.

Experiment	**Test**	**Treatment**	**p-value**
H1	Calima vs. SAB 686	Ambient	0.012
H1	Calima vs. SEF 60	Ambient	0.045
H1	Calima vs. SAB 686	Greenhouse control	0.113
H1	Calima vs. SEF 60	Greenhouse control	0.053
H1	Calima vs. SAB 686	Greenhouse night heat	0.081
H1	Calima vs. SEF 60	Greenhouse night heat	0.900
H2	Calima vs. SAB 686	Ambient	0.886
H2	Calima vs. SAB 686	Greenhouse night heat	0.358

Table 3.6: Two sided permutation tests for a comparison of leaf thickness group means between genotypes for each treatment of the H1 and H2 experiments.

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Chapter 4

Modelling the trade-off between saving water and exposure to heat stress

4.1 Introduction

Chapter 3 considered the magnitude of transpirational cooling at the plant scale and explored the relationship between cooling and heat tolerance in common bean. Chapter 4 shifts the scale of analysis to a farmers field and explores the relevance of transpirational cooling to modelling the trade-off between saving water and resilience to heat stress in the Indian Punjab - one of South Asia's most important rice growing regions. This chapter begins by describing why this trade-off is important. It then goes on to highlight the key uncertainties in modelling the trade-off and how they relate to transpirational cooling before summarizing the aims and objectives of the chapter.

4.1.1 The Food-Water Nexus

Under future climate change, the global area of rice exposed to high temperature stress during the flowering period is expected to expand. Using a high temperature stress threshold of 36°C, Gourdji et al (2013) estimate that between the

2000s and the 2050s, this area will increase from 8 to 27 % (Gourdji et al. 2013). Teixeira et al (2011) use a threshold of 35°C to project that by the 2070s more than 120 million hectares of land currently used for growing rice will be exposed to sustained periods of high temperature stress (Teixeira et al. 2013). Simultaneously, increasing scarcity of water resources for irrigation is driving a shift from continuously flooded (CF) fields to water saving technologies. This transition reduces the availability of water in the field for transpirational cooling and increases the probability that the crop will experience combined heat and drought-induced sterility during flowering (Jagadish et al. 2015).

The state of Punjab in NW India is one of the world's major rice growing regions and is experiencing this confluence of rising temperatures and the need to switch to water saving technologies. Following the green revolution, there has been a rapid rise in irrigated rice production in Punjab, which is now responsible for producing 60 percent of the rice that goes into India's central stock, whilst representing only 1.6 percent of the nation's land area (Devineni and Perveen 2014). This has resulted in plummeting water tables (Kaur et al. 2011). In 2012, 80 percent of blocks (administrative units for water) were found to be over-exploited (CGWB 2012). As a result, some farmers have already shifted production to alternate wetting and drying (AWD) irrigation methods (Subash et al. 2015).

The interplay between exposure to high temperatures and the need to reduce the amount of water in the field is likely to strengthen in the future. The most recent IPCC Working Group I report projects an increase in mean temperatures across South Asia (high confidence) and an increase in the number of extremely hot days and nights (IPCC 2013). Northern India is singled out as a hotspot likely to experience mean temperature changes above the regional average. It is therefore crucial to be able to accurately model the combined impact of rising temperatures and less water intensive methods of paddy farming on yield.

4.1.2 Uncertainties in modelling the interaction between high temperature stress and irrigation

Understanding the trade-off between saving water and resilience to high temperature requires quantification of the most important uncertainties in modelling the interactions between high temperature stress and limited water availability. A recent inter-comparison of rice models finds a large spread in the simulation of both historical variability and future yield projections at the Ludhiana field site in Punjab (Li et al. 2015). It was hypothesised that this spread was related to whether or not they simulated heat-induced spikelet sterility. Li et al. (2015) also suggested that threshold effects play an important role in the spread of yield projections, since present day temperatures at Ludhiana are closer to high temperature stress thresholds than at the other sites in the inter-comparison.

Although growth of the rice plant can be damaged by high temperatures during any part of the season, a review of heat stress in cereals notes that yield sensitivity is greatest during the reproductive phase of the growth cycle (Rezaei et al. 2015; Hedhly 2011; Prasad et al. 2017). High temperature stress is found to reduce grain weight and pollen germination through a combination of increased panicle abortion, lower density of spikelets and a larger share of infertile spikelets.

A key uncertainty in modelling the impact of high temperature stress on rice, is determining the temperatures that induce spikelet sterility. A common approach is to use the threshold at which spikelet sterility has been observed in rice in experiments conducted under controlled conditions. This threshold has been identified as 35 °C (Yoshida et al. 1981). A weakness of this approach is that considerable differences exist between tolerant and susceptible varieties (Matsui and Omasa 2002). For example, in a lowland variety (IR64) and an upland variety (Azucena), exposure to temperatures greater than or equal to 33.7 °C engendered spikelet sterility under durations of less than or equal to one hour (Jagadish et al. 2007). Spikelet sterility thresholds of between 32 °C and 36 °C have been witnessed in growth chamber experiments (Ishimaru et al. 2016).

Another potential approach would be to use the air temperature observed to result in spikelet sterility under field conditions. However, the temperature at which spikelet sterility occurs under field conditions is not well constrained. There is no clear consensus on the temperature at which rice experiences spikelet sterility under field conditions, and as is the case under controlled conditions, temperature thresholds have been found to vary amongst different cultivars (Prasad et al. 2006). A large multi-variety field trial conducted in India found that temperatures above 33 °C resulted in significant increases in spikelet sterility (Bheemanahalli et al. 2016). A literature review combining field, laboratory and experimental greenhouse studies across sub-species and varieties of rice found that 37 °C is the mean critical threshold for spikelet sterility during anthesis (Sánchez et al. 2014).

One of the main reasons for differing heat sterility thresholds in controlled and field experiments is the variation between panicle and air temperatures under field conditions. In conditions where relative humidity is low and vapour pressure deficit is high, the rate of evapotranspiration is increased at high temperatures, thereby enhancing cooling. When relative humidity is high and vapour pressure deficit low, the rate of evapotranspiration is lowered, thereby reducing cooling (Van Oort et al. 2014). In a chamber-based experiment, Weerakoon et al. (2008) showed that spikelet fertility is dependent on relative humidity, as this determines the degree of transpirational cooling and subsequently the panicle temperature experienced by the spikelet (Weerakoon et al. 2008). Julia and Dingkuhn (2013) found the same to be true under a variety of field conditions. Air temperatures at the hottest site in this study exceeded 40 °C, yet all varieties were able to avoid heat-induced sterility through early flowering and transpirational cooling (Julia and Dingkuhn 2013).

The range of the difference between air and panicle temperatures varies in different environments. In the Julia and Dingkuhn (2013) study of four contrasting environments, panicle temperature was found to be between 9.5°C cooler and 2°C warmer than air temperature. In a study in the Japanese Kanto region, this range was found to be between 2°C cooler and 3°C warmer (Yoshimoto et al. 2011). In irrigated rice grown in the Jianghan basin in China, warm and humid conditions with low windspeeds led to panicle temperatures exceeding air temperatures by 4 °C (Tian et al. 2010).

This chapter examines the impact of uncertainties in the spikelet sterility threshold and the difference between panicle and air temperatures in the context of modelling the trade-off between saving water and exposure to heat stress in Punjab. The impact of uncertainty in the spikelet sterility threshold is tested by performing crop modelling simulations over the historical period in Ludhiana Punjab whilst using a panicle temperature model to vary the spikelet sterility threshold to account for transpirational cooling during flowering. Differences in spikelet sterility and yield from the inclusion of transpirational cooling in the model set-up are assessed.

4.1.3 Aim and Objectives

The aim of this chapter is to understand the implications of uncertainty in modelling spikelet sterility and the implications for attempts to model the trade-off between saving water and exposure to heat stress. This can be split into three objectives with corresponding hypothesis tests. The first objective is to assess the extent to which modelled spikelet sterility is sensitive to including transpirational cooling in the heat stress routine. The second objective is to assess the extent to which modelled yield is sensitive to including transpirational cooling in the heat stress routine. The third objective is to assess whether modelled spikelet sterility and yield differ between potential and AWD conditions, and whether this is influenced by including transpirational cooling.

4.1.3.1 Hypothesis test for objective 1

H_o: Simulated spikelet sterility is the same when using the physiological spikelet sterility threshold and when including transpirational cooling.

H_a: Simulated spikelet sterility is not the same when using the physiological spikelet sterility threshold and when including transpirational cooling.

4.1.3.2 Hypothesis test for objective 2

H_o: Simulated yield is the same when using the physiological spikelet sterility threshold and when including transpirational cooling.

H_a: Simulated yield is not the same when using the physiological spikelet sterility threshold and when including transpirational cooling.

4.1.3.3 Hypothesis test for objective 3

H_o: Modelled spikelet sterility is the same for both potential and AWD conditions.

H_a: Modelled spikelet sterility is not the same for both potential and AWD conditions.

4.2 Materials and Methods

4.2.1 Study Site

The field experiments used in this paper tested the impact of different irrigation regimes on the rice variety PAU201. They were conducted at the Punjab Agricultural University in Ludhiana (30°54 N, 75°98 E) at 247 m above sea level. Figure 4.1 provides a climatology for the rice growing season in Ludhiana (June-November). The highest maximum temperatures occur during the vegetative period. On average, maximum temperatures are very close to the maximum temperature for panicle initiation (31.4-34.8 °C) during the reproductive period and several degrees below the threshold for spikelet sterility during the reproductive period (35.8-38.2 °C) (Sánchez et al. 2014). Minimum temperatures do not closely follow maximum temperatures and remain high for the vegetative period and majority of the reproductive period, before declining sharply during the ripening period. Climatologically, there is adequate rainfall for most of the growing season. Rainfall is lowest during the very early stages of the vegetative period

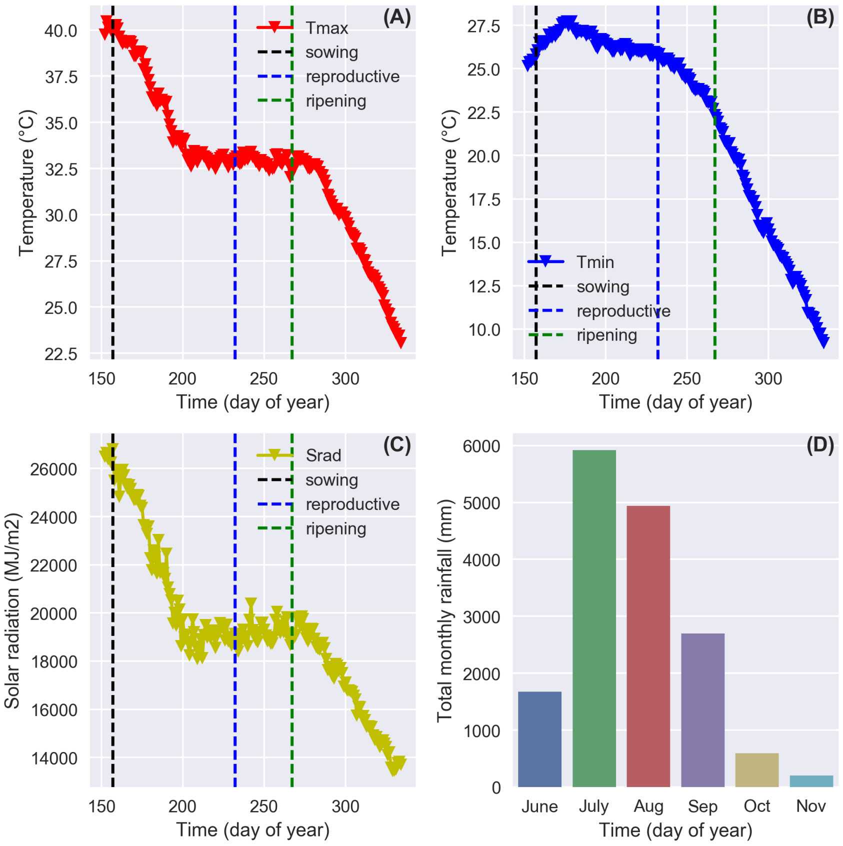

Figure 4.1: Daily climatology for the study site a) Mean daily Tmax b) Mean daily Tmin c) Mean daily Solar Radiation d) Mean monthly Precipitation using ERA-interim data 1980-2010 (Dee et al. 2011)

and for parts of the ripening period. There is a large range in solar radiation over the course of the growing season. Solar radiation declines strongly during the vegetative period before recovering slightly for parts of the reproductive period and falling sharply again throughout the ripening period (Figure 4.1).

4.2.2 Field Experiment Data

The field experiments on clay loam soil with varying irrigation treatments were used to parameterize the ORYZA V3 rice model. The site was laser levelled before establishment of the experiment and the fields were puddled before transplanting. The medium duration variety PAU-201 rice crop was transplanted on the 5th and

Treatment	**Name**	**Irrigation frequency**	**Irrigation amount**
Continuously flooded	CF	daily	50 mm
Alternate wetting and drying	AWD	soil water tension 20 kPa	50 mm

Table 4.1: Summary of Treatments

6th of July in the years 2008 and 2009 in rows that were 20 cm apart with plants spaced 15 cm apart.

The experiments consisted of four treatments. One treatment was continuously flooded while the other three experiments were conducted under alternate wetting and drying irrigation with minimum soil water tension of 20, 40 and 70 kPa respectively at 20 cm. When the minimum soil tension was reached, the AWD treatments were topped up to a standing water depth of 50 mm. Soil water tension was measured using tube tensiometers with a ceramic cup depth of 18-20 cm between 8 am and 9 am each morning to determine irrigation requirements that day.

Regionally recommended nitrogen application and practices for controlling pests and diseases were applied to all 4 fields. A comprehensive description of these experiments can be found in (Sudhir et al. 2011a) and (Sudhir et al. 2011b). In this chapter, only the fully flooded experiment and the AWD treatment with minimum soil water tension at 20 kPa was used. This is because the other AWD experiments fall well below the safe threshold for AWD (Humphreys et al. 2010) and are therefore not realistic adaptation choices for farmers in the region. The two treatments simulated are summarised in Table 4.1 and will be referred to using their acronyms (CF and AWD) for the rest of this chapter.

4.2.3 Weather Data

Weather data for running the historical simulations was taken from the AgMERRA data set (Ruane et al. 2015). AgMERRA is a global meteorological data set, combining station data, satellite observations and re-analysis from models to provide a suite of meteorological variables designed for use in crop modelling (Ruane et al. 2015). The AgMERRA data set covers the period 1980-2010 at a 0.25 by 0.25 degree resolution. In this study, the grid cell containing Punjab Agricultural University was extracted and used to run ORYZA over the years 1980-2010. AgMERRA is used widely in the Agricultural Model Intercomparison and Improvement Project and is freely available from Ruane et al. (2018). AgMERRA is chosen for this study because it enhances the replicability of the study, performs better than previous products used for agricultural modelling (Ruane et al. 2015) and facilitates comparison with other studies. CO_2 data was taken from the Mauna Loa observatory (Tans and Keeling 2019).

4.2.4 Model description and selection

The ORYZA V3 rice model is used for the simulations in this chapter. A detailed summary of the ORYZA V3 model and the way in which heat and drought stress are simulated can be found in the methods chapter of this thesis (sections 2.3.1.4 and 2.3.1.3). The rationale for choosing ORYZA V3 is also described at length in the methods chapter of this thesis (section 2.1).

4.2.5 Calibration process

Calibration in ORYZA is a multi-tiered process. Standard genetic parameters for a common rice variety (IR64) were adjusted to reflect the variety simulated using field observations of plant development over the growing season. In this case, the variety PAU201 was parameterized using observations from the 2008 growing season. The 2008 growing season was chosen because the distribution of rainfall in the 2009 growing season was uneven, and plants experienced above average solar radiation. In the first stage of calibration, the development rate parameters were calibrated from observed air temperatures and phenology data for each of the four development stages. The DRATES program, which is provided online with the ORYZA v3 software (IRRI 2020) was used for this part of the calibration process.

In the second calibration stage, assimilate partitioning factors were calibrated for each development stage. Further, parameters constraining leaf area growth, specific leaf area and the rate of senescence were also included in this stage of calibration. Finally, the relative transpiration ratio was calibrated in order to model variety specific drought tolerance. ORYZA's auto-calibration program was then used to select values for these parameters that minimise the Root Mean Squared Error between observed and simulated values of: weight of the storage organs, weight of above ground biomass, weight of green leaves, weight of stems and leaf area index.

During the auto calibration procedure, the calibrated parameters are constrained to vary within a physiologically consistent range. The Autocalibration 3 program was used for this process and is also freely available online (IRRI 2020). A full list describing the parameters calibrated, their acronyms within the model, a description of what they do and the range defining their constraints are included in table 4.2. This ensures that the calibration procedure is fully replicable.

4.2.6 Methodological Choices

A number of modelling choices were made in setting up these simulations. These include user choices on how to model specific processes. In this subsection choices made in model set-up are outlined. The Penman-Monteith model was selected for estimating ET over the other options provided by ORYZA. This decision was made in response to the recent guidelines issued by the Food and Agriculture Organisation (FAO) (FAO 2020). In these guideline, the Penman-Monteith model is offered as the sole recommended method for simulating ET. There are a number of different ways in which different irrigation schedules can be represented in the model set-up. Continuously flooded irrigated was represented by running the model under potential conditions. Irrigation in the AWD treatment was represented using the soil water tension routine. Irrigation was therefore set to be topped up whenever the simulated soil tension dropped below 20 kPa. The nutrient fixed supply method was selected for nitrogen uptake from the soil. This choice was made because the soil nutrient module exhibited high sensitivity to initial conditions and some of the parameters required for setting initial conditions

Parameter	**Description**	**Range**
DVRJ	Rate of development during the juvenile stage (Bouman 2001)	NA
DVRI	Rate of development during the photoperiod-sensitive stage (Bouman 2001)	NA
DVRP	Rate of development during the panicle development stage (Bouman 2001)	NA
DVRR	Rate of development during the reproductive stage (Bouman 2001)	NA
RGRLMX	Upper limit of the relative growth rate of leaf area (Bouman 2001)	0.25
RGRLMN	Lower limit of the relative growth rate of leaf area (Bouman 2001)	0.25
FNTRT	The Fraction of Nitrogen translocated from the stems and leaves to the storage organs (Bouman 2001)	0.25
FSTR	The Fraction of carbohydrates partitioned to the stems and stored as reserves (Bouman 2001)	0.25
FSHTB	The Fraction of total dry matter partitioned to the shoot by development stage (Bouman 2001)	0.25
FSOTB	The Fraction of total dry matter partitioned to the storage organs by development stage (Bouman 2001)	0.25
FLVTB	The Fraction of total dry matter partitioned to the leaves by development stage (Bouman 2001)	0.25
FSTTB	The Fraction of shoot dry matter partitioned to the stem by development stage (Bouman 2001)	0.25
DRLVT	The leaf death coefficient by development stage (Bouman 2001)	0.25
SLATB	Specific leaf area by development stage (Bouman 2001)	0.25
KDFTB	The extinction coefficient by development stage (Bouman 2001)	0.25
SWIRTRF	The Relative transpiration ratio (Bouman 2001)	0.25

Table 4.2: Calibrated Parameters and the range used in the autocalibration procedure

were not directly available from the experimental data.

4.2.7 Modelling the impacts of evaporative cooling

Transpirational cooling is simulated in the experiments in this chapter by changing the sterility threshold. This is an approach, which has been taken by Gabaldón-Leal et al. (2016) and Barlow et al. (2015). These approaches are built upon by dynamically altering the sterility threshold each year by adding the sum of the mean daily difference between maximum air temperature and calculated panicle temperature during the flowering period to the physiological heat sterility threshold derived from controlled experiments. This approach is summarized in equation 4.1 below.

$$T_{evapcooling} = 35 + (\sum_{dvs=0.96}^{dvs=1.2} Tmax(t)_i - Tpan(t)_i/t) \tag{4.1}$$

where, the term $Tpan$ refers to the calculated panicle temperature and $Tpan$ is derived following Van Oort (2014) (Van Oort et al. 2014).

$$T_{pan}(t) = b_1 T_{air}(t) + b_2 RH(t) \tag{4.2}$$

where b1 = 0.78, b2 = 0.073 and RH refers to relative humidity. In the Van Oort study, calculated panicle temperature was found to be a good predictor of observed panicle temperature over a range of environments (Van Oort et al. 2014).

4.2.8 Simulations

Two sets of simulations were performed to test the impact of uncertainty in the spikelet sterility threshold on yield over the historical period. The first set of simulations (R1) modelled crop growth with the spikelet sterility threshold set

Run Set	Threshold	Description	Time period
R1	35 °C	Physiological threshold	1980-2010
R2	R1 + Tcooling	Physiological threshold + Tcooling	1980-2010

Table 4.3: Simulations Performed, Tcooling = transpirational cooling

at 35 °C, the physiological threshold derived from experiments in controlled conditions. The second set of simulations modelled crop growth with the spikelet sterility threshold set to the sum of the physiological threshold and panicle cooling.

4.3 Results

4.3.1 Calibration results

Comparison of observed and simulated values for the 2008 CF experiment (Figure 4.2) show that the weight of above ground biomass and the weight of storage organs were slightly overestimated (13.8 and 11.4 percent respectively). Grain yield was overestimated by 29 percent and season length was accurately simulated (1 day different)

Comparison of the evolution of growth through the season (Figure 4.3) shows that the weight of above ground biomass was accurately simulated throughout the season (mean percentage difference = 13.1) and slightly overestimated at the end (percentage difference = 13.8). The shape of the distribution was well simulated over the course of the season. Similarly, the weight of stems was accurately simulated for the majority of the season (mean percentage difference = 11.4) and slightly overestimated towards the end of the season (mean percentage difference of the last 3 points = 13.6). The shape of the distribution was well simulated over the course of the season. The weight of green leaves and the leaf area index were reasonably simulated throughout the season (mean percentage differences of 20.1 and 19.7 respectively), with similar distributions and peaks. Both appear to peak late (though the peaks cannot be known exactly from these observations, since the observed data does not necessarily capture the peak). This suggesting that the model did not simulate the timing of leaf senescence perfectly.

Comparison of observed and simulated values for the 2008 AWD experiment (Figure 4.2) shows that the weight of above ground biomass and the weight of storage organs was reasonably overestimated (22.4 and 16.3 percent respectively). Grain yield was also slightly overestimated (14.6 percent). Season length was accurately simulated (1 day different).

Model performance of the evolution of growth in the AWD treatment of the 2008 growing season (Figure 4.4) was similar to the CF case. Above ground biomass was accurately simulated throughout the growing season (mean percentage difference = 16.2) and overestimated at the end of the season (percentage difference = 22.4). Weight of stems follows a similar pattern (mean percentage difference = 23) and the mean percentage difference of the last three points was 22.9. For both the weight of above ground biomass and the weight of stems, the shape of the distribution was well simulated. As was the case for the CF experiment, the weight of green leaves was reasonably simulated (mean percentage difference = 23.9) and the distribution and peak of the weight of green leaves was well simulated. In this case, modelled senescence began on time. The evolution of Leaf Area Index (LAI) was reasonably simulated (mean percentage difference = 27.6) and the shape of the distribution was reasonably simulated, the peak appears to be slightly overestimated and model simulation of the decline in LAI was late.

Comparison of observed and simulated values for the 2009 CF experiment (Figure 4.5) shows that weight of above ground biomass, the weight of storage organs and grain yield were all accurately simulated (differences of 0.5,1.6 and 4 percent respectively). Season length was reasonably simulated (4 days difference).

Comparison of simulated and observed evolution of growth throughout the season (Figure 4.6) shows that the evolution of above ground biomass was reasonably simulated (mean percentage difference = 31.0) and the shape of the distribution was well simulated. The evolution of the weight of green leaves was underestimated at times and over-estimated at times (mean percentage difference = 51.9) though the shape of the distribution was reasonably simulated. The timing of leaf

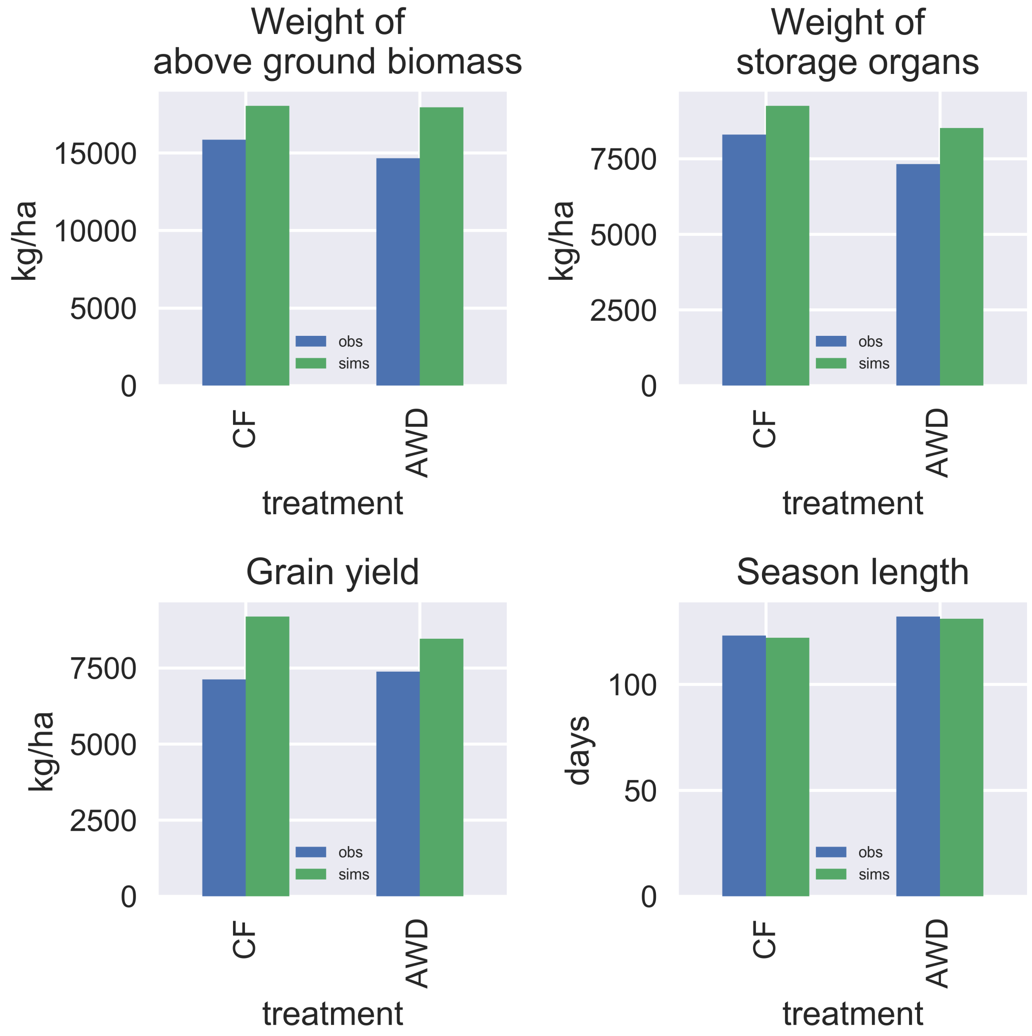

Figure 4.2: Observed vs. simulated end of season variables for the 2008 growing season. CF = continuous flooding treatment and AWD = alternate wetting and drying treatment (obs = observed values, sims = simulated values)

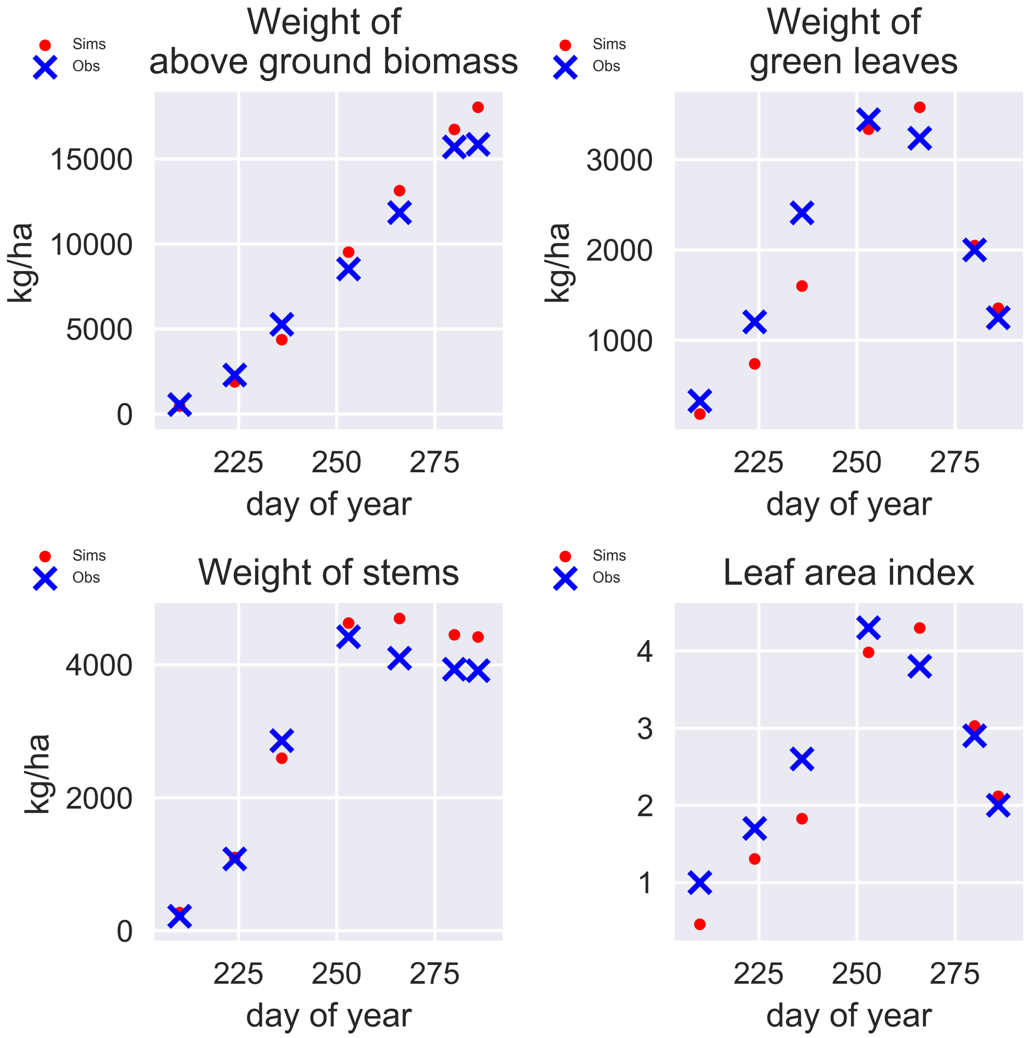

Figure 4.3: Observed vs. simulated values throughout the 2008 season for the continuously flooded (CF) treatment (obs = observed values, sims = simulated values).

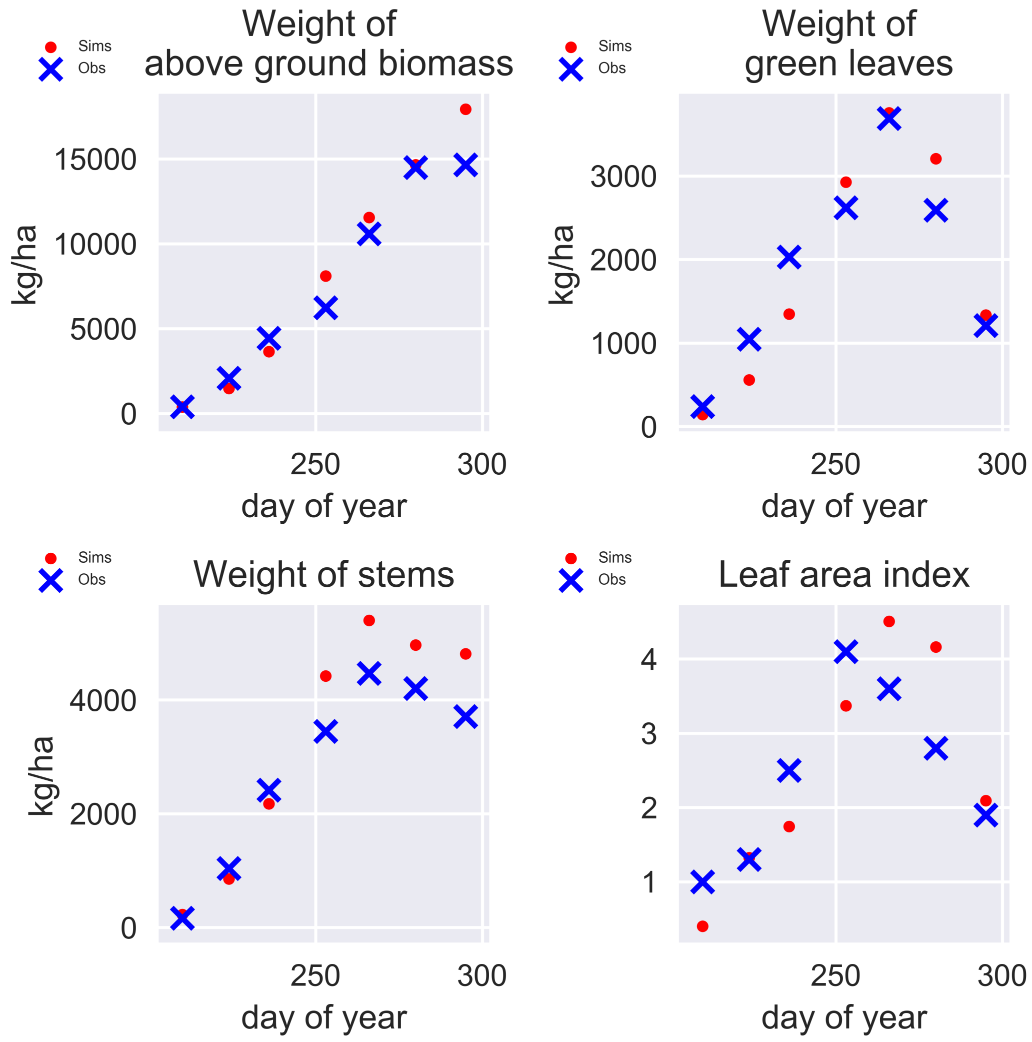

Figure 4.4: Observed vs. simulated values throughout the 2008 season for the alternate wetting and drying (AWD) treatment (obs = observed values, sims = simulated values).

senescence appears to be slightly late. The evolution of the weight of stems was reasonably simulated (mean percentage difference = 22.0) and the shape of the distribution of the weight of stems was reasonably simulated. The timing of the peak appears well simulated but the peak of stem weight appears to be underestimated. The leaf area index was underestimated (mean percentage difference = 56.1) and peaked late.

Comparison of observed and simulated values for the 2009 AWD experiment (Figure 4.5) show that weight of above ground biomass, weight of storage organs and grain yield were accurately simulated (4.5, 2.5 and 11.9 percent respectively). Season length is reasonably simulated (5 days difference). The simulated growing season length was less well simulated than for CF conditions (6 days difference).

Comparison of simulated and observed evolution of growth throughout the season (Figure 4.7) shows that the distribution of the weight of above ground biomass was reasonably simulated (mean percentage difference = 30.7), though the rate of increase was underestimated in the middle of the season. The shape of the distribution was well simulated. The evolution of the weight of green leaves exhibited larger differences between simulations and observations (mean percentage difference = 43.5). The shape of the distribution of the weight of green leaves was reasonably simulated, though the the weight of green leaves peaked late. The weight of stems was reasonably simulated (mean percentage difference = 23.3) but appeared to peak late. Although the peak of the leaf area index was well simulated, LAI clearly peaked late and the mean percentage difference was 46.9. This suggests that senescence did not begin quickly enough in the model.

Over both the calibrated and evaluated year for both potential and AWD conditions, end of season biomass, weight of storage organs and season length were simulated reasonably accurately. Both the evolution of biomass and the weight of stems were reasonably simulated across experiments, while the weight of green leaves and the leaf area index developed late.

The aim of this chapter is to assess the sensitivity of modelled sterility and yield to the inclusion of transpirational cooling. This requires reasonable end of season biomass and weight of storage organs and reasonable simulation of phenology.

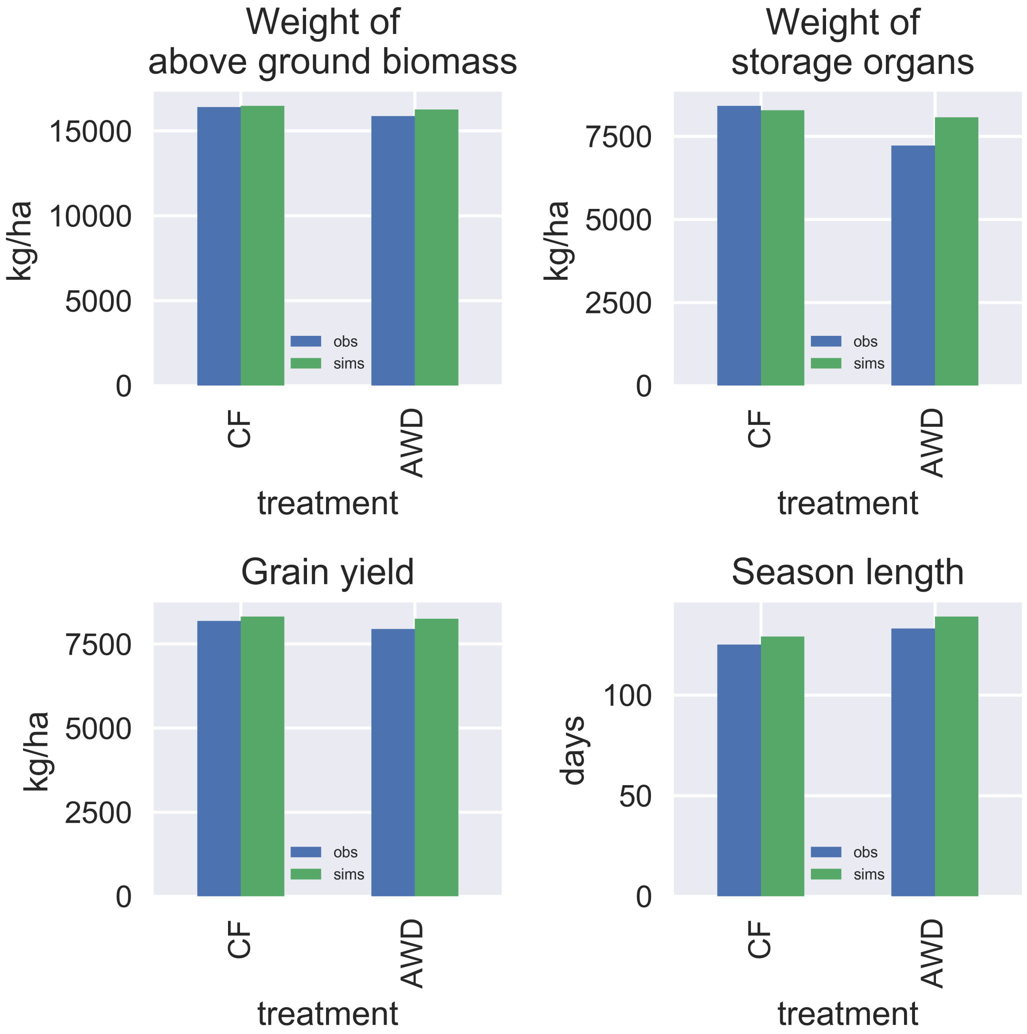

Figure 4.5: Observed vs. simulated end of season variables for the 2009 growing season. CF = continuously flooded treatment, AWD = alternate wetting and drying treatment (obs = observed values, sims = simulated values).

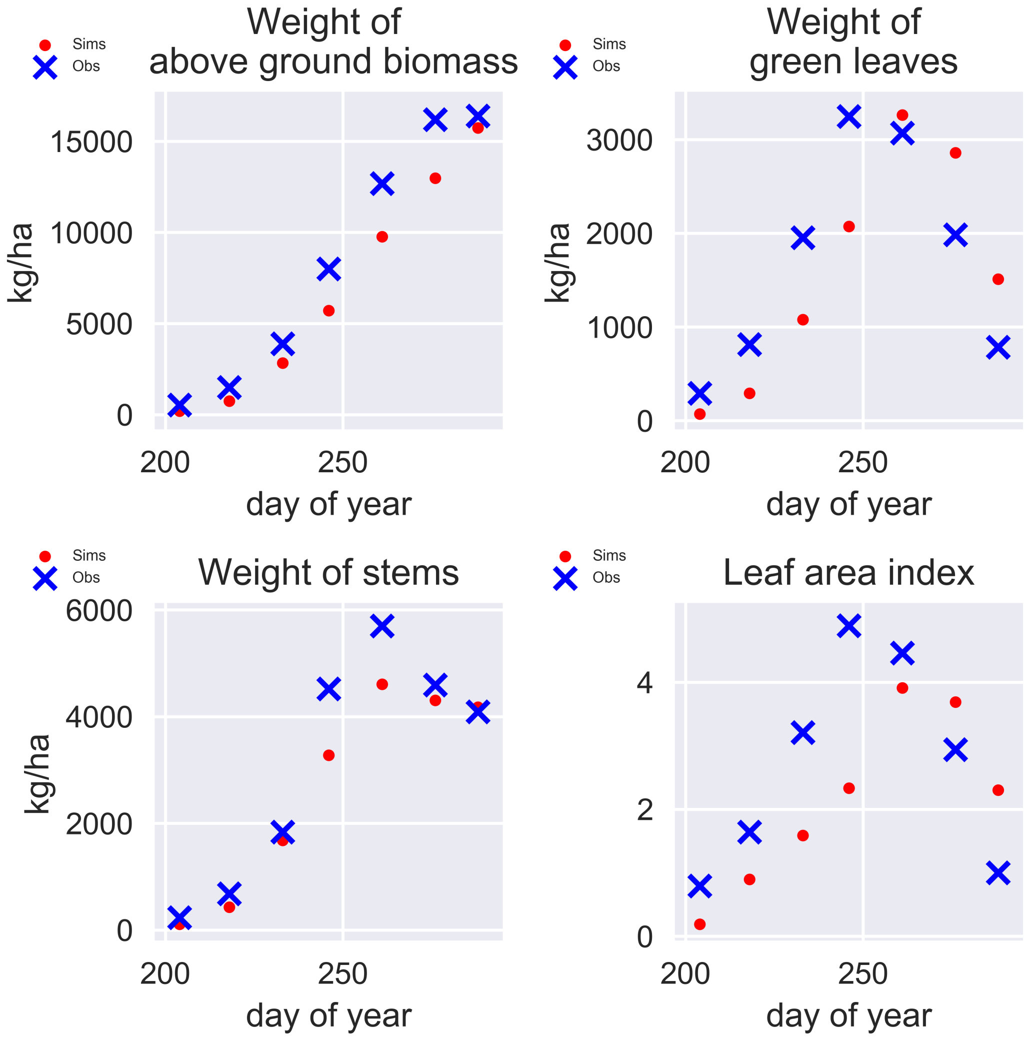

Figure 4.6: Observed vs. simulated values throughout the 2009 season for the continuously flooded (CF) treatment (obs = observed values, sims = simulated values).

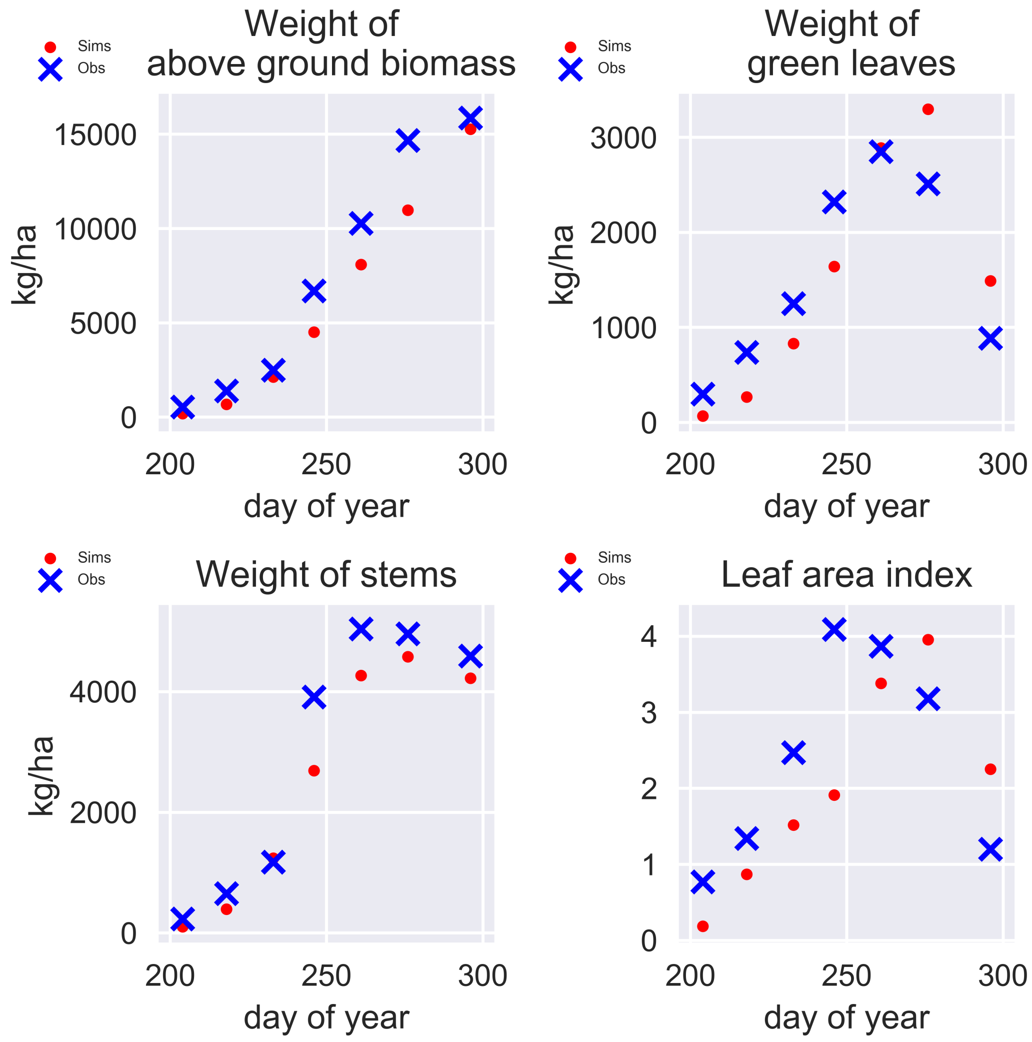

Figure 4.7: Observed vs. simulated values throughout the 2009 season for the alternate wetting and drying (AWD) treatment (obs = observed values, sims = simulated values).

The model meets these requirements over the two seasons for which data were available. Reasonable simulation of the weight of stems suggests that biomass partitioning between root and stem does not change radically between potential and AWD conditions. Plants received lower than average solar radiation in the 2008 growing season and greater than average solar radiation in the 2009 growing season. Overestimation in the 2008 growing season and underestimation in the 2009 growing season therefore suggests that model calibration is weighted towards average conditions.

4.3.2 Simulated spikelet sterility is sensitive to the inclusion of transpirational cooling

In both the CF and AWD runs, there was very little spikelet sterility in any of the 30 growing seasons simulated when transpirational cooling was included (Figure 4.8 panels a and c). A high value of the spikelet sterility factor indicates low spikelet sterility (see equations 2.2 and 2.4). When the physiological threshold for spikelet sterility was employed, inter-annual variability in spikelet sterility was high and spikelet sterility was very high in many of the years simulated (Figure 4.8 panels a and c).

4.3.3 Simulated yield is sensitive to the inclusion of transpirational cooling

Spikelet sterility explained just under a fifth of yield in the CF runs with transpirational cooling switched on (Figure 4.8 panel b). Since the model was set to potential water conditions with adequate amounts of fertilizer, yields remained high in the majority of years. Even though spikelet sterility was low, it was still significantly correlated with yield ($r = 0.42$, $p= 0.02$). This suggests that even very small amounts of spikelet sterility can contribute to yield variability.

Spikelet sterility explained just under 80 percent of variability in yield in the CF runs when the physiological threshold was used and transpirational cooling was switched off (Figure 4.8 panel b). Spikelet sterility and corresponding yield shocks occurred in many growing seasons. Spikelet sterility was highly correlated with yield (r=0.89, p = 0.00). This suggests that when the physiological threshold for spikelet sterility was used, sterility was the dominant source of variability in yield.

Spikelet sterility was not significantly correlated with yield in the AWD runs (r = 0.08, p =0.66) when transpirational cooling was switched on. This suggests that when AWD conditions are simulated and transpirational cooling is included in the model, spikelet sterility is not a meaningful determinant of yield (Figure 4.8 panel d). In this set of runs, transpirational cooling resulted in very few seasons in which the rice crop experienced spikelet sterility.

Spikelet sterility explained just over three quarters of the variability in the AWD runs when the physiological thresholds was used (Figure 4.8 panel d). This suggests that when the physiological threshold is used, spikelet sterility is the dominant source of variability in yield. As was the case for the CF runs, the rice crop experienced spikelet sterility in a large number of seasons. There was a clear impact on grain yield in majority of simulated years. Spikelet sterility was highly correlated with yield (r = 0.87, p = 0.00).

4.3.4 There are small differences in simulated spikelet sterility by treatment

Spikelet sterility was slightly larger in the AWD simulations and more variable in the CF simulations when the physiological threshold was used (Figure 4.9 panels a and c). When the physiological threshold was used, spikelet sterility in the CF and AWD simulations were significantly correlated (r = 0.36, p = 0.05). When the transpirational cooling threshold was applied, there was very little difference between the distribution of spikelet sterility in the CF and AWD simulations (Figure 4.9 panels b and d). Spikelet sterility in the CF and AWD runs were not correlated (r = 0.04, p = 0.85) when the transpirational cooling threshold was applied.

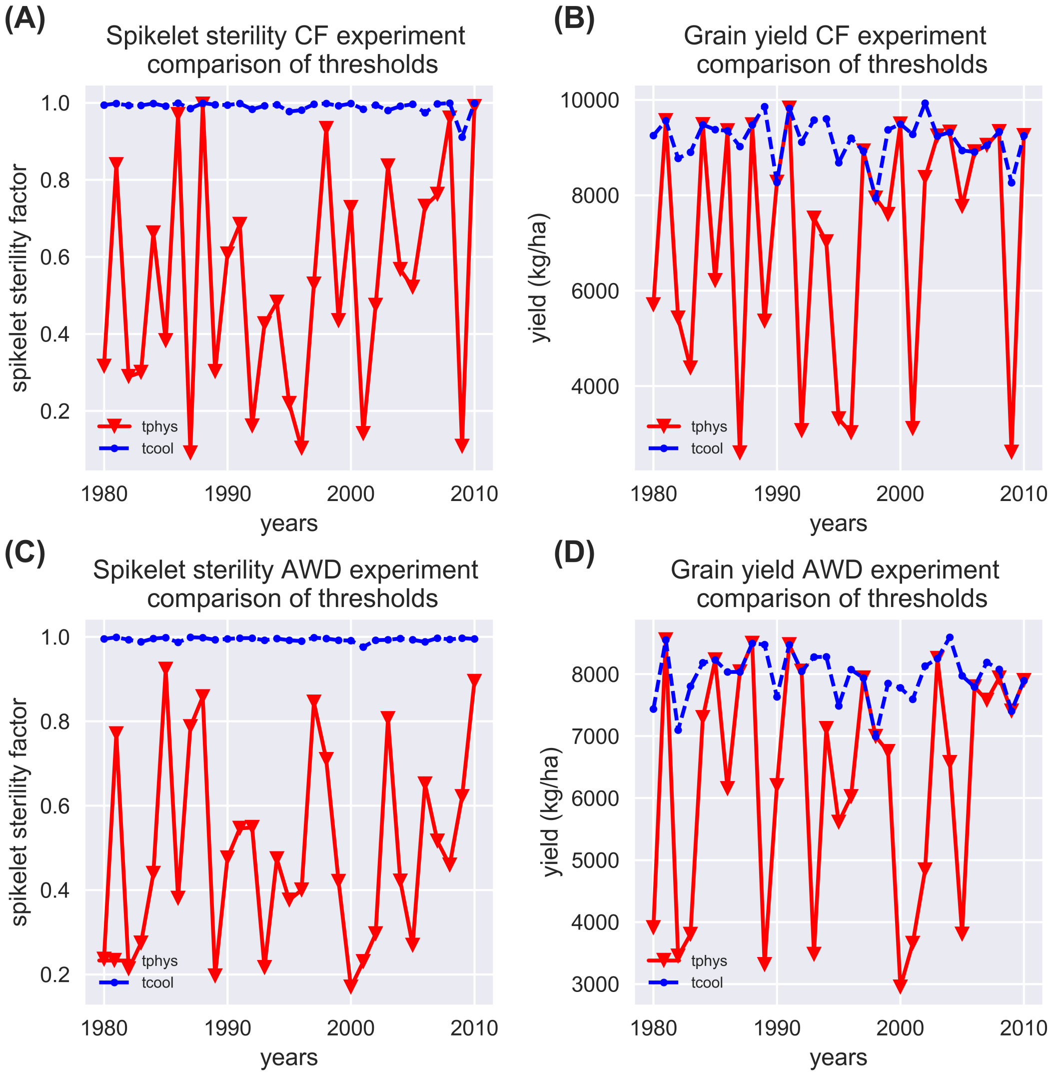

Figure 4.8: A comparison of modelled spikelet sterility and yield over the period 1980-2010 using the physiological threshold and including transpirational cooling. CF = continuously flooded treatment and AWD = alternate wetting and drying treatment (tphys = physiological threshold, tcool = transpirational cooling based threshold). A high value of the spikelet sterility factor indicates low spikelet sterility

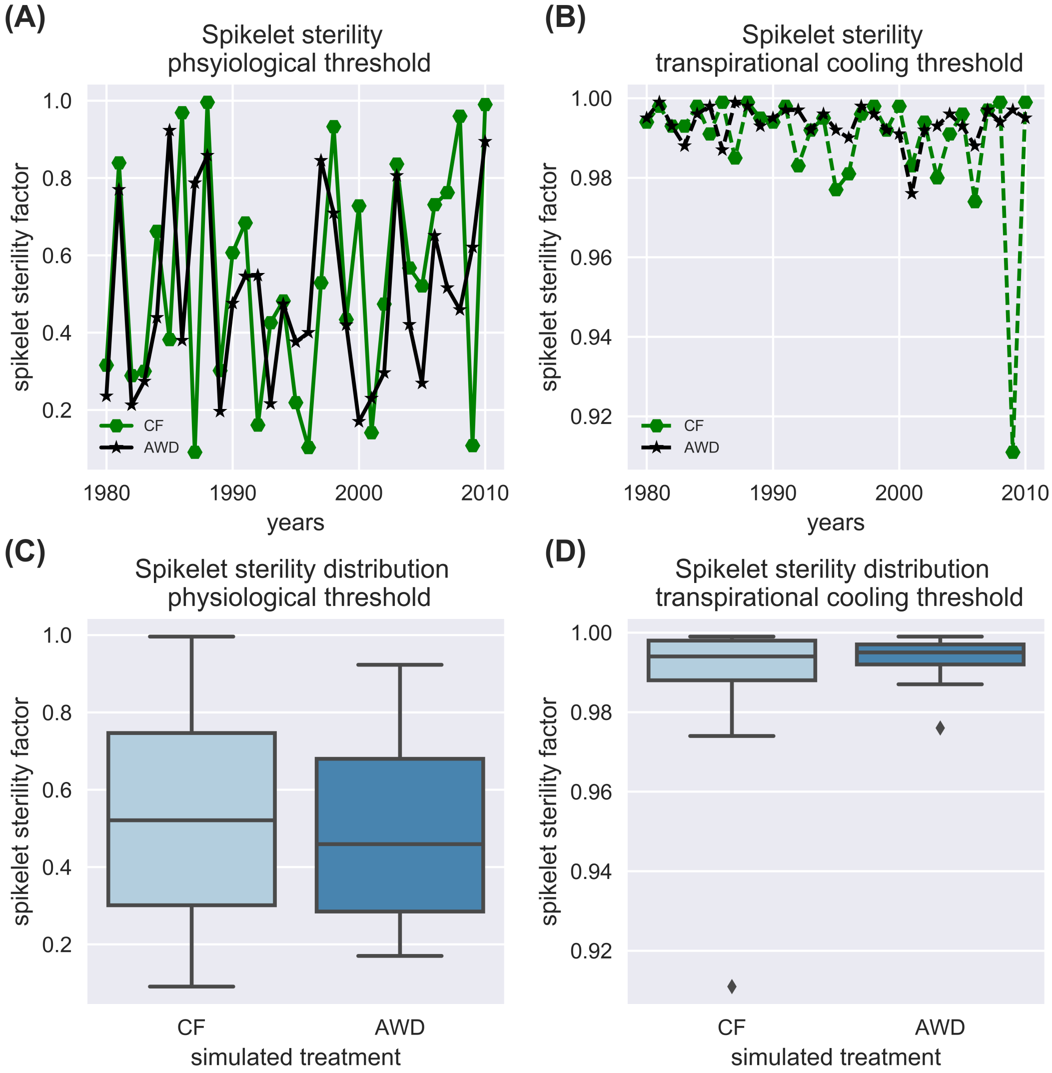

Figure 4.9: A comparison of modelled spikelet sterility in the continuously flooded (CF) and alternate wetting and drying (AWD) treatments. A high value of the spikelet sterility factor indicates low spikelet sterility.

4.4 Discussion

In both controlled environments and field conditions, large differences between panicle and air temperatures have been recorded. A growing body of evidence discussed in the introduction suggests that this is partially driven by transpirational cooling (Van Oort et al. 2014). In this chapter, the effect of transpirational cooling on panicle temperatures was dynamically added to a state of the art rice model. The sensitivity of spikelet sterility and crop yield to transpirational cooling was simulated over a 30 year period in Ludhiana Punjab, a hot environment, where mean air temperatures frequently cross the physiological threshold for spikelet sterility during the flowering period.

Simulated spikelet sterility and impacts on yield were extremely sensitive to the inclusion of transpirational cooling in the model in both fully flooded and alternate wetting and drying conditions. In both cases, use of the physiological threshold for spikelet sterility resulted in many years with high levels of spikelet sterility. In both sets of simulations, spikelet sterility was a dominant source of variability in grain yields. When the impacts of transpirational cooling were included in the model, spikelet sterility was infrequent and the magnitude was small.

Differences in the frequency and magnitude of spikelet sterility were observed for the fully flooded and AWD simulations when the physiological threshold was employed. The median spikelet sterility was larger in AWD conditions, however the range was greater in the CF simulations. This suggests that delayed flowering from water limitations prevents the most severe occurrences of spikelet sterility experienced in the CF simulations. However, on average, the influence of leaf rolling on panicle temperature outweighs the heat avoidance from late flowering

These results also support the body of literature suggesting that accurate simulation of heat stress during the flowering period requires the inclusion of transpirational cooling (Siebert et al. 2014) (Siebert et al. 2017). Depending on the choice of sterility threshold, spikelet sterility either dominates historical simulations of yield or makes a small/negligible impact on yield variability. These results support the hypothesis made by Li et al. (2015) that the large envelope of uncertainty in model simulations of grain yield under climate change in this location was attributable to differences in the way that spikelet sterility was represented in the rice models.

The over-arching purpose of this chapter was to understand the implications of uncertainty in modelling spikelet sterility and the impacts on attempts to model the trade-off between saving water through AWD and exposure to heat stress in India's most important rice growing region. These results show that the choice of whether or not to include transpirational cooling in modelling spikelet sterility had a far greater impact on simulated yields than changing the treatment simulated. This suggests that in order to accurately assess this trade-off, it is necessary to model transpirational cooling accurately.

In order to do so, it is necessary to consider the strengths and weakness of existing approaches in the context of multiyear simulations and the appropriate degree of physiological complexity when less data is available. The next two sections explore the limitations of the current approach in ORYZA V3 and the limitations of integrating more complex approaches into the model.

4.4.1 Strengths and weakness of simple approaches

Formulation of heat stress during the flowering period in ORYZA requires the average maximum temperature over the flowering period to be greater than the sterility threshold. However, in reality, spikelet sterility can occur in less than an hour (Jagadish et al. 2007). ORYZA (and most crop models) are driven by daily weather data and run at a daily timestep. There is therefore a mismatch between the timescale at which the process occurs, and the timescale at which the process is modelled. Further, in general, rice tends to flower in the late morning and not at midday when maximum temperatures typically occur (Julia and Dingkuhn 2012).

Solutions to both these challenges have been attempted in an early version of the ORYZA rice model. van Oort et al. (2015) incorporated equations for describing diurnal variation in panicle temperatures, population flowering times and transpirational cooling using the Julia and Dingkuhn (2013) approach. These authors tested the model in two arid environments and found significant improvements in simulation of yields. They note that this approach differs from less arid and more humid conditions in rice growing regions in Asia. The extent to which this has the potential to improve historical or future simulations depends upon three factors: the extent of knowledge of flowering times, the accuracy of diurnal cycle approximations when applied to gridded weather output and the accuracy of equations for calculating panicle temperatures.

Julia and Dingkuhn (2012) show that there is significant within species variation in flowering times, and that flowering time is also influenced by minimum temperatures in the 7 days preceding anthesis. Detailed data sets on the evolution of flowering times for varieties grown in Punjab between 1980 and 2010 were not available. Apriori, it is therefore unclear whether the introduction of the van Oort et al. (2015) method has the potential to bring simulations closer to reality or introduces further uncertainties to historical simulations of the type performed in this chapter (which undoubtedly represent an upper estimate).

The authors of the diurnal cycle model used in van Oort et al. (2015) note the site dependency of their model (Ephrath et al. 1996). It would therefore be necessary to weigh the introduction of uncertainties from sub-daily weather simulations compared with the degree of overestimation from simulating noon temperatures. Future work could include a comparison of the simple dynamical method used in this chapter with van Oort et al. (2015)'s integrated approach over the historical period under a range of genotypic assumptions. This would involve integrating the van Oort approach into the ORYZA version 3 model and changing parts of their approach to make the underlying assumptions more suited for a monsoon climate. For example, replacing their assumption that the dewpoint temperature can be approximated by the minimum temperature

In this chapter, the impact of evaporative cooling was represented in the model by dynamically adjusting the sterility threshold depending on the weather in the season being simulated. This method had the advantage of low input data requirements, few assumptions about genotypic differences and no introduction of additional parameters to the model. The simplicity of this approach was well suited to testing model sensitivity to transpirational cooling in CF and AWD conditions. However, studies that wish to make policy relevant statements about the trade-off between saving water and heat stress impacts will need to demonstrate an ability to navigate the physiological complexity of modelling spikelet sterility and the extent of existing knowledge and data. Next,the suitability of more complex approaches is assessed.

4.4.2 Strengths and weakness of more complex approaches

More in depth models of panicle temperature have been formulated. Yoshimoto et al. (2011) employ a detailed energy balance model integrating the energy balance above and within the rice canopy. Julia and Dingkuhn (2013) include time of anthesis, the height of the upper boundary of the panicle layer and the vapour pressure deficit in their model to obtain accurate simulations of canopy temperature across 2 seasons and 2 environments.

Both of these approaches achieve high levels of skill in the particular environments that the models are tested on. However, while the models show skill across several environments, temporal and genotypic coverage is very low. Yoshimoto et al. (2011) test their model on two plots (potential vs. water limited) for two varieties in one growing season. Julia and Dingkuhn (2013) test their model on two seasons in hot and dry environments in Senegal and a more humid environment in the Philippines using four varieties.

It is therefore difficult to know how dependent model skill is on specific growing seasons, and therefore to estimate the uncertainty from using these complex models over climatic time scales. Further, these models are both tested on a few specific varieties, and transpirational conductance of rice panicles has been shown to exhibit significant genotypic variation (Fukuoka et al. 2012). In summary, it is not clear that more complex approaches are necessarily more reliable for simulations over longer time scales. More detailed models make more assumptions about: the time of day at which flowering happens, canopy scale meteorology and genotypic properties of the canopy determining transpirational conductance.

Future work should test the robustness of these models to parameter uncertainty when information on the genotypic properties are not known. This is the typical situation for simulations at climate time scales when the genotype grown would have changed many times during the time period simulated. The integration of more complex models for simulations over long time scales will need to consider: the extent of knowledge about the uncertainties introduced by extra parameters, the degree to which model performance is improved by their introduction and whether or not sufficient data is available to define these parameters across environments (Falloon et al. 2014). The answers to these questions will determine if more complex methods are appropriate.

Although answering these questions will be a huge step forward for modelling spikelet sterility over climate time scales, simulating panicle temperatures alone, does not account for differences between leaf and air temperatures throughout the season. Differences between leaf and air temperatures would likely influence the rate of photosynthesis and development, which in turn influences the carbohydrate available for spikelet and grain formation. There is therefore a need to combine both leaf temperature and spikelet temperature models to improve simulation of heat stress.

4.5 Conclusion

This chapter set out to test three hypotheses. The first hypothesis was that spikelet sterility is reduced when including the effects on transpirational cooling in the model set-up. This hypothesis is strongly supported by the results of this chapter. The second hypothesis was that simulated yield is increased when including the effects of transpirational cooling in the model set-up. This hypothesis was also strongly supported by the results of this chapter. The third hypothesis was that simulated spikelet sterility differs in continuously flooded and alternate wetting and drying experiments. It was shown that when the physiological threshold is employed in the model, spikelet sterility is slightly higher in alternate wetting and drying conditions and more variable in continuously flooded conditions. It was also shown that there is very little difference between the two simulated treatments when transpirational cooling is included in the model set-up.

This chapter has demonstrated that modelling the trade-off between saving water and exposure to heat stress in India's most important rice growing region is extremely sensitive to the inclusion of transpirational cooling in modelling spikelet sterility during the flowering period. Simulations of yield are far more sensitive to the inclusion of transpirational cooling than they are to the choice of fully flooded versus AWD treatments. Current models of transpirational cooling of the spikelet are trained and evaluated on few seasons and genotypes. Future work is required to build models that perform well over climate timescales and are provably robust to environmental and genotypic variation.

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Chapter 5

Interactions between flooded irrigation, heatwaves and rice yields on the Indian subcontinent

5.1 Introduction

Chapter 4 considered the trade-off between saving water and resilience to heat stress at field scale. The focus was to explore the extent to which transpirational cooling is important in modelling interactions between saving water and impacts on yield from changes in heat stress. Chapter 5 shifts the scale of analysis to explore the relationship between current flood irrigation practices and the atmosphere at district level. This chapter examines the relationship between the extent of current flood irrigation and meteorological heatwaves. Further, it examines the relationship between heatwaves and rice yields. The combination of these two analyses contributes to an understanding of how water saving practices may have influenced rice yields through landscape wide effects on the atmosphere. As water saving practices in India change under the pressure of water scarcity (Tiwari et al. 2009; Subash et al. 2015), it is important to understand how previous rice management practices may have influenced meteorological extremes in the past.

Farm management practices which aim to reduce groundwater depletion aim to either reduce seasonal evapotranpsiration, or to reduce run off and deep drainage. Recommended technologies include alternate wetting and drying, delayed transplanting and the adoption of shorter duration varieties (Humphreys et al. 2010). All of these options involve either ending flooded irrigation practices over the length of the rice growing season, or maintaining ponded water for a shorter period of time. Any of these changes in management practices will mean a reduction in the amount of time during which flooded rice fields dominate the landscape in agricultural regions. Understanding the potential impact of water saving technologies on meteorological heatwaves requires an understanding of how soil moisture interacts with atmospheric drivers of heatwaves.

This chapter begins with a summary of the process of heatwave generation and why irrigation may or may not be expected to interrupt these processes. This is followed by a short summary of the literature on heatwaves in India, and the evidence for a link between heatwaves and rice yields. Finally, an aims and objectives section discusses the knowledge gaps in the chain between irrigation, heatwaves and rice yields and offers a high level description of how they will be addressed in this chapter.

5.1.1 Heatwave generation

Heatwaves around the globe share common physical drivers. Often, advection of warm air is combined with a high pressure synoptic system that prevents warm air masses from clearing (Perkins 2015). High temperature increases evaporation from the earth's surface, which in turn reduces soil moisture. This can induce a negative feedback loop between drier soils and increased sensible heating, which further increases surface temperatures (Perkins 2015). Recent work suggests the presence of a third ingredient in the generation of mega-heatwaves. In both the 2003 and 2010 mega-heatwaves over Europe, high pressure synoptic systems and soil desiccation led to a deepening of the atmospheric boundary layer, progressively increasing heat storage over the duration of the heatwave (Miralles et al. 2014).

The interaction between drying of the land surface and heatwave development is mediated by ecosystem characteristics. The rate of evapotranspirative decline is controlled by the response of both transpiration and evaporation from the soil to heating (Miralles et al. 2019). Conceptually, evaporation from the soil will continue until a critical soil moisture threshold is reached, after which it may decline (Miralles et al. 2019; Seneviratne et al. 2010). This response is complicated by negative feedbacks between transpiration and soil evaporation. As soil moisture declines, many plants control transpiration by reducing stomatal conductance. The extent of stomatal regulation varies widely amongst plants, and even within plant species (Roche 2015).

5.1.2 Heatwaves and irrigation

Large-scale irrigation reduces surface temperatures. The higher specific heat capacity of water relative to land allows water to absorb more heat, and changes the balance between latent and sensible heating at the land surface (Sacks et al. 2009). Higher rates of evaporation over irrigated areas leads to increased water vapour content in the atmosphere (Boucher et al. 2004), which can influence both macro and meso scale circulations (Douglas et al. 2009). Irrigation induced cooling is consistently borne out in modelling studies (Thiery et al. 2017) and also supported by a limited number of observational studies. At wider landscape scales, the presence of large-scale irrigation has been shown to reduce daily mean (Bonfils and Lobell 2007) and daily maximum temperatures (Lobell and Bonfils 2008).

In addition to impacting daily mean and maximum temperatures, theory suggests that irrigation may also interrupt the mechanisms involved in heatwave generation. The section above describes the positive feedback loop between sensible heating and soil drying as being important to heatwave generation. Wet soils increase the proportion of shortwave radiation converted to latent heat flux, reducing the amount of energy available for sensible heating. This suggests an interruption to the cycle of progressive soil drying and heat build up (Perkins 2015).

The body of literature examining the impact of irrigation on heatwaves is smaller and less mature than the evidence base for impacts on surface temperature. In a global modelling study, Thiery et al. (2017) found that irrigation reduces the duration of heatwaves. Lu and Kueppers (2015) conducted a regional study testing the impact of irrigation on 15 heatwave indices across the contiguous US. They found that irrigation reduces the frequency, duration and intensity of heatwaves in heavily irrigated regions. In less irrigated regions, the relationship between irrigation and heatwaves was weaker, and fewer associations between irrigation and heatwave characteristics were significant. Lobell and Bonfils (2008) compared daily temperature extremes in irrigated and non-irrigated areas in California and Nebraska. They found a similar level of cooling from irrigation on both normal and extremely hot days. No significant differences in the duration of heatwaves were found.

The relationship between irrigation and heatwaves may also depend on the kind of heatwaves that are being considered. Kang and Eltahir (2018) performed historical regional simulations for the North China plain both with and without irrigation. They found that including irrigation increased the frequency of maximum wet bulb temperature occurrences, leading to heatwaves that would be more intensely experienced by human beings. They also performed future simulations for the same region. These projections suggested that the combination of widespread irrigation and increasing temperatures results in an increase in the number of days above the wet bulb threshold for human habitability. Im et al. (2017) suggest that irrigation may be a contributing factor to climate projections of increased extreme wet bulb temperatures for densely populated agricultural regions in the Indo-gangetic plains.

A priori, there are also theoretical arguments to suggest that the relationship between irrigation and heatwaves may be more complex than a simple reduction. Widespread irrigation has been shown to affect macro and meso scale circulation patterns, which can change where cloud cover and convection occur (Douglas et al. 2009). For example, irrigation has been shown to weaken the Indian monsoon in some parts of India and to shift rainfall from the east to the west (Tuinenburg et al. 2014). Since the impact of irrigation is an integrated effect on forcing and changes to atmospheric circulation, implications for impacts on extreme temperature events are not obvious to first order.

5.1.3 Heatwaves in India

Although the literature on heatwaves has been more focused on Europe, America and Australia, a fast growing body of literature on heatwaves in India suggests similar causal mechanisms. Rohini et al. (2016) analyses heatwaves in India over the period 1961-2013 for April-June. They found that heatwaves in northern India were associated with anomalous regions of high pressure originating from sub-tropical highs linked to quasi-stationary Rossby waves in the mid-latitudes. These conditions lead to clear skies. Low soil moisture was also identified as being associated with variability in heatwaves over this part of the country.

Ratnam et al. (2016) found that there are two types of heatwaves in northern and central India between March and June. The first type is associated with quasi-stationary Rossby wave activity along the African jet, which generates high pressure systems associated with typical heatwave conditions. This supports the theory put forward by Rohini et al. (2016). The second set of conditions is set off by anomalous westerlies, which weakens the land-sea breeze over the eastern coast of India. This prevents the inflow of cooler air from the ocean, which makes heatwaves more likely (Ratnam et al. 2016).

Analysis of heatwaves over India have largely focused on the months before the monsoon starts, as this is when the danger to human beings is greatest (Pai et al. 2013). Severe heatwaves during the rice growing season are more often associated with weak monsoons, active breaks in the monsoon and dry soils (Panda et al. 2017). Causal mechanisms supporting this theory are supported by observational analysis. Ramarao et al. (2016) found that variability in temperatures during the monsoon season are associated with variability in rainfall, which influences variability in soil moisture and increases sensible heating. Their work supported previous modelling studies demonstrating an increase in sensible heating when soil moisture was low (Asharaf and Ahrens 2013; Asharaf et al. 2012). Ramarao et al. (2016) found that the power of this effect was stronger in the drier central and north-west of India and was weak in wetter areas. Sharma and Mujumdar (2017) found that the concurrence of droughts and heatwaves has increased between 1951-1980 and 1981-2010.

While a consensus is forming around the impact of soil moisture variability on heatwave formation in the Indian summer, less is known about the relationship between heatwaves and irrigation in India. Kumar et al. (2017) found that the contrast in temperature between urban and rural areas is higher in heavily irrigated regions in the north of India, which suggests a role for irrigation above and beyond the impact of wet soils. Kumar and Mishra (2019) used the Community Land Surface Model (CLM) to investigate differences in extreme day and night time temperatures. They found that irrigation resulted in a decrease in the number of extremely hot nights in the Indo-Gangetic plains (IGP), which also suggests a potential role for irrigation in reducing the frequency of heatwaves. Roy et al. (2007) used both observations and modelling to investigate the impact of irrigation on land surface temperatures in central and north western India. They find evidence of reduced land surface temperatures in irrigated areas of India, providing further support for the hypothesis that irrigation could reduce heatwaves in India.

5.1.4 Heatwaves and rice yields

Extreme temperatures impact rice yields through different mechanisms during the day and at night. Maximum daytime temperatures impact rice yields by reducing photosynthesis and sink capacity (Rezaei et al. 2015). Rice is most sensitive to high temperatures during the reproductive period (Prasad et al. 2017). High temperatures during flowering can accelerate grain filling (reducing time for grain accumulation), reduce pollen production, and increase sterility (Rezaei et al. 2015). High night time temperatures reduce growth by increasing maintenance respiration, which reduces the carbon available for growth (Peng et al. 2004).

Although a large body of literature exists examining the impact of high temperatures on rice at field scale (Jagadish et al. 2015), much less is known about the impact of high temperatures on rice yields at larger spatial scales. At the global scale, empirical analysis has focused on the impact of individual variables aggregated to seasonal timescales. Lobell and Field (2007) found that increases in maximum temperatures from 1961-2002 had a small negative impact on rice yields. Lesk et al. (2016) found a strong and significant relationship between extreme temperatures and rice yields at global scale. Osborne and Wheeler (2013) examined the relationship between variability in temperature and precipitation on yield variability and found that significant changes in climate variability have influenced rice yields in India. Lobell (2007) found a negative association between increasing diurnal temperature range and rice yields in China, India and Bangladesh over the years 1961-2002.

Fewer detailed studies on temperature extremes and crop yields have been conducted for rice yields over the Indian subcontinent. Vogel et al. (2019) performed a grid scale analysis of the impacts of climate extremes over the globe at a spatial resolution of 1.5 degree by 1.5 degree. They used heatwave indicators and found that a composite of extreme climate indices are able to explain 26 percent of yield variability for rice in Asia. Kumar et al. (2011) considered the combined impact of temperature and rainfall on Indian rice yields between 1961 and 2007. They found that a combination of high minimum temperature and low precipitation has had strong negative impacts on rice yields. To date, no studies provide a disaggregated analysis of the relationship between specific heatwave indices and district level rice yields in India over a long hisorical time period.

5.1.5 Aims and Objectives

This chapter addresses three knowledge gaps in the literature. First, studies conducting heatwave climatology over India have largely focused on the pre-monsoon season, as this is when heatwaves are most dangerous to human beings. To the authors knowledge, no studies have made a detailed comparison of how the duration and frequency of heatwaves differs in the monsoon season. The first objective of this chapter is to provide such an analysis.

The second gap in the literature explored in this chapter is the relationship between heatwaves and rice yields at district level in India over more than 50 years. There have been a number of global studies looking at extreme temperatures and crop yields, which have included grid cells in India, and a few studies looking at broad measures of heatwaves and rice yields globally (for example Vogel et al. (2019)). Unlike previous studies, this study assesses how different aspects of each heatwave definition are associated with rice yields. In particular, a comparison is made between spatial patterns of association for frequency and duration of heatwave indices separately. This chapter makes use of higher resolution rice yield data than previous studies and newly available climate data published by the Indian Meteorological Department (IMD) at a comparable scale.

The third gap in the literature is empirical analysis between flooded rice irrigation and heatwaves in India. Although previous studies (for example Roy et al. (2007)) have conducted empirical analysis of the relationship between irrigation and surface temperatures over India, to the authors knowledge, no studies have conducted a thorough analysis of the impact of flooded rice irrigation on heatwaves in India. In this chapter, permutation sampling is employed to assess whether irrigation reduces the frequency and duration of heatwaves. To the authors knowledge, use of this technique has not been employed in the empirical literature on irrigation and heatwaves and confers many advantages over previous methods.

5.2 Data and Methods

5.2.1 Data Sets

District level production, area planted and irrigated area data sets from the Icrisat (2015) data set were used. Data were available for 19 of the 29 states in India for the years 1966 to 2011. Daily maximum and minimum temperature data from the Indian Meteorological Department were used, available at a spatial resolution of 1 degree by 1 degree for the years 1951-2018 (Srivastava et al. 2009). Rainfall data from the Indian Meteorological Department was available at a spatial resolution of 0.25 degrees by 0.25 degrees for the years 1901-2018 (Pai et al. 2014). All of these data sets are freely available online.

5.2.2 Variable Definitions

The irrigated fraction per grid cell was calculated by dividing the irrigated rice area by the district area. The definition of irrigated area was constrained to irrigated rice area because rice is cultivated in flooded fields, which would be expected to alter both sensible and latent heat fluxes.

$$IrrigatedFraction = irrigatedricearea(000ha) \div districtarea(000ha) \tag{5.1}$$

Rice yields were calculated by dividing rice production by area of rice planted for each district.

$$Riceyield = riceproduction(kg) \div riceareaplanted(ha) \tag{5.2}$$

5.2.3 Data Preparation

District level data was gridded to a spatial resolution of 1 degree by 1 degree to match the weather data. Grid cells were assigned the value of the district covering the largest share each grid cell. Grid cells with missing data for more than 25 percent of years between 1966-2011 were removed. This was done to prevent misclassification of grid cells based on an incomplete time series. Grid cells that overlapped with the sea were also removed using the National Center for Atmospheric Research (NCAR) land sea mask (National Center for Climate Research 2019). The mask for this process is freely available online (see bibliography for the web address).

5.2.4 Study Region

Rice yields have followed a consistent upward trend from 1966-2011, with considerable inter-annual variation (Figure 5.1). The rate of increase has been par-

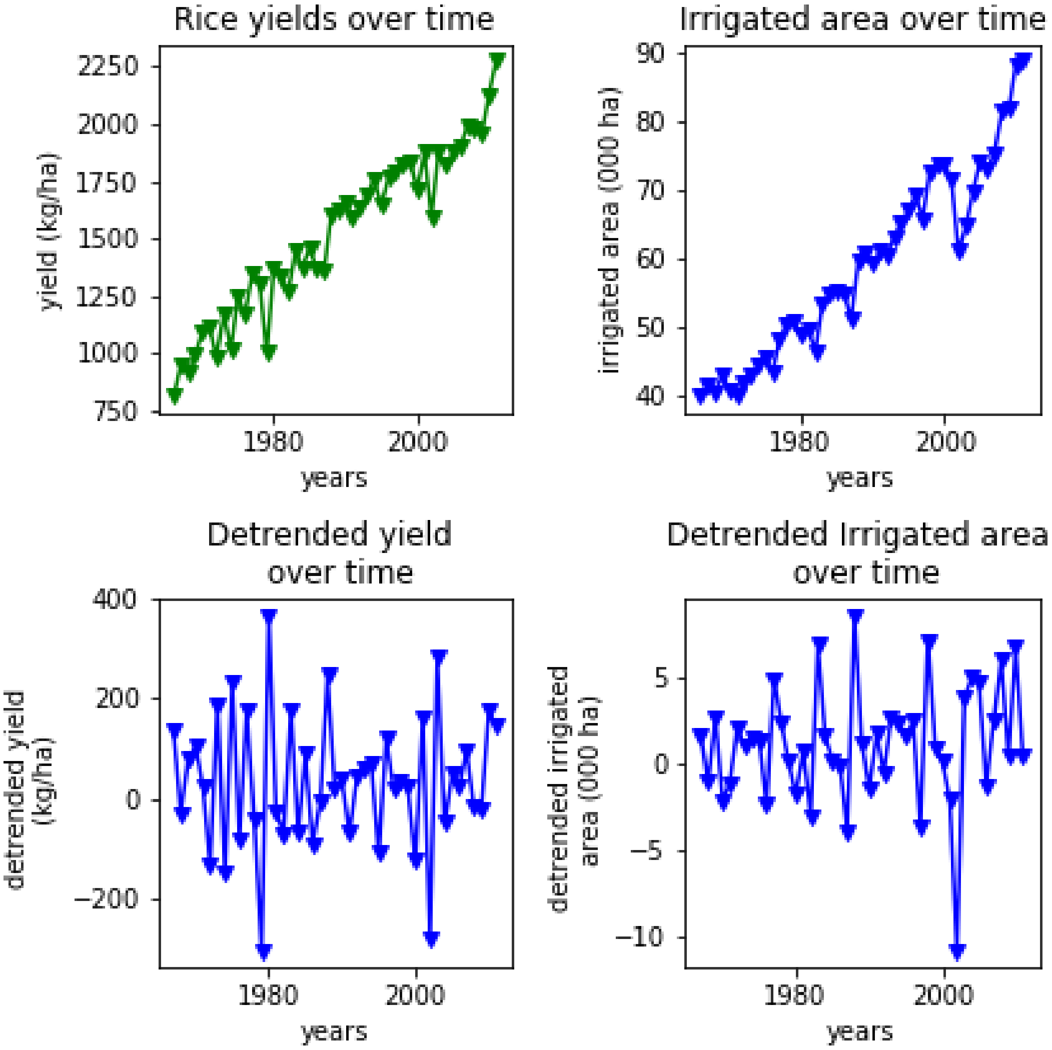

Figure 5.1: Mean rice yields and irrigated area 1966-2011 for 19 states in India

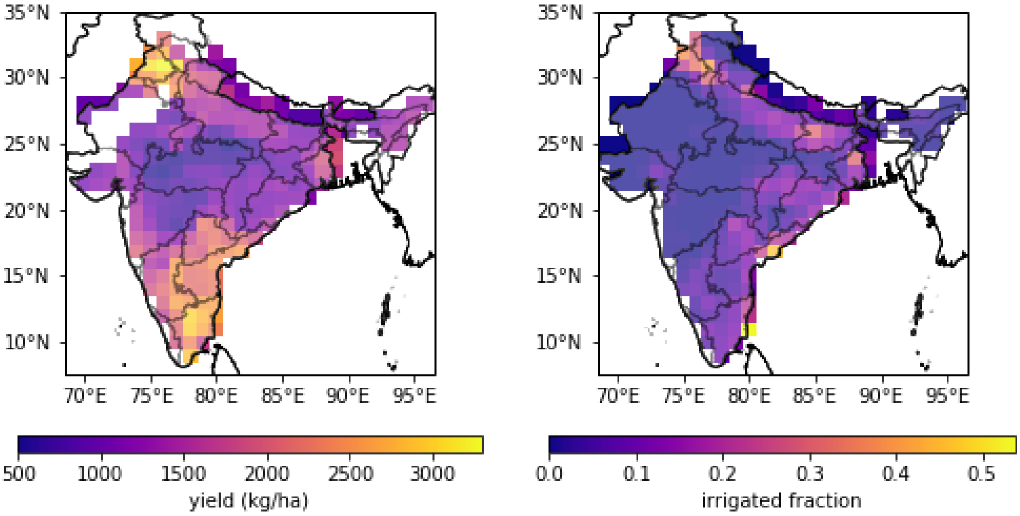

Figure 5.2: Mean rice yields and irrigated fraction by grid cell 1966-2011 (1 degree by 1 degree)

ticularly sharp in the most recent decade shown. Irrigated area has also followed an upward trend between 1966 and 2011, and has also shown considerable interannual variability. There was a drop in irrigated area in the early part of the first decade of the 21st century. However, as was the case for rice yields, the rate of increase has been particularly sharp in the most recent decade available.

There is significant variation in rice yields across India, ranging from 500 kg/ha to more than 3000 kg/ha (Figure 5.2). The highest yielding areas are in the north west and the south of the country. There is a clear gradation in yield from the north west of the Indo-gangetic plains to the north east. The lowest yielding areas are found in the centre of India. The mean irrigated fraction ranges from zero to slightly over 0.5. The mean irrigated fraction is larger in the east of the country and the highest irrigated fractions are found in the north west and south east of the country. Areas with substantial irrigated fractions (greater than 0.1) can be found across diverse climatic and agroecological regions.

The highest yielding areas in the north west and south east of the country are also some of the hottest and driest parts of the country (Figure 5.3). The Indo-Gangetic plains receives increasing amounts of rainfall during the growing season from west to east. The coolest daytime maximum temperatures are found in

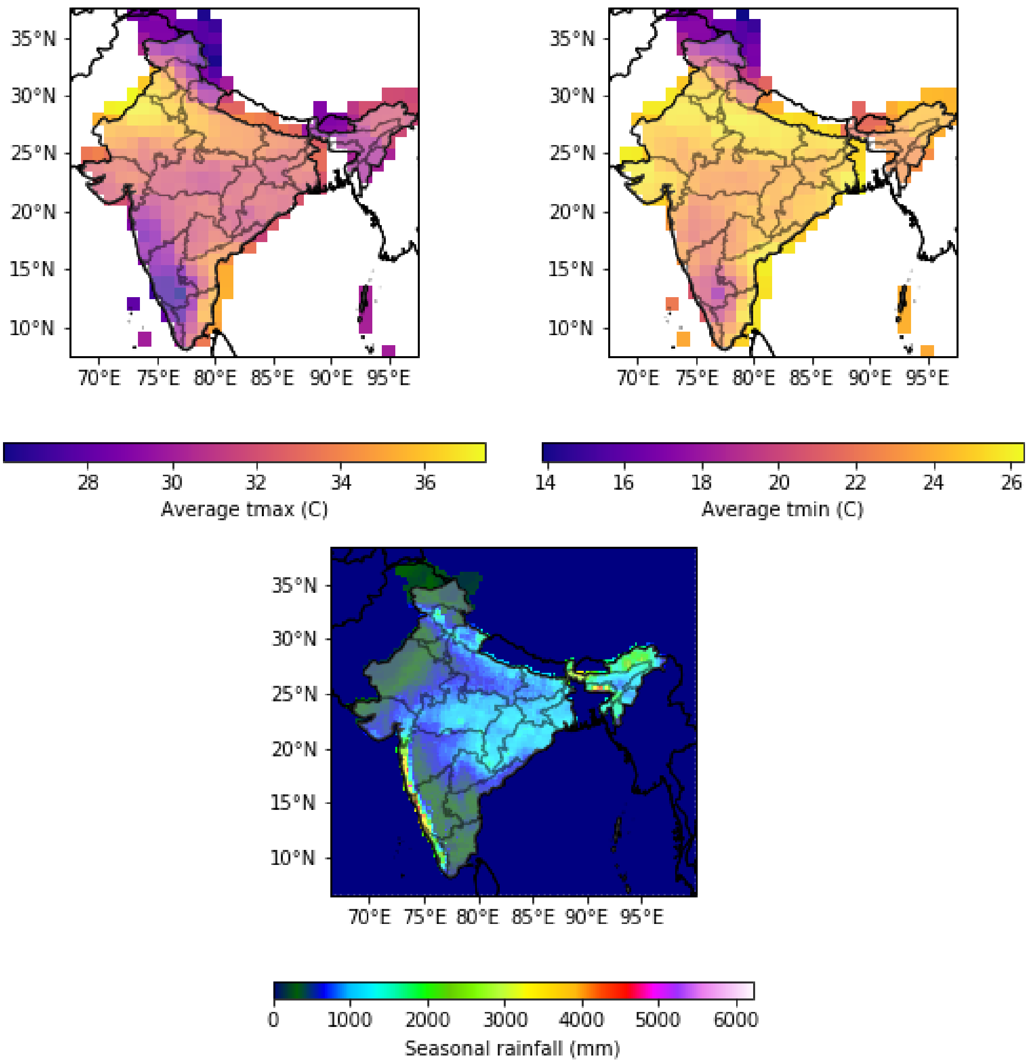

Figure 5.3: Climatology of Tmax, Tmin and Total precipitation over the rice growing season for the period 1966-2011. Seasonal rainfall refers to the mean total precipitation over the rice growing season.

areas of high elevation in the far north and south west of the country and in very wet areas in the far east of the country.

5.2.5 Heatwave definitions

Percentile based heatwave definitions were used in this study, as grid cells cross many different climates, soils and topographies. To ensure a fair test of the impact of irrigated fraction on heatwaves, it was necessary to use indices that are defined relative to climatology. The three heatwave definitions selected by Perkins and Alexander (2013) were used in this study, to ensure applicability across climates. These indices were calculated for all grid cells between 1966 and 2011.

1. CTX: 3 consecutive days with Tmax >90th percentile based on a 15 day window around the calendar day.
2. CTN: 3 consecutive days with Tmin >90th percentile based on a 15 day window around the calendar day.
3. EHF: 3 consecutive days with the Excess Heat Factor >1.

The Excess Heat Factor Nairn and Fawcett (2015) is calculated as follows:

$$EHF = EHI_{sig} \cdot max(1, EHI_{accl}) \tag{5.3}$$

Where if T = maximum temperature, T_{95} = the 95th percentile based on a 15 day window around the calendar day, $\mathrm{EHI_{sig}}$ is defined as follows,

$$EHI_{sig} = (T_i + T_{i+1} + T_{i+2}) \div 3 - T_{95} \tag{5.4}$$

and $\mathrm{EHI_{accl}}$ is defined as:

$$EHI_{accl} = (T_i + T_{i+1} + T_{i+2}) \div 3 - ((T_{i-1} + ...T_{i-30}) \div 30) \tag{5.5}$$

The first two heatwave definitions account for the extremity of an event relative to intra-seasonal variation in maximum and minimum temperature throughout the summer season. This chapter follows Perkins and Alexander (2013) in arguing that the 90th percentile provides a reasonable balance between the extremity of the event and frequency of occurrence. The Excess Heat Factor considers the intensity of a heatwave based on the local climate, and the potential for acclimation over the previous 30 days.

Definition 1 employs maximum temperatures, which occur during the daytime and is commonly referred to as CTX in the literature. Definition 1 will therefore be referred to as CTX for the remainder of the text. Definition 2 employs minimum temperatures, which occur during the night and is commonly referred to as CTN in the literature. Definition 2 will therefore be referred to as CTN for the remainder of the text. By using both CTX and CTN heatwaves, it is possible to analyse the impact of irrigation on daytime and nighttime heatwaves and to explore the impact of daytime and nighttime heatwaves on rice yields separately. Definition 3, commonly referred to as the Excess Heat Factor (EHF) in the literature combines an understanding of how hot a particular event was relative to intra-seasonal climatology and relative to the previous month. Definition 3 will therefore be referred to as the EHF for the remainder of the text.

Since the irrigation and yield data is on a seasonal time scale, seasonal aggregates for all three defintions were taken, where the season was defined as the beginning of June to the end of September. This season definition was chosen to coincide with the part of the rice growing season when the fields were most likely to be flooded. Following Perkins and Alexander (2013), the number of heatwaves per season and the duration of the longest heatwave per season for all three definitions were considered. The number of heatwaves per season will be referred to as heatwave number (HWN) and the maximum duration of the longest heatwave per season as heatwave duration (HWD) for the remainder of the text.

5.2.6 Irrigation definitions

Grid cells were classified based on the mean irrigated fraction over the time period 1966-2011. In total, there are 253 grid cells for which 75 percent of the time series is available. Grid cells with a mean irrigated fraction of less than 0.05 were classified as non-irrigated, since such a small irrigated fraction is not expected to affect surface temperatures at the grid scale (Thiery et al. 2017). There were 149 non-irrigated grid cells. Grid cells with a mean irrigated fraction between 0.1 and 0.2 were classified as medium-irrigated, there were 43 medium-irrigated grid cells. Grid cells with a mean irrigated fraction greater than 0.2 were classified as highly-irrigated, there were 19 highly irrigated grid cells.

5.2.7 Hypothesis tests

The following hypotheses were tested in this chapter. The first hypothesis tested was that the number of heatwaves per year is associated with rice yields, which can be expressed as follows:

H_o: The number of heatwaves per year is not associated with rice yields.

H_a: The number of heatwaves per year is associated with rice yields.

The Spearman correlation between the total number of heatwaves per year and detrended rice yields between 1967 and 2011 was calculated for each grid cell. Since technology improves over time, crop yields contain a technology trend, which needs to be removed to avoid spurious correlation (Swinton and King 1991). Yields were detrended by taking the first difference of each year following Lobell and Field (2007). By taking the first difference of yields, the impact of changes which occur at longer time scales are removed from the correlation analysis. This process reduced the length of the time series by 1 year, as it is not possible to calculate the first difference for the first year of available data. Correlations between heatwave characteristics and rice yields were tested to see if they were significantly different from zero using a two sided t-test at the 95 percent confidence level. The widely used equation for this test is given below,

$$t = corr \cdot \sqrt{n-2} \div \sqrt{1-corr^2} \tag{5.6}$$

if t >1.96 or t <-1.96, then the null hypothesis is rejected at the 95 percent confidence level. Ninety five percent of the area under the t distribution can be found between these two values of t.

The hypothesis that there are fewer heatwaves per year in areas with a larger fraction of irrigated rice area was tested. This test can be expressed as follows:

H_o: The mean number of heatwaves per year in a given grid cell is not affected by the irrigated fraction in that grid cell.

H_a: The mean number of heatwaves per year is lower in grid cells with larger mean irrigated fractions.

The hypothesis that the maximum duration of heatwaves per year is reduced in areas with a larger fraction of irrigated rice area was tested. This test can be expressed as follows:

H_o: The maximum duration of heatwaves per year in a given grid cell is not affected by the irrigated fraction in that grid cell.

H_a: The maximum duration of heatwaves is shorter in grid cells with larger mean irrigated fractions.

Testing for differences in meteorology above irrigated and non-irrigated conditions in India presents a number of statistical challenges. First, count data of meterological events is not normally distributed. Second, since farmers did not randomly choose where to irrigate, observations cannot be described as random samples and it is therefore not safe to assume that observations are independently and identically distributed. For this reason, classical parametric statistical inference tests are unsuitable. A third challenge associated with the potentially non-random spatial distribution of irrigated and non-irrigated grid cells is that other factors such as differences in elevation or climatology must be considered in the statistical method chosen. The permutation test was chosen with these challenges in mind. The permutation test was chosen as a response to the challenges highlighted above and is used extensively throughout this thesis for statistical inference with non-parametrically distributed data.

A one sided permutations test (Ludbrook and Dudley., 1998) for a difference in means between non-irrigated, medium-irrigated and highly-irrigated grid cells at the 95 percent confidence level was conducted. Grid cells were randomly split into separate arrays with lengths equal to the number of observations in each category being compared (permuted samples). The mean difference between the permuted samples was then taken. This procedure was performed 100 000 times, resulting in 100 000 mean differences. The p-value was then calculated by finding the proportion of times in which the mean difference of the permuted samples exceeded the observed difference.

5.3 Results

5.3.1 Comparison of heatwave definitions

5.3.1.1 Heatwave number

Figure 5.4 (a,c,e) shows that there is a north-south gradient visible in all three heatwave indices of heatwave number. In general, there are a greater number of heatwaves in the north and a smaller number of heatwaves in the south. This gradient is more pronounced for the CTN and EHF heatwaves than for the CTX heatwaves. Further, in all three definitions, fewer heatwaves are experienced in the far east of the country. The number of heatwaves experienced varies substantially across definitions. Large numbers of grid cells experience upwards of three heatwaves a year on average using the CTX definition. A much smaller share of grid cells experience upwards of three heatwaves a year using the CTN definition and very few grid cells experience an average of one heatwave a year using the EHF definition.

There is also significant spatial variation between heatwave definitions. In both the CTX and the CTN definitions, there is a band of northern-central India that experiences an average of more than 3 heatwaves during the rice growing season. On average, the largest number of daytime heatwaves are experienced in northern-central parts of India, while the largest number of nighttime heatwaves are experienced in the far west. In both definitions, the smallest mean number of heatwaves is experienced in the far east of the country.

There are large differences in the spatial variation and mean number of heatwaves experienced when comparing the EHF definition with the CTX and CTN definitions. The largest number of heatwaves are found in a band along the eastern Indo Gangetic Plains. Further, there is a band of grid cells going from the southern tip of the country to the western edge of the country, in which, on average, very few or no heatwaves are experienced.

5.3.1.2 Heatwave duration

Figure 5.4 (b,d,f) shows that there is also a north-south gradient in the climatology of the maximum heatwave duration. The climatalogical maximum duration of daytime heatwaves was larger than that of nighttime heatwaves, and the mean maximum duration of EHF heatwaves was very low (probably as a result of low occurrence). On average, the longest duration of daytime heatwaves ranged between 1.5 and 4.5 heatwaves per rice growing season, while nighttime heatwaves ranged between 1.2 and 3 heatwaves per rice growing season. The climatological maximum duration of EHF heatwaves ranged between 0 and 1 days.

Spatial variation was similar for the climatological maximum duration of daytime heatwaves and the climatology of daytime heatwaves. Northern-central India experienced both the greatest number and the longest heatwaves. Spatial variation was also similar for the climatology of the number of heatwaves and the longest duration. However, the largest number of nighttime heatwaves were experienced in the western tip of the country, while the longest duration of heatwaves were experienced in northern-central India. Spatial variation of the number and duration of EHF heatwaves was most closely aligned.

5.3.2 Heatwaves are associated with rice yields

Both the number and maximum duration of CTX heatwaves are mostly associated with reductions in rice yields. Panel a) and b) of Figure 5.5 show that the majority of grid cells display negative correlations between heatwave number/duration and rice yields. A large number of these negative correlations are significant. Significant correlations are mostly located in the north and centre of India. There are a smaller number of grid cells exhibiting positive correlations between CTX heatwaves and rice yields in the southern and eastern tips of India bu the vast majority of these are insignificant.

Both the number and maximum duration of CTN heatwaves were associated with both increases and decreases in rice yields (Panels c) and d) of Figure 5.5). The vast majority of grid cells did not exhibit significant correlations between CTN heatwaves and rice yields. There are small numbers of grid cells in the north west and north east of the country that exhibited significant negative correlations.

Both the number and maximum duration of EHF heatwaves are mostly associated with reductions in rice yields. Panel e) and f) of Figure 5.5 show that there are both negative and positive correlations between EHF heatwaves and rice yields. The vast majority of grid cells with significant correlations between EHF heatwaves and rice yields exhibited negative correlations. In Figure 5.5, there is a band of significant negative correlations spread across the Indo-gangetic plains and a very small block of significant positive correlations on the eastern tip of India. In Figure 5.5 the band of significant negative correlations is spread across central India and there are fewer significant positive correlations. Fewer significant correlations in southern India very likely reflects the lack of EHF heatwaves recorded in this part of the country.

5.3.3 Heatwaves and Irrigation

There were fewer CTX heatwaves in medium and highly irrigated areas than in non-irrigated areas (Table 5.1). These differences were highly significant. There was no difference in the duration of CTX heatwaves in medium irrigated areas and

Test	**HW type**	**Mean diff**	**p-value**	**Significance**
Non irrig vs. medium irrig	CTX hwn	-0.25	0.01	99 percent
Non irrig vs. highly irrig	CTX hwn	-0.33	0.02	98 percent
Non irrig vs. medium irrig	CTX hwd	0.00	0.48	Not significant
Non irrig vs. highly irrig	CTX hwd	-0.18	0.04	96 percent
Non irrig vs. medium irrig	CTN hwn	-0.38	0.00	99.9 percent
Non irrig vs. highly irrig	CTN hwn	-0.70	0.00	99.9 percent
Non irrig vs. medium irrig	CTN hwd	-0.11	0.03	97 percent
Non irrig vs. highly irrig	CTN hwd	-0.29	0.00	99.9 percent
Non irrig vs. medium irrig	EHF hwn	-0.02	0.29	Not significant
Non irrig vs. highly irrig	EHF hwn	-0.05	0.18	Not significant
Non irrig vs. medium irrig	EHF hwd	-0.84	0.28	Not significant
Non irrig vs. highly irrig	EHF hwd	-0.89	0.10	90 percent

Table 5.1: Permutation tests of differences in heatwave number per season and maximum duration in differently irrigated grid cells. Irrig = irrigation, diff = difference, hwn = heatwaves number, hwd = heatwave duration. Mean differences are given in the same units as heatwave type.

non-irrigated areas, but CTX heatwaves were shorter in highly irrigated areas.

There were fewer CTN heatwaves in medium and highly irrigated areas than in non-irrigated areas (Table 5.1). These differences were highly significant. CTN heatwaves were shorter in medium and highly irrigated areas than in non-irrigated areas. These differences were highly significant.

There was no difference in the number of EHF heatwaves in medium and highly irrigated areas and in non-irrigated areas. There was also no difference in duration between medium and highly irrigated areas and non-irrigated areas.

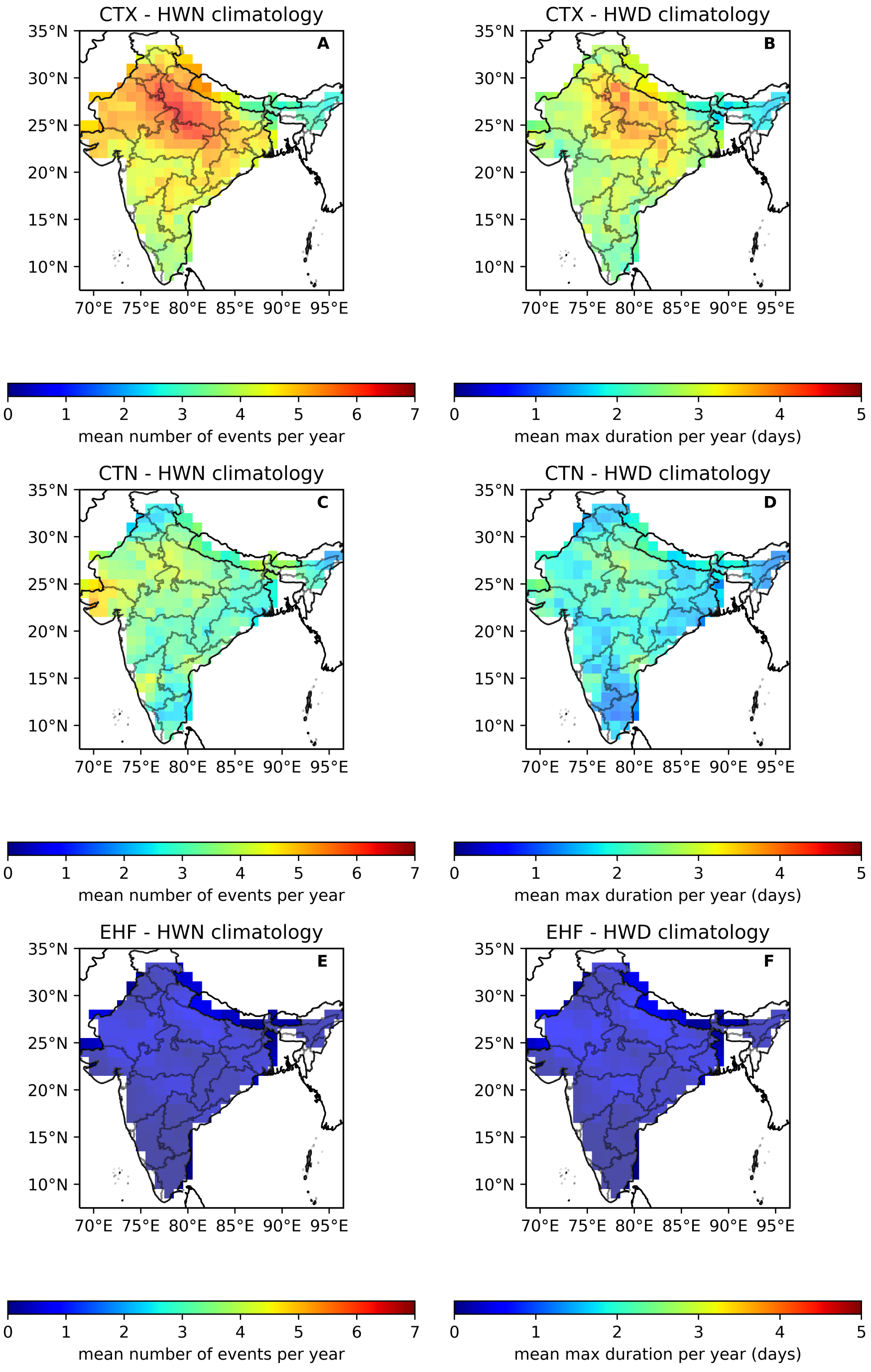

Figure 5.4: Climatology of heatwave number and maximum duration during the rice growing season over the period 1966-2011 for a) CTX heatwave number b) CTX maximum heatwave duration c) CTN heatwave number d) CTN maximum heatwave duration e) EHF heatwave number f) EHF maximum heatwave duration. HWN = heatwave number, HWD = maximum heatwave duration.

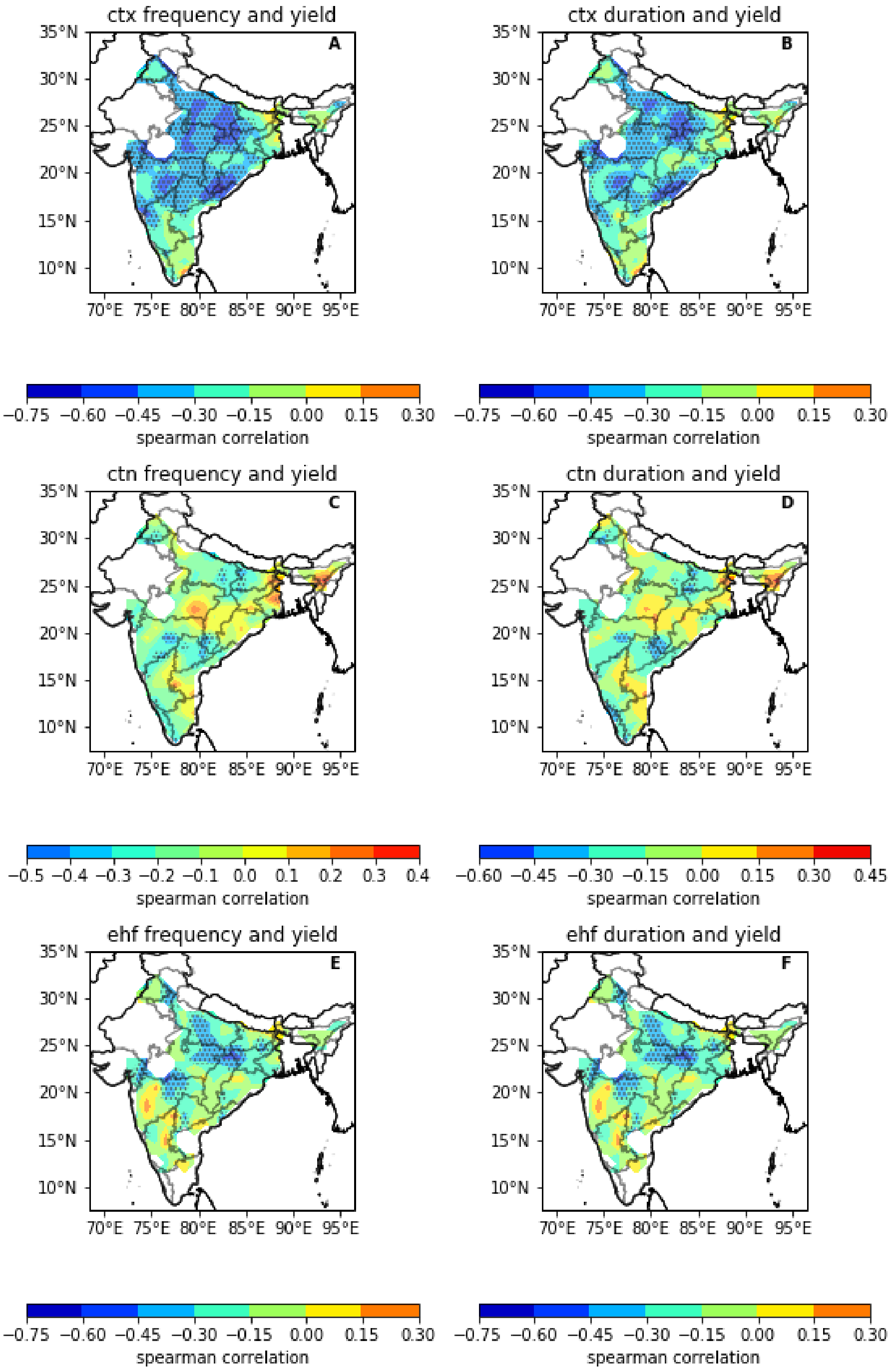

Figure 5.5: Spearman correlations between detrended heatwaves indices and detrended rice yields. Significant correlations are marked with stippling

5.4 Discussion

5.4.1 Climatology of heatwaves over the rice growing season

Sections 5.3.1.1 and 5.3.1.2 demonstrated that CTX heatwaves occurred more frequently and for a longer duration than either CTN or EHF heatwaves during the rice growing season. They were also more spatially coherent and occurred over a larger area. The very small number and short duration of EHF heatwaves suggests that the heatwaves that do occur during this season are usually part of a longer warm spell. Rice plants have therefore been unlikely to experience extreme heat shocks during the growing season and may have had time to partially acclimatise to the hotter conditions over the historical period.

Longer and more frequent CTX than CTN heatwaves were also found for a study of heatwaves between 1981 and 2013 for the period January- September at the same spatial resolution (Panda et al. 2017). There are however, important differences in spatial variation between heatwaves in June-September (the monsoon period in which rice is grown) and heatwaves from January - September (which includes the hottest parts of the year before monsoon onset begins).

in June to September the highest number of CTX heatwaves is found in the central and north-western parts of the country. This was found to be different in Panda et al. (2017)'s analysis of the January to September period, in which the frequency of both CTX and CTN heatwaves was greatest in the far east, mid-west and northern tip of India. The highest number of CTN heatwaves between June and September was found in the mid-west of the country, which was also the case in Panda et al. (2017)'s January to September analysis.

Between June and September, the duration is highest in the central and north-western part of the country for CTX and CTN heatwaves, with regions in the west of the country also experiencing relatively longer heatwaves. This contrasts with Panda et al. (2017)'s January to December analysis, which found that although there is significant spatial agreement for CTX heatwaves, CTN heatwaves were longer in the far north and central-south west of the country.

For CTX and CTN heatwave metrics analysed over the rice growing season, both frequency and duration are lowest in the far east, south and south-western coast. This pattern is not seen in Panda et al. (2017)'s January - September analysis.

It seems likely that differences in spatial patterns reflects the influence of the Indian summer monsoon on heatwave dynamics. The areas where the lowest number and shortest duration of heatwaves is observed corresponds well to areas with high annual mean rainfall (Figure 5.3). These results support the hypothesis that heatwave dynamics may be very different in the hot period (March - June) and the cooler and wetter period (June - September). These mechanistic differences may explain the differences in the spatial pattern of heatwave metrics between January - September and June - September.

5.4.2 Heatwaves and rice yields

The results presented in section 5.3.2, demonstrate that over the historical period, daytime heatwaves are more closely associated with reductions in yield than nighttime temperatures. This suggests that maximum daytime temperature thresholds have been crossed more frequently than nighttime thresholds during the rice growing season.

Correlations appear weaker in heavily irrigated areas. The correlation between both the number and duration of daytime heatwaves is clearly weaker in heavily irrigated Punjab than for the rest of the Indo-gangetic plains. The same pattern is seen for both the frequency and duration of EHF heatwaves. This does not appear to be the case for the CTN heatwaves, which suggests that if the weaker correlation between daytime heatwaves and yield is influenced by irrigation, then this affect does not carry over to high nighttime temperatures.

One possible reason for a smaller impact of nighttime heatwaves on rice yields is that in the absence of solar radiation, the beneficial chain between heating and evaporative cooling is not present. In some areas nighttime heatwaves are positively associated with rice yields. It is unlikely that periods of high nighttime temperatures benefit yield. It is more likely that they are associated with periods of high mean temperature, which may increase yield in areas where temperatures are limiting to growth, and remain below heat stress thresholds.

The magnitude of the negative correlations between CTX heatwaves and rice yield are consistent with the share of variance explained by extreme weather events found in Vogel et al. (2019), rather than the stronger impacts found in Lesk et al. (2016) for many areas. However,the breakdown provided in this chapter shows that there are areas with very strong negative correlations between CTX heatwaves and rice yields, while other areas exhibit weaker correlations or correlations of the opposite sign.

While the negative correlations dominate between CTX heatwaves and rice yields, this is not necessarily the case for CTN and EHF heatwaves. In these cases, while the majority of significant correlations are still negative, they are smaller and there are also small patches where correlations of the opposite sign dominate. This suggests that differences in soil, elevation, management practices and pests and diseases may have greater explanatory power than high nighttime temperature events in some parts of major rice growing regions in India. This may also be the result of differences in elevation and local micro-climates, which needs to be explored further.

5.4.3 Irrigation and heatwaves

Section 5.3.3 demonstrated that irrigated grid cells experience fewer of both daytime and nighttime heatwaves. Irrigated grid cells experience shorter daytime heatwaves, and highly irrigated grid cells experience shorter nighttime heatwaves. Irrigation does not appear to have an impact on EHF heatwaves. However, these heatwaves did not occur often and were not present at all in many parts of India.

These results support the theory that high levels of soil moisture interrupt the generation of daytime and nighttime heatwaves. These findings are in agreement with the model-based findings of Thiery et al. (2017), and contrary to the Lobell and Bonfils (2008) findings in California. Fewer and shorter heatwaves in irrigated rice areas suggest that the layer of ponded water on top of rice fields has a quantitatively stronger impact on heatwaves than wet soil. During the monsoon season, the soil would be wet in many non-irrigated parts of the country.

If the fraction of irrigated rice area reduces the frequency and duration of day and nighttime heatwaves, then the introduction of water-saving techniques such as direct seeding of rice may change the exposure of rice cropping systems to heat extremes. Rice systems may then be more vulnerable to heat extremes as a result of reduced transpirational cooling (Jagadish et al. 2015), whilst simultaneously being more likely to experience damaging heatwaves.

5.4.4 Limitations

An inherent limitation to bi-variate statistical analysis is the inability to assess causation. Orlowsky and Seneviratne (2010) note the potential for omitted variable bias in observation based approaches to assessing land surface-atmosphere interactions. In the Indian context, establishing causation in some irrigated rice regions is complicated by the co-variation of irrigation and ozone accumulation in parts of the Indo-gangetic plains (Bonfils and Lobell 2007).

A second important limitation to this observational approach is the underlying assumption that an irrigated fraction means the same thing across grid cells in India. This is fundamentally an assumption about rice growing practices and the amount of water the field is irrigated with. This chapter is therefore making the simplifying assumption that irrigation over the period 1966-2011, was sufficiently similar in nature to interact with heat fluxes analogously. This assumption is intuitively sensible for flooded rice cultivation. Although, the depth of flood water is likely to vary with access to groundwater and electricity, all rice growing fractions of a grid cell would still present a ponded layer of water to the atmosphere. In areas with irrigation that differ by type, for example sprinkler vs. flood irrigation - this assumption would not necessarily hold. Future work could look in more detail at specific geographic regions of India such as Punjab and Harayana, where farmers are likely to have used broadly similar irrigation practices over the period 1966-2011.

A second assumption relevant to the interpretation of the results of this work is that the temperature impacts of irrigation in one grid cell can be separated from rainfall-temperature interactions in neighboring grid cells. This argument also assumes that the impacts on heatwaves from large areas of pooled water are likely to be orders of magnitude larger than any accompanying rainfall-temperature impacts in neighboring grid cells at the resolution of this analysis. However, it should be conceded that downstream impacts of moisture advection may influence temperature in surrounding grid cells. In future work climate and land surface models will be used to study the magnitude of changes to the moisture budget in relation to heatwave occurrence, and compare the impacts of different methods of irrigation.

5.4.5 Future Work

The analysis in this chapter considers the relationship between the fraction of irrigated area and heatwave number and duration. Future work should build upon this result with a more detailed analysis of the impacts of irrigation on heatwaves at higher resolution in each of the major crop growing regions in India. Satellite data can be used to pinpoint the exact location of irrigation and a similar analysis could be conducted with weather station data to test the hypothesis put forward in this paper at more local scales. Lu and Kueppers (2015) found that the impacts of irrigation on heatwaves was significant in highly irrigated landscapes, rather than being a local effect. Testing this hypothesis in the Indian context would be a useful aid to policy makers as sustainable water saving practices become more widespread.

The complex nature of interactions between irrigation and the climate suggests that modelling studies will be needed to further test the hypothesis that irrigation has reduced heatwaves in rice growing regions in India. Coupled land-atmosphere models can be used to explore the relative importance of changes to the energy balance versus impacts on the Indian monsoon and local convection. They can also provide insight into whether the impacts of irrigation varies by environment. Regional scale convection permitting models will be required for these analyses to ensure that the relationship between local increases in the moisture budget, orography and cloud formation are appropriately represented.

As discussed in the limitations section, the analysis in this paper does not distinguish between the amount of irrigation applied in different areas. Modelling studies can test the sensitivity of the relationship between irrigation and heatwaves through systematic sensitivity runs using different amounts of water. This would help policy makers to assess the sensitivity of land surface-atmosphere interactions to different irrigation techniques (for example highly targeted drip irrigation vs. sprinkler vs. flooding). This would require model development, and a next step could involve offline model development of the JULES land surface model (Best et al. 2011) for targeted agricultural applications.

In this chapter, three globally used heatwave metrics examining heatwave number and duration were used to make the results comparable with studies in other parts of the world. These definitions included different aspects of mean, minimum and maximum temperatures. Given the findings in chapters three and four of this thesis, it would also be useful to perform the same analysis for heatwave metrics which include relative humidity. In earlier chapters, it was demonstrated that transpirational cooling is dependent on both temperature and humidity. Metrics that include relative humidity may therefore be better suited to explaining variability in rice yields. Observed relative humidity data was not available for the time period analysed in this study. Future work could use re-analysis data to assess the explanatory power of heatwave metrics that include relative humidity on the variability of rice yields.

5.4.6 Conclusions

Spatial variation in heatwave frequency and duration differs between the rice growing season and the rest of the year. During the rice growing season, daytime heatwaves have been more prevalent than nighttime heatwaves and have had a larger negative impact on yield. Heatwaves that sharply differ from the temperature of the preceding month have been rare during the rice growing period. This suggests that episodes of heat shock have not been common. In the past, the rice crop is likely to have had time to acclimatize to high temperatures over the course of the growing season. Rice yields have been more strongly influenced by longer warm spells than by heat shocks.

This analysis has provided the first empirical analysis of the association between irrigation and heatwaves in India over the historical period. It suggests that irrigation has reduced the frequency and duration of both day and nighttime heatwaves. It is therefore potentially the case, that as new more water saving rice practices are introduced, exposure to damaging heatwaves may increase.

Now that firm empirical foundations have been laid, future work should focus on understanding how the complex interactions between changes to the energy balance, moisture availability and dynamic circulations interact with the mechanisms for heatwave generation. Given the dual needs for adapting to groundwater decline and rising temperatures, model development will certainly be required. The next generation of crop and land surface models will need to ensure that different options for simulating irrigation strategies, heat tolerance and alternative cropping systems are coupled with convection permitting climate models.

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Chapter 6

Discussion and Conclusions

The overarching objective of this thesis was to understand the relationship between crop evapotranspirative cooling and heat stress across scales. This section begins by revisiting the aims and objectives of the thesis and providing a short summary of the relevant findings. This is followed by a synthesis section, which integrates the findings relating to individual objectives with the overarching goal of the thesis. An implications section is then offered to explore the relevance of these findings for the crop breeding and crop modelling communities and to suggest future work.

6.1 Completion of Aims and Objectives

6.1.1 Is transpirational cooling important to heat avoidance and heat tolerance in common bean?

Measurements of leaf and air temperatures for a variety of common bean genotypes were taken from 5 experiments covering ambient, drought stress, heat stress and soil nutrient stress conditions. These observations were compiled into a large data set comprising approximately 7000 observations, and the distribution of leaf and air temperatures were compared. This comparison represented the first comprehensive evaluation of leaf cooling in common bean. The magnitude and variability of leaf cooling was compared for heat tolerant and heat sensitive genotypes in both ambient and humid conditions and in hot and dry conditions. Both physiological and morphological investigations were conducted to understand these differences. This study is the first assessment of the relationship between heat tolerance and leaf cooling in common bean. Machine learning techniques were used to develop a genotype specific leaf temperature model.

This study demonstrated that transpirational cooling is an important heat avoidance mechanism. The magnitude of leaf cooling was found to be large and played an important role in keeping the temperatures experienced by the plant within a photosynthetically functional range. A link between heat tolerance and enhanced transpirational cooling was established. Heat tolerant genotypes were better able to regulate the temperature of their leaves, and this advantage increased in hotter and drier conditions. Heat tolerant genotypes exhibited far higher stomatal conductance and the association between VPD and leaf cooling was also greater for heat tolerant genotypes. These results suggest heat tolerant genotypes are better able to regulate their leaves through enhanced transpirational cooling. It was shown that leaf temperatures can be accurately estimated for heat tolerant and heat sensitive genotypes.

6.1.2 Is transpirational cooling important in modelling the trade-off between saving water and resilience to heat stress?

Transpirational cooling was integrated into the set-up of a state of the art crop model (ORYZA v3). ORYZA v3 was then run for 30 seasons between the years 1980 and 2010 for a grid cell in the Indian Punjab. Two sets of runs were conducted to compare heat stress under current irrigation techniques versus water saving techniques, with and without transpirational cooling. The first set of runs simulated farmers continuously flooding their rice fields throughout the season with transpirational cooling switched on and off. The second set of runs simulated farmers alternate wetting and drying their rice fields with transpirational cooling switched on and off. The runs were then compared to assess the impact of transpirational cooling and irrigation management techniques on the heat stress experienced by the rice crop.

Simulated heat stress and grain yields were found to be extremely sensitive to the inclusion of transpirational cooling in both the continuous flooding runs and the alternate wetting and drying runs. Simulated heat stress reductions in grain yield were far more sensitive to the inclusion of transpirational cooling than to the irrigation management technique applied in the model. These results suggest that modelling the trade-off between saving water and resilience to heat stress is not possible without including transpirational cooling in model set-up. It follows that until uncertainties in modelling transpirational cooling in rice models are resolved, these models will not be able to appropriately inform decision making on one of the greatest challenges to food security in present day south Asia.

6.1.3 Has evapotranspirative cooling from irrigation had an impact on heatwaves?

Seasonal irrigation fraction data sets were prepared and gridded to match available 1 degree by 1 degree air temperature data for the period 1966–2011 for 19 states in India. Globally used heatwave metrics were calculated from maximum and minimum temperatures for the same period. These metrics covered daytime heatwaves, nighttime heatwaves and episodes of heat shock. Grid cells were categorized into non-irrigated, medium irrigated and highly irrigated based on the irrigated fraction data. A permutation test was then used to test whether medium and highly irrigated grid cells experienced fewer and shorter heatwaves than non-irrigated areas.

Fewer daytime and nighttime heatwaves were experienced in irrigated grid cells than in non-irrigated grid cells. Episodic heatwave shocks did not differ in frequency or duration in irrigated and non-irrigated areas. This is likely because they occurred so infrequently during the rice growing season. These results suggest that changes to evapotranspiration from region-wide irrigation has likely reduced the number and duration of heatwaves experienced in rice growing regions. It follows that a move from continuous flooding to water saving practices may increase the risk of damaging heatwaves as temperatures warm. Whether or not this turns out to be the case is a more complicated question than can be answered empirically from historical data; global heating induced changes to the Indian monsoon and regional circulation and dynamics will interact with reductions in region-wide irrigation and hotter temperatures.

6.1.4 Synthesis

The scientific investigations in this thesis have examined the importance of evapotranspirative cooling for heat avoidance across spatial and temporal scales. At the plant scale it has been shown that evapotranspirative cooling plays an important role in both heat avoidance and heat tolerance. At the field scale it has been shown that the simulated trade-off between saving water and heat stress is dominated by evapotranspirative cooling. At the region-wide scale, there is evidence to suggest that evapotranspirative cooling may have reduced the frequency and duration of heatwaves experienced in irrigated areas. This implies an atmospheric mechanism through which evapotranspirative cooling can mediate the impacts of global heating on future yields.

Each of these scales involves a trade-off between evapotranspirative cooling and water use. For breeders, selecting for genotypes which exhibit enhanced transpirational cooling only reduces heat stress if sufficient water is available to take advantage of greater stomatal conductance. In hot and wet environments, there is a clear advantage to enhanced transpirational cooling, while in environments where hot and dry conditions often occur concurrently, water spending may be a disadvantage. At the field scale, simulations suggest a trade-off between the use of water saving technologies and evapotranspirative cooling. At the regional scale, empirical analysis suggests a potential trade-off between groundwater availability and the frequency and duration of heat extremes.

Decisions made at each scale may be interlinked. Breeding programs that aim to select for plants with an enhanced ability for transpirational cooling are influencing water use patterns at field scale. Farmers choosing to save water through irrigation management techniques, or by switching to non-irrigated crops are also choosing new land use patterns. If enough farmers do so, land surface–atmosphere interactions may be altered. Evapotranspirative cooling across spatio-temporal scales emerges as a useful lens through which to analyse how decisions at one scale can impact the likelihood of heat and drought stress at others.

6.2 Implications for breeders and future work

One of the most fundamental theories in plant science states that greater stomatal conductance increases assimilation of carbon and subsequently increases yield (Roche 2015). It is also well established that greater stomatal conductance increases potential transpiration and evaporative cooling. The connection between leaf temperature and yield under potential, drought and heat stress conditions has been well studied in wheat. The evidence to date suggests that wheat genotypes that exhibit enhanced transpirational cooling are higher yielding in potential (Aisawi et al. 2015), hot and dry conditions (Amani et al. 1996; Mason and Singh 2014). Advances have also been made in understanding the physiological mechanisms underlying differences in leaf cooling, and recent work suggests a common genetic basis for cooler wheat plants (Pinto and Reynolds 2015). The advent of aerial measurements of canopy temperature has advanced the potential for using canopy temperature in wheat breeding programs (Deery et al. 2019).

No such consensus on the importance of canopy temperature for heat tolerance exists for common bean. The results of this thesis represent a first step towards testing the hypothesis that enhanced transpirational cooling may increase heat tolerance in common bean. Initial results are encouraging; the heat tolerant variety exhibited both increased stomatal conductance and cooler leaf temperatures. When viewed in combination with previous studies, which show that cooler common bean varieties exhibit greater rooting depth, some initial similarities between the findings of this thesis and the more comprehensive work done in wheat breeding programs are noted. The results in chapter 3 have resulted in ongoing collaborations with the CIAT bean breeding program to explore the possibility that enhanced transpirational cooling is associated with heat tolerance in common bean. A second test of association between leaf cooling and heat tolerance has been conducted, and the results support the conclusions presented in chapter 3.

Future work will require bean breeding programs to test more heat tolerant and heat sensitive common bean genotypes to see if these results hold in a larger sample of genetic material. The heat tolerant genotype most tested in chapter 3 is an Andean genotype. As discussed in chapter 1, recent trials at CIAT have found that Tepary and common bean crosses exhibit higher levels of heat tolerance. In chapter 3, the heat sensitive Andean genotype with a Tepary cross were compared in ambient temperatures and in more humid conditions. Initial results showed that the Tepary cross did cool more than the heat sensitive Andean genotype in ambient conditions, but data was not available to test if the difference in cooling increased at higher temperatures. Future work should test whether greater stomatal conductance is also a mechanism for enhanced leaf cooling in the Tepary cross.

In addition to testing for enhanced cooling in Tepary crosses, it will also be necessary to understand the share of enhanced cooling attributable to evapotranspiration. The results from chapter 3 suggested that the heat tolerant genotypes may also have had thicker leaves. Although differences in leaf thickness were not always statistically significant, they were consistent. This raises the possibility that enhanced leaf cooling may be the integrated effect of greater transpirational cooling and morphological features that favour thermal stability. Disentangling these effects will be important to understanding trade-offs in different environments. It will also help advance understanding of the evolutionary underpinnings of enhanced leaf cooling.

If enhanced transpirational cooling is robust across a wide range of heat tolerant genotypes, it will also be necessary to test how the strength of the effect varies in different environments. The relationship between air temperature, relative humidity and leaf temperature identified in this thesis suggests that the strength of any advantage conferred through enhanced transpirational cooling is likely to vary by environment. Harnessing enhanced transpirational cooling for heat avoidance will require careful categorisation of the target population of environments in which an advantage is conferred.

A combination of big data and models can be employed by bean breeding programs for this purpose. Infra-red measurements of canopy temperatures has been successfully used in wheat breeding programs (Deery et al. 2019), and can be used to assess differences in canopy temperature between genotypes. This can be combined with large samples of multi spectral data taken using the handheld MultispeQ device to evaluate the hypothesis advanced in this thesis at both the plant and field scales. The model developed in this chapter (and future models built on similar principles) can be used to estimate the potential value of enhanced transpirational cooling across target population of environments of interest.

In addition to examining a broader GxE evidence base for an association between enhanced transpirational cooling and heat tolerance, it will also be necessary to conduct a multi-environment trial testing the hypothesis that enhanced transpirational cooling results in higher yields. As discussed at length in Tardieu (2011) it is possible for a trait to be advantageous in some environments and detrimental in others. The clear trade-off between heat avoidance and water use inherent to greater evaporative cooling suggests that this trait may not be advantageous in water-limiting circumstances. Given the heat tolerance of Tepary bean crosses, which evolved in arid conditions, it remains possible that heat and drought tolerance co-evolved. If this is the case, then enhanced transpirational cooling may have co-evolved with deeper rooting, which would confer an advantage in a wider range of water limiting conditions. The CIAT bean breeding program have embarked upon a series of experiments to test whether enhanced transpirational cooling remains advantageous under water limiting conditions.

Leaf temperature models can be applied directly to assess the impact of genotypic differences in transpirational cooling on summary statistics such as threshold exceedence or accumulated degree days (Neukam et al. 2016). However, in order to understand the emergent effects of differences in transpirational cooling, leaf temperature models would need to be introduced to process-based crop models. These models are able to simulate complex feedback effects between plant and environment (Bertin et al. 2009) and provide the integrated impact of leaf cooling on plant growth and development. The introduction of transpirational cooling to crop models may not be a simple job. Functions within crop models are often parameterized using air temperatures and these functions would need to be rewritten to accommodate leaf temperatures (Neukam et al. 2016).

6.3 Implications for crop and land surface modellers and future work

The work in this thesis has demonstrated that leaf cooling in common bean is large enough to be an important heat avoidance mechanism. This supports the argument made that both crop and land surface models need to incorporate canopy temperature to improve heat stress assessments (Webber et al. 2016) (Dong et al. 2017). It has also been shown that the magnitude of transpirational cooling dominates attempts to quantitatively assess one of south Asia's most pressing food security challenges.

Although there is now consensus in the literature that models should use the temperature of the plant rather than the temperature of the air, there is no consensus on the approach or specific methods by which this should be done. To date, most models of canopy / organ temperature are trained on experimental data for one or two seasons in one or two locations. These models are often able to perform well on subsets of the data that are used to build them (Neukam et al. 2016; Julia and Dingkuhn 2013; Van Oort et al. 2014; Webber et al. 2016).

Section 1.4.3.1 of the Introduction chapter discusses a recent multi-model comparison of canopy temperature models employed in crop models demonstrates that empirical models, energy balance models and more complex models all obtain low levels of accuracy when tested across a greater number of field experiments and environmental conditions (Webber et al. 2018). In general, empirical models and more complex energy balance models performed better than standard approach energy balance models. Neither empirical nor complex energy balance models consistently out performed the other.

The modelling work in chapter 3 of this thesis suggests that low accuracy is unlikely to be the result of genotypic differences in transpirational cooling. Model accuracy was very high even when using temperature and relative humidity as inputs and not including a genotype dummy variable. One possible explanation is that the model generated in chapter 3 uses air temperatures close to the canopy, rather than 2 meter air temperatures. If crop canopies are creating their own micro-climates, this would explain low skill when using inputs collected at 2 meters. Future work could test for differences between 2 meter air temperatures and temperatures just above the canopy.

All of the energy balance models used in the inter-comparison employ the Penman Monteith equation to derive canopy temperature from the estimated latent heat flux (Webber et al. 2018). This equation was designed for estimating average ET over large areas (Dong et al. 2017) and does not consider differences in canopy structure and boundary layer dynamics, which are known to influence tissue temperatures (see 3.3.3) (Dong et al. 2017). In chapter 3, it was shown that within - species variation in stomatal conductance, leaf thermoregulation and within-canopy temperatures can be large in common bean. If such differences can be large within-species, it follows that differences between crops are likely to be at least as large or larger. Simple energy balance models, do not distinguish between crops, which suggests that these differences limit their accuracy.

Based on the results of this thesis and progress in canopy temperature modelling to date, the following avenues of future work are proposed. The first avenue could explore the benefits of empirical canopy temperature modelling based on large data sets that represent the genotypic and environmental variation observed in field conditions. The advent of open source MultispeQ data promises a move from generating canopy temperature models on a handful of field experiments to hundreds of thousands of data points uploaded from experiments all over the world. Machine learning techniques (such as the one used in chapter 3) can be specifically designed to navigate the bias-variance trade-off inherent to empirical approaches.

The success (or lack thereof) of this first avenue of enquiry will provide a quantification of the potential for empirical approaches to capture the complex dynamics of canopy temperature. Such models can be designed to differentiate within and across species. The data on which current models are trained is far too small to provide a genuine understanding of the limits to predictive power for modelling canopy temperature.

The second avenue of enquiry could build on larger scale energy balance approaches to modelling canopy temperature at an ecosystem scale. At these scales, it is not realistic to expect data on leaf orientation, canopy structure and the myriad subtleties involved in a detailed micro-meterological approach. Advances in thermal imaging data from satellites provide a second newly available data source for estimating the difference between canopy and air temperatures (Still et al. 2019). This data source could be used to develop models of canopy-air temperature differential at ecosystem and regional scale.

Different approaches at different spatial scales may be necessary to ensure that model complexity is suitably matched with available observations. Challinor and Wheeler (2008) and Falloon et al. (2014) argue that model complexity should reflect the potential to constrain parameterisations with observations. At plant and field scale, tools like MultispeQ and rapid throughput thermal cameras allow detailed observations to be taken of both micro-meterology and leaf thermal attributes (Deery et al. 2019). At the land surface scale, such observations are not available, and this situation is unlikely to change soon.

The need to vary approaches by scale also reflects scaling issues observed in real-world systems. Jones et al. (2009) shows that extrapolation techniques taken from measurements of leaf temperature in controlled conditions do not scale to the level of the canopy in field observations. Further, controls on canopy temperature can be more or less tightly coupled with meterological conditions throughout the day (Kim et al. 2016). Kim et al. (2016) show that there is a stronger relationship between daily temperatures and soil moisture than is true for 30 minute temperatures. Further, they show that during the warmer afternoon period, canopy temperatures are less closely coupled to air temperatures, as net ecosystem exchange becomes the dominant control on canopy temperature depression (Kim et al. 2016).

Finally, the approach to canopy temperature simulations should reflect the purpose at which model output is directed. There is a need for highly detailed machine learning approaches aimed at genotypic selection. Equally, there is a need for far more zoomed out approaches concerned primarily with improving simulations of energy fluxes above vegetation. Remote sensing from satellites will undoubtedly contribute to the development of next generation land surface models (Good et al. 2017). The availability of these data sets, combined with recent successes using deep learning algorithms to estimate crop productivity from satellite images (You et al. 2017), provide an interesting route for further exploration.

6.4 Conclusion

This thesis has demonstrated that evapotranspirative cooling enables heat avoidance at plant, field and regional scales. At the plant scale, chapter 3 provides the first empirical evidence that heat avoidance is a pathway to heat tolerance in common bean. At the field scale, chapter 4 suggests that transpirational cooling is the dominant process in modelling the trade-off between saving water and heat stress in one of South Asia's most important rice growing regions. Irrigation decisions at the farm scale are linked to heat avoidance at regional scale. Chapter 5 showed that irrigated areas experienced fewer and shorter heatwaves than non-irrigated regions.

This thesis was motivated by applied science goals. The first of these goals was to contribute towards efforts to breed heat tolerant beans. Chapter 3 provides a first step in building the evidence base for a breeding program based on heat avoidance as well as providing modelling tools to test the value of enhanced cooling in target population environments of interest. This work provided the foundation for ongoing collaboration with the CIAT breeding program to explore the possibility of developing a large-scale breeding program based on canopy cooling. This approach has been successful for breeding heat tolerant varieties of wheat, and early signs suggest that the same may be possible for beans.

The second applied science goal of this thesis was to explore the trade-offs between employing water saving technologies and retaining resilience to heat stress in Punjab's rice growing system. Chapter 4 suggests that transpirational cooling is a dominant process in assessing this trade-off. It also suggests that state of the art crop models are unable to simulate the complex interactions between water and heat with sufficient confidence to quantify this trade-off. Chapter 5 suggests that, as cropping systems in Punjab adapt to reduced groundwater availability, planning may need to incorporate the combined effects of rising temperatures and changes in land surface properties.

Future work will need to engage in model development to improve simulation of evapotranspirative cooling across scales. This has become a recent focus in the crop modelling and land surface communities, as the importance of plant temperature in heat stress assessments has gained consensus. However, model accuracy at the field scale remains low. The advent of new sources of open source rapid phenotyping data, combined with machine learning techniques designed to navigate the bias-variance trade-off present a new avenue of exploration that may improve model performance. At wider scales, advances in thermal imaging from remote sensing may aid land surface models in moving past the limitations of simplistic energy balance based approaches of the past. The same approaches are unlikely to work across scales. Model complexity and data sources may therefore vary for simulation of plant temperatures at different scales.

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