Leaf- to field-level compound effects of warm and dry conditions on crops and potential mitigating strategies

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Leaf- to field-level compound effects of warm and dry conditions on crops and potential mitigating strategies

Abstract

Ongoing climate change has been threatening global food security. Under climate change, increasing risk of hot and dry conditions (termed compound events) is projected in many agricultural regions. Compound events cause detrimental effects on crops, yet their effects have rarely been quantified based on modeling approach. In this thesis, we established mechanistic and statistical models to analyze crop canopy temperature, transpiration rate, and yield responses to compound effects. We aimed to explore the compound effects on crops and help identifying adaptation strategies. Our results suggested that hot and dry conditions interacted in enhancing canopy temperature, i.e. the risk of potential crop heat stress, and crop yield losses. Both canopy temperature and yield losses increased from wet-cool conditions to dry-hot conditions. Short-term intra-seasonal conditions and growing season averages were equally important in assessing crop responses to compound events. More intermittent precipitation regimes and longer dry spells negatively affected canopy temperature and yields even when the mean climatic conditions remained unaltered. Rainfed crop yields showed yield maximizing precipitation, which increased with temperature. As one of the adaptation strategies, irrigation could alleviate but not cancel the negative effects of adverse climate. Another adaptation is a shift from annual to perennial grain crops. Whether perennial grain crops are less vulnerable to heat and water stress depends on some key plant traits, such as leaf area index, which should be targeted for future breeding program to adapt to climate change.

Keywords: Climate change, compound effect, adaptation, canopy and leaf temperature, crop yields, modeling.

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Blandade effekter av löv till fältnivå av varma och torra förhållanden på grödor och potentiella mildrande strategier

Sammanfattning

Den globala livsmedelssäkerheten hotas av de pågående klimatförändringarna. Klimatförändringar förväntas leda till ökande risk för varma och torra förhållanden (här benämnda samverkande effekter) på många platser där jordbruk bedrivs. Samverkande effekter skadar jordbruksgrödor, men det finns få studier av effekten av samverkande effekter på jordbruksgrödor baserade på modelleringsmetodik. I denna avhandling etablerade vi mekanistiska och statistiska modeller för att analysera hur bladtemperaturen, transpirationshastighet och grödans avkastning påverkas av samverkande effekter. Vårt syfte var att utforska hur grödor påverkas av samverkande effekter, samt hjälpa till att identifiera anpassningsstrategier för att minska de negativa effekterna. Våra resultat indikerade att kombinationen av varma och torra förhållanden gav den högsta bladtemperaturen, och därmed den högsta risken för värmestress hos grödan och minskad avkastning. Både bladtemperaturen och avkastningsförlusterna var högre med våta och svala förhållanden än med torra och heta förhållanden. Hur temperatur och nederbörd varierade inom säsongen och deras säsongsmedel spelade lika stor roll för hur de samverkande effekterna påverkade grödan. Mer periodisk nederbörd och längre torrperioder ökade bladtemperaturen och minskade avkastningen även när de genomsnittliga klimatförhållandena förblev oförändrade. Grödor som inte bevattnats hade en specifik mängd nederbörd som var gynnsam, och denna ökade med ökad temperatur. Bevattning av grödan visade sig kunna minska men inte eliminera de negativa effekterna av samverkande effekter. En annan anpassning är en övergång från årliga till fleråriga spannmålsgrödor. Huruvida fleråriga spannmålsgrödor är mindre utsatta för värme och vattenstress beror på vissa viktiga växtegenskaper, såsom bladyteindex, något som framtida växtförädlingsprogram bör rikta in sig på för att anpassa grödor till framtida klimat.

Nyckelord: Klimatförändringar, samverkande effekter, anpassning, och bladtemperatur, avkastning, modellering.

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Dedication

To my parents

“Be fruitful and increase in number; fill the earth and subdue it.”
Genesis 1:26

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Luan, X. & Vico, G. (2021). Canopy temperature and heat stress are increased by compound high air temperature and water stress, and reduced by irrigation–A modeling analysis. Hydrology and Earth System Sciences, 25, pp. 1411-1423.

II. Luan, X., Katul G.G., & Vico, G. (2021). Comparing leaf temperature and transpiration rates in annual and perennial grain crops (manuscript)

III. Luan, X., Bommarco, R., Scaini, A. & Vico, G. (2021). Combined heat and drought suppress rainfed maize and soybean yields and modify irrigation benefits in the USA. Environmental Research Letters, 16(6), p. 064023.

IV. Luan,X., Bommarco, R., & Vico, G. (2021). Yield maximizing precipitation increases with temperature for rainfed maize and soybean in the U.S. (manuscript)

The contribution of Xiangyu Luan to the papers included in this thesis was as follows:

I. Main author. Developed the codes of the model and wrote the paper with GV, performed analyses, ran simulations and created the figures. GV conceived the idea and developed the model.

II. Second author. Ran simulations and created most figures. GV conceived the idea, developed the model with the support from GGK, and led the writing.

III. Main author. Conceived idea and wrote the paper together with GV and RB, collated and analyzed the data, developed the codes of the model, and created the figures with GV.

IV. Main author. Collated and analyzed the data, created the figures, developed the codes of the model, and led the writing. GV and RB conceived the idea and supported the data analysis and paper writing.

Symbols and Abbreviations

Symbols	Description
P_{CHS}	Fraction of days that T_c exceeds threshold temperature
T_c	Crop canopy temperature
CDD_{GS}	Duration of the longest dry spell during growing season
P_{GS}	Precipitation total (depth) during growing season
T_{CDD}	Average temperature during CDD_{GS}
T_{GS}	Average temperature during growing season

Abbreviations	Description
eCO_2	Elevated carbon dioxide
LAI	Leaf area index
LMM	Linear mixed model
WUE	Water use efficiency

1. Introduction

1.1 Burgeoning food demand and the food security issue.

Feeding humanity with increasing food demand is a well-recognized issue for next 30 years. The factors that influence food demand are manifold, among which, rising population, dietary preferences, and increasing biofuel consumption play important roles (Keating et al., 2014). By 2050, the global population will peak ~10 billion (UN, 2013) with a rising level of affluence. Increasing population will directly drive the food demand, and increasing level of affluence is usually concomitant with more animal products consumption (Robinson & Pozzi, 2011). Indeed, dietary preferences, especially the amount of animal products that we consume is a pivot to estimate food demand (Bajželj et al., 2014). Currently, crops are the major forage to animal feeds. Due to the low conversion coefficient from crop to animal products, consuming animal products means enhancing the needs of crop production, which in turn, requires more environmental resources (Davis et al., 2016). Consistent projections reveal that food demand will drastically drop if we shifted in diets with fewer animal products (Stehfest et al., 2019; Alexander et al., 2016; Davis & D'Odorico, 2015; Bajželj et al., 2014). In addition, a need to enhance energy security, reduce greenhouse gas, and strengthen rural development stimulate the use of biofuels (Koizumi, 2015). Crop also makes up a major share of biofuel feedstock (Davis & D'Odorico, 2015; Koizumi, 2015). As a result, more crop production is needed to meet increasing biofuel demand. Taking all these factors together, we need to double the crop production to meet the food demand by 2050 (Tilman et al., 2011).

Increasing crop production has different pathways, wherein sustainable ones are widely advocated, which are often termed as ‘sustainable intensification’ (Foley *et al.*, 2011; Tilman *et al.*, 2011; Godfray *et al.*, 2010). One important notion of sustainable intensification is to increase crop yields rather than further expand croplands, because the latter meet the food demand at the cost of reducing biodiversity and increasing greenhouse gas emissions (Garnett *et al.*, 2013). In the past decades, yields of staple cereal crops including wheat, maize, and soybean have achieved continuous increase at the global scale (Ray *et al.*, 2013). However, recent evidence in many regions shows that crop yields have already stagnated (Ray *et al.*, 2012), which implies a caveat that the past yield increase may not persist in the future.

Climatic conditions, particularly temperature and precipitation, are key factors affecting crop yields (Matiu *et al.*, 2017). In the past decades, climate variability explained up to 60% of the yield variability (Ray *et al.*, 2015), and more than half of the food shocks (Cottrell *et al.*, 2019). In the context of climate change, crops face warming temperature and altered precipitation regime, which bring uncertainties in predicting the crop yields and hinders future enhancement of crop yield. Indeed, climate change has already adversely impacted crop yield (IPCC, 2019; Moore & Lobell, 2015; Osborne & Wheeler, 2013; Lobell *et al.*, 2011; Lobell & Field, 2007), and will continue to do so in many regions in the future (IPCC, 2019; Challinor *et al.*, 2014; Rosenzweig *et al.*, 2014). Thus, it is vital to advance the understanding of crop responses to the changing climate, especially its responses to temperature and precipitation. This advancement in knowledge will ensure food security for now and future, and guide us in providing suitable adaptation strategies.

1.2 Climate change: its evolution in the past and future projections

The changing climate affects not only the mean climatic conditions, but also their variability. Under climate change, many climatic factors are altered, such as temperature, precipitation, and atmospheric concentration of CO_2. Here, we focused on two major factors – precipitation and temperature, to introduce their observed changes, projections in both climatic mean conditions and variability. In addition, their covariance, i.e., the concurrent low precipitation and high temperature is discussed.

1.2.1 Change in temperature

The emission of anthropogenic greenhouse gases is the dominant cause of global warming (IPCC, 2014). Earth surface temperature has successively increased in the last three decades, and became warmer than any preceding decade since 1850 (IPCC, 2014). During the past century, the average temperature for the earth surface has increased by 0.85°C (IPCC, 2014), and ~1°C of increase for croplands (Zhao et al., 2017).

On the basis of the current rate of temperature increase, global average temperature is expected to increase by 1.5 to 2°C by 2050 (IPCC, 2014). The scenario of 2°C warming will bring more severe consequences than 1.5°C warming. It is noteworthy that land and sea exhibit different magnitudes of warming under climate change, i.e., land warms more than sea. In addition, in many land regions, heat extremes warm faster than seasonal mean temperatures (Horton et al., 2016). Under the warming scenario of 2°C, there is a strong evidence suggesting that the frequency, intensity, and duration of heat extremes will increase in all land regions (IPCC, 2018). Thus, in the future, croplands will be exposed to warmer growing seasons, with higher average temperature and more frequent and severe heat extremes.

1.2.2 Change in precipitation

Globally, the impacts climate change on precipitation are less certain compared with temperature for the past and future (IPCC, 2018). The mid-latitude of the northern hemisphere, on average, had shown precipitation increase since 1901. Other latitudes had less certainty, both positive and negative long-term precipitation trends were found (IPCC, 2014).

Projections in the change of mean precipitation show a marked difference between the warming of 1.5 °C and 2 °C. At warming of 2°C, the Mediterranean region is predicted to decrease in precipitation, while high latitude regions show precipitation increase. Even under mild warming levels, meteorological droughts (defined as droughts due to the deficit precipitation) will be amplified in many regions (Taylor *et al.*, 2018; Lehner *et al.*, 2017; Wartenburger *et al.*, 2017), due to the increased natural variability (Berg & Hall, 2015). Also, soil water loss can be further intensified via enhanced soil evaporation under warming temperature, which in turn can exacerbate soil water deficit.

1.2.3 Change in the compound event (combination of low precipitation and high temperature), and its definition.

In many regions, the combination of rising temperature and altered precipitation patterns leads to increasing risks of concurrent high temperature and low precipitation – compound event hereafter.

According to IPCC (IPCC, 2012), the compound event is categorized as three types:

"(1) two or more extreme events occurring simultaneously or successively, (2) combinations of extreme events with underlying conditions that amplify the impact of the events, or (3) combinations of events that are not themselves extremes but lead to an extreme event or impact when combined. The contributing events can be of similar (clustered multiple events) or different type(s)."

In this thesis, we followed the definition of compound event given by IPCC, but excluded the compound events that are comprised by successive extreme events.

The risk of compound event has continuously increased in the past decades (Ridder *et al.*, 2020; Manning *et al.*, 2019; Mazdiyasni & AghaKouchak, 2015). Compound events aggravate yield losses in agriculture. Assessing one climatic driver or event at a time can result in incomplete perception of climatic risk (Trnka *et al.*, 2014). For instance, assessing either low precipitation or high temperature alone can potentially underestimate the risks as they co-occur (Zscheischler *et al.*, 2018). Hence, a rigorous assessment of the agricultural risk should involve in multi-climatic factors, particularly when the combination of factors causes additional effect.

1.3 Key abiotic factors to crops physiological responses

Crops respond to both mean climatic conditions, and their variability (Porter & Semenov, 2005). As discussed in the section of 1.2.2, altered precipitation patterns result in either increase or decrease precipitation totals, whereas temperature is more certain to increase. Intensified droughts and heat stress are also anticipated when considering the change of intra-seasonal conditions (IPCC, 2018). In addition, warming without increment precipitation can enhance the evapotranspiration rates. Under these climatic conditions, four relevant physiological stressors are most likely to occur and were included in this thesis: they are heat, water stress, water excess, and heat and water combined stress.

1.3.1 Crop responses to heat stress (high air temperature)

Temperature negatively affects crop growth and development once crop temperature ranges (or cardinal temperatures) are exceeded. For each crop species, its temperature range is unique, and varies with developmental stages. These ranges are defined by minimum, optimum, and maximum temperatures (Sanchez et al., 2014; Hatfield et al., 2011). Crop key physiological responses to temperature, including growth rate, enzyme activity, photosynthesis, and respiration rates generally follow bell shapes (Figure 1). The response rates, such as photosynthesis and enzyme activity, rise quickly from minimum temperature, and peak at optimum temperature. The response rates start to decline as temperature exceeds the optimum, and is commensurate with the rising rates. As temperature exceeds maximum temperature (upper cardinal temperature), crop response rates cease. The maximum temperature is often regarded as a threshold of crop heat stress, above which crops are subject to severe, or irreversible damage (Lamaoui et al., 2018).

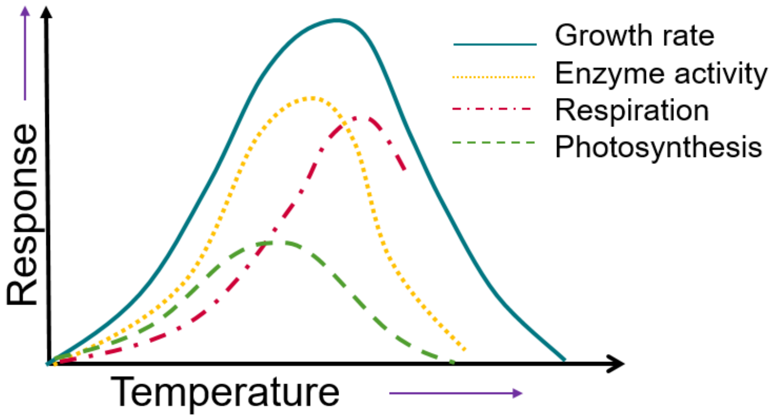

Figure 1. Crop physiological responses to temperature. Specific responses are noted in legend (Source: Hasanuzzaman et al., 2013).

High temperature above this threshold affects crop in many aspects, including crop growth, development, and reproductive processes (Iizumi &

Ramankutty, 2016; Hatfield & Prueger, 2015; Asseng *et al.*, 2011). Observations from fields or controlled environments reveal that high temperature can reduce leaf chlorophyll, photosynthetic capacity, seed set, grain number per spike; cause kernel abortion, and pollen sterility (Narayanan *et al.*, 2015; Pradhan & Prasad, 2015; Lobell *et al.*, 2012). In addition, high temperature cause leaf senescence and accelerate crop growth and development, which shortens the period of crop photosynthesis (Rashid *et al.*, 2019; Lobell *et al.*, 2012). Ultimately, the exceedance of temperature above threshold can lead to drastic yield losses (Schlenker & Roberts, 2009), as a synthesized outcome of all negative effects from physiological processes.

1.3.2 Crop responses to water stress

Soil water is essential to crop growth and development. Low precipitation can result in soil water deficit, which reduces plant stomatal conductance, in turn affecting plant photosynthesis. Water stress also limits cell expansion and hence crop growth and development (Farooq et al., 2009). As a result, water stress renders small leaf size, reduced stem elongation, plant height, and root proliferation. Similar to the effect of high temperature, the damaging effect of water stress also depends on species and their developmental stage (Daryanto et al., 2017). In addition, water stresses with different intensity, frequency, and duration lead to different magnitudes of crop damage (Gupta et al., 2020). Ultimately, water stress impairs crop yield quantity and quality, for instance, grain weight, and grain yields are decreased (Anjum et al., 2017; Lawlor & Tezara, 2009).

1.3.3 Crop responses to water excess

Apart from water stress, water excess is also detrimental to crop growth and yields. Water excess can occur during wet years or heavy rainfall events. Water excess limits crop growth via nutrient leaching, anoxic environment due to waterlogging, increasing plant disease and insect infestation because of proliferous fungi and bacteria (Kleinman et al., 2006; Rosenzweig et al., 2002; Rosenzweig et al., 2001). Past evidence based on modeling approach confirmed large yield losses under water excess (Li et al., 2019; Rosenzweig et al., 2002).

1.3.4 Crop responses to combined stress (combined heat and water stress)

The plant physiological signaling pathways to heat and water stresses are largely unique. Hence, the final damaging effects cannot be simply summed as the effects from individual stresses (Zandalinas et al., 2018; Suzuki et al., 2014). Water stress inhibits crops' thermoregulation ability by evaporative cooling. Limited evaporative cooling adds extra warming on crop canopy regardless of the levels of ambient air temperature (Neukam et al., 2016; Siebert et al., 2014). As a consequence, crops are more likely to drift from their optimum temperature ranges, when they are subject to combined stress.

Indeed, as heat and water stress co-occur, more severe crop damage can be observed in plants. The crop damage usually displays a synergistic pattern, which means the damaging effect is larger than the sum of their individual effects. Observations from the field and controlled-environment experiments reveal that crop growth and physiological processes, including photosynthesis rate, chlorophyll content, life cycles, are synergistically damaged under the combined stress conditions (Hlaváčová et al., 2018; Mahrookashani et al., 2017; Prasad et al., 2011). Consequently, at the reproductive stage, most crop yield traits, including spikelet fertility, grain numbers, grain weight, harvest index, and grain yield, show synergistic damaging pattern under combined stress (Cohen et al., 2021; Hlaváčová et al., 2018; Mahrookashani et al., 2017; Prasad et al., 2011).

1.4 State of the art of studies on compound events on crops, and major challenges

Despite the well-known physiological mechanisms of crop responses to the combined stress on causing synergistic damage to crops, the simulation and quantification of such damage on crops growth and yields are largely lacking or remain elusive (Rötter *et al.*, 2018; Matiu *et al.*, 2017; Tubiello *et al.*, 2007). As aforementioned, heat and water stresses can occur with different characteristics, which differ in timing, duration, and intensity during crop growing periods. The co-occurrence of two stressors is thus complex in determining crop damage due to many combinations of two stressors varying in their characteristics. This renders the assessment via experiments exploiting combination unpractical. Crop models can serve as a powerful tool to enable the quantification and assessment of potentially damaging effects on plant physiology and crop yield. Further, crop models can help identifying or optimizing adaptation strategies, to reduce the negative effects of different climatic scenarios (Peng *et al.*, 2020).

Crop models, in general, can be categorized into two types: mechanistic (process-based) models, and statistical (empirical) models. Mechanistic models rely on physical and biological principles, which allows the simulation to be transferable to other locations by altering the simulation parameters. However, the parameterization for the models is not always effortless. Sophisticated mechanistic models usually thoroughly describe the processes by including a series of mechanisms. As a consequence, these models require a number of parameters, which to some occasions, are not directly available. In addition, mechanistic models also allow for simulating the use and allocation of captured resources, such as water and nutrient, which is helpful in assessing the advantages and disadvantages of various adaptation strategies to environmental conditions (Jones *et al.*, 2017). For instance, by using mechanistic models, suitable irrigation strategies (Grassini *et al.*, 2011), management measures, such as early sowing and nitrogen fertilizer applications, as well as crop traits and breeding recommendations were explored to adapt to the changing climate (Hernandez-Ochoa *et al.*, 2019). In contrast, the statistical models require less effort in quantifying the impacts of certain climatic conditions on crop damage, which makes the model advantageous in assessing crop responses to certain climatic conditions without much model parameterization. However, simulation results from statistical models can be confounded by other factors that are not accounted in the models, which can yield biased results if applied to other locations with dissimilar conditions of these unaccounted factors.

Most crop models, both mechanistic and statistical ones, currently focus on dealing with the effects of heat and water combined stress without consideration of their interactions (Rötter et al., 2018), i.e. the compound effects. This renders the impact assessment, for instance, heat stress on the crop temperature and yield losses underestimated under dry conditions, or overestimated under wet conditions (Matiu et al., 2017; Siebert et al., 2017). It is thus essential to well represent the compound effects of water and heat stress in crop modeling simulations, for both mechanistic and statistical models, to provide rigorous adaptation assessment.

Current mechanistic crop models underperform in simulating compound events (Liu *et al.*, 2016; Barlow *et al.*, 2015), especially when estimate crop yield losses under extreme climate (Schewe *et al.*, 2019). One explanation for model suboptimal performance is the complex crop physiological responses to combined abiotic stressors are not well represented in the model (Peng *et al.*, 2020). For example, most models employ air temperature instead of canopy temperature to quantify crop heat stress, without properly integrating canopy energy budget and plant hydraulics in their simulations. Yet, crop key growing stages like reproduction, crop spike, and grain physiological activities are more related to the canopy temperature than ambient air temperature (Jagadish *et al.*, 2021; Matsui *et al.*, 1997). Canopy temperature shows more accurate estimations on the compound effects on crop yield (Gabaldón-Leal et al., 2016; Siebert et al., 2014; Rezaei et al., 2015), mainly because it can reflect extra warming once the crop is subject to water stress and reduce its stomatal conductance. However, the state-of-art canopy temperature models do not explicitly include the canopy energy balance (Webber *et al.*, 2016; Fang *et al.*, 2014), or use semi-empirical approaches to incorporate plant water availability into simulations (Webber *et al.*, 2018; Webber *et al.*, 2017). Canopy temperature models that more mechanistically account for plant water status, together with more explicit calculation of canopy energy balance, are needed to assess the impacts of compound events.

In parallel, few state-of-art statistical models consider the interaction of heat and water stress on crop yields. Currently, models that consider the compound effects are done at the national level (Matiu et al., 2017; Zscheischler et al., 2017; Hawkins et al., 2013), or field level (Carter et al., 2018), and confirm the synergistic yield reduction. At the regional level, statistical analyses that account for the compound effects have rarely been done. In addition, most statistical models utilize the yield data without differentiating the yields from rainfed cropping and irrigated cropping, which can confound the true soil water status. Consequently, yields losses from the mixture of rainfed and irrigated land can be underestimated in rainfed-dominated regions, and overestimated in irrigated-dominated regions.

We need to advance the model performance by considering the compound effects on crops. Specifically, for mechanistic models, accurate simulation on yields under compound events requires employing canopy temperature instead of air temperature to represent certain physiological processes. It is thus requires rigorous modeling for obtaining crop canopy temperatures, which should be based on the more mechanistic calculation of energy balance compared to current ones, and more direct relationship of plant water availability and stomatal conductance. In statistical models, the interactions of heat and water stress should be considered when regressing crop yields by temperature and precipitation. In addition, crops harvested from irrigated cropping and rainfed cropping should be discerned, because of the buffering role of irrigation on crop responses to water and heat stresses.

1.5 Potential adaption strategies to climate change.

Irrigation is beneficial to mitigate the crop damage caused by adverse climatic conditions (Vogel et al., 2019; Li & Troy, 2018; Tack et al., 2017; Zhang et al., 2015). Irrigation can directly alleviate soil water deficit, and buffer the negative heat stress imposed by enabling evaporative cooling. However, major river basins across the globe had already faced groundwater shortages due to over-used irrigation (Wada et al., 2010; Molle et al., 2007). Further expansion of irrigation in these regions or the region where irrigation application is restricted by the socio-economic factor (Rosa et al., 2020) is thus impractical. In addition, the application of irrigation could bring negative environmental impacts on soil salt content and nearby water bodies (Daliakopoulos et al., 2016; Scanlon et al., 2007). These aspects should be sufficiently considered when determining irrigation as an adaptation strategy.

Crop species have different responses to abiotic factors, such as heat and water stress (Hatfield *et al.*, 2011). Hence, crop substitution, for instance, cultivating more heat-tolerant species to replace the original ones, can be used for adapting to climate change (Rezaei *et al.*, 2015). Within each species, crop variety selection can further enhance crop adaptability to climate change. Indeed, the majority of crops can be drawn from existing crop varieties for adaptation under moderate warming, whereas 39% of global croplands will need new varieties to counter the negative effects of climate change (Zabel *et al.*, 2021). Currently, climate variability and uncertainty are not sufficiently considered for breeding programs and variety selection practices (Kahiluoto *et al.*, 2019). Available major crop varieties are mostly capable of dealing with single stressors, i.e. heat or water stress, which shows the importance of breeding for cultivars that are tolerant to combined stress (Tack *et al.*, 2016).

In particular, perennial crops have been advocated as an alternative to annual crops. Perennial crops can reduce negative environmental impacts and enhancing ecosystem services (Crews *et al.*, 2018; Glover *et al.*, 2010). Known advantages of cultivating perennial crops include more belowground resources investment (Vico *et al.*, 2016), which allows for better utilizing water and nutrient (Sprunger *et al.*, 2018; Culman *et al.*, 2013), reducing nutrient leaching and greenhouse gas emissions (Kim *et al.*, 2021; Culman *et al.*, 2013). If perennial crops are more adapted to tolerate heat and water stress, they can be an ideal crop to be cultivated under climate change because of their values in the environment and ecosystem services.

There are other management practices effective in coping with compound events, and their performance and suitability depend on the local conditions. For instance, early sowing shows promising results in regions like Australia, where is subject to both water and heat stress (Hunt *et al.*, 2019). In addition, crop migration is an effective approach to help crops escaping from high-temperature exposures (Sloat *et al.*, 2020). However, crop migration is restricted by socio-economic and political factors, and in some cases, is at the cost of undermining the environment.

2. Aims and research questions

Compound events have severely damaging effects on crops, yet current crop models do not explicitly quantify such effects on crop canopy temperature and yield. For mechanistic modeling, a more mechanistic approach needs to be incorporated into simulating the dependence of stomatal conductance on water stress so that the compound effects on canopy temperature can be more accurately simulated. To advance the model predictive performance, statistical modeling that is used for estimating crop yields needs to account for precipitation and temperature interactions (i.e. compound effects) on crop yields. By the development of these models, we can shed new light on crop physiological and yield responses to compound events and better inform choices of adaptation strategies to cope with compound events. We established mechanistic and statistically-based crop models to meet two aims:

1. Quantify the compound effects on crop canopy temperature and yield.
2. Identify adaptation strategies that can reduce the damaging effect of compound events. Adaptation strategies mainly include irrigation and crop species and traits.

Specifically, these aims can be expressed as four research questions:

1. How do the precipitation regime and air temperature jointly affect canopy temperature, especially when they lead to high canopy temperature corresponding to crop heat stress? (Paper I)
2. How do the compound effects of precipitation and air temperature translate into actual yield losses? (Paper III, IV)
3. For the rainfed cropping system, what is the precipitation condition at which crops attain maximum yields, and how does that change with temperature? (Paper IV)

4. How effective are irrigation and crops with specific traits in coping with compound events as potential adaptive strategies? (Paper I, II, III)

The synopses of aims for each paper and the modeling approach they adopted were specified in Figure 2.

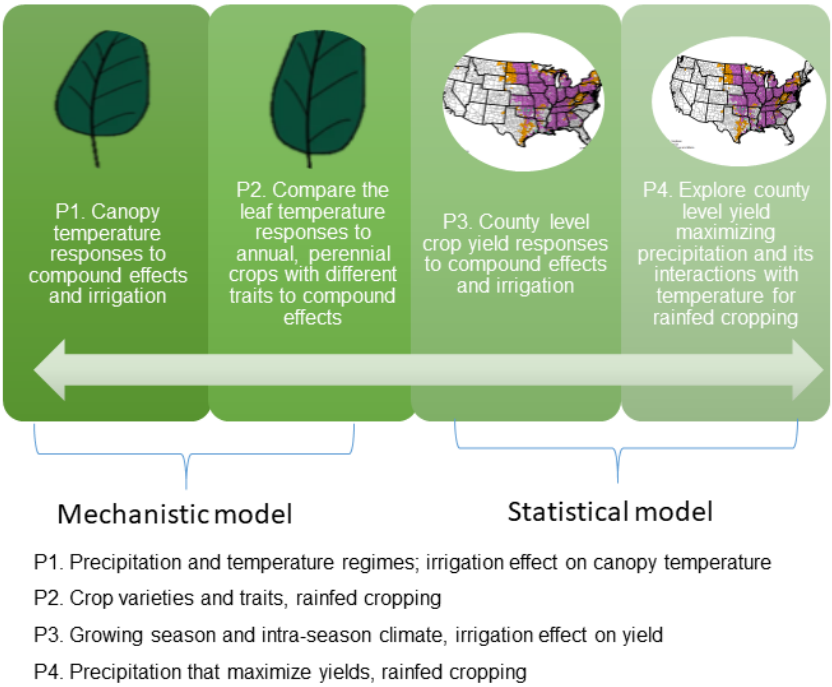

Figure 2. Schematic illustration of the papers within this thesis. Synopses of papers are described within the boxes, the types of model applications to each paper are specified within the brackets. The differences of key feature of each papers were stated at the bottom.

3. Methods

At the outset, we selected three staple crops: wheat (Paper I), maize and soybean (Paper III, and IV). Wheat varieties characterized by different life habits, annual wheat, and perennial wheatgrass were also explored (Paper II) to analyze how they and their traits respond differently to compound events (Details of crop parameters see Paper I, Table S2; and Table 1 in Paper II). In Paper I and II, annual wheat and perennial wheat were parameterized based on literature data to simulate crop canopy and leaf temperature and transpiration rates. In Paper III and IV, we utilized maize and soybean yields data spanning 1970 to 2010, which are available at county level in the U.S. (Details of dataset see methods in Paper III and IV). Further, we discerned rainfed and irrigation cropping for these yield data, either adopted both to compare the responses of these two cropping (Paper III), or purely analyze rainfed yield response to compound events (Paper IV).

3.1 Big-leaf and vertically explicit mechanistic models of canopy water and energy balances

Mechanistic models were established aiming to determine canopy or leaf temperature, and transpiration rates, as a function of precipitation regimes, air temperature, as well as other environmental factors that are key to crop leaf and canopy temperatures (wind velocity, air relative humidity, solar radiation). In addition, the models were developed to assess the efficacy of irrigation, and the role of crop traits in defining their vulnerability to compound events. These results can inform irrigation strategies and future breeding programs.

3.1.1 Big-leaf vs multi-layered model.

We used two variants of canopy temperature models: big-leaf model in Paper I, and a multi-layered model (vertically explicit model) in Paper II. Two models' similarities and differences were presented in Figure 3. The big-leaf model is a simplified model, which lumps the canopy as a 'big-leaf', and scales up the leaf-level carbon and water fluxes by assuming the same environmental conditions prevail in the entire canopy. This assumption reduces parameters and computation requirements (looping times), but the big-leaf models do not account for the environmental differences along the vertical dimension inside canopy. Instead, parameters for crop physiological responses summed as one value to represent entire canopy. Due to the non-linearity of most processes involved, the values of parameters cannot be taken as averages or measure directly from canopy. As a result, common parameterization approach relies on plausible assumptions (Dai *et al.*, 2004). Despite so, the big-leaf model provides the means to assess the effects of changing climatic conditions on crop canopy temperature, and represents an improvement with respect to models currently used for this aim, thus meeting the goals of Paper I. While being more computationally intensive, multi-layered models provide a representation of phenomena closer to reality and allow explicitly accounting for aspects such as the coupling between the canopy and the atmosphere, including the role canopy height and leaf area density. This fulfills the aims of Paper II. The differences of model structures were presented in Figure 3.

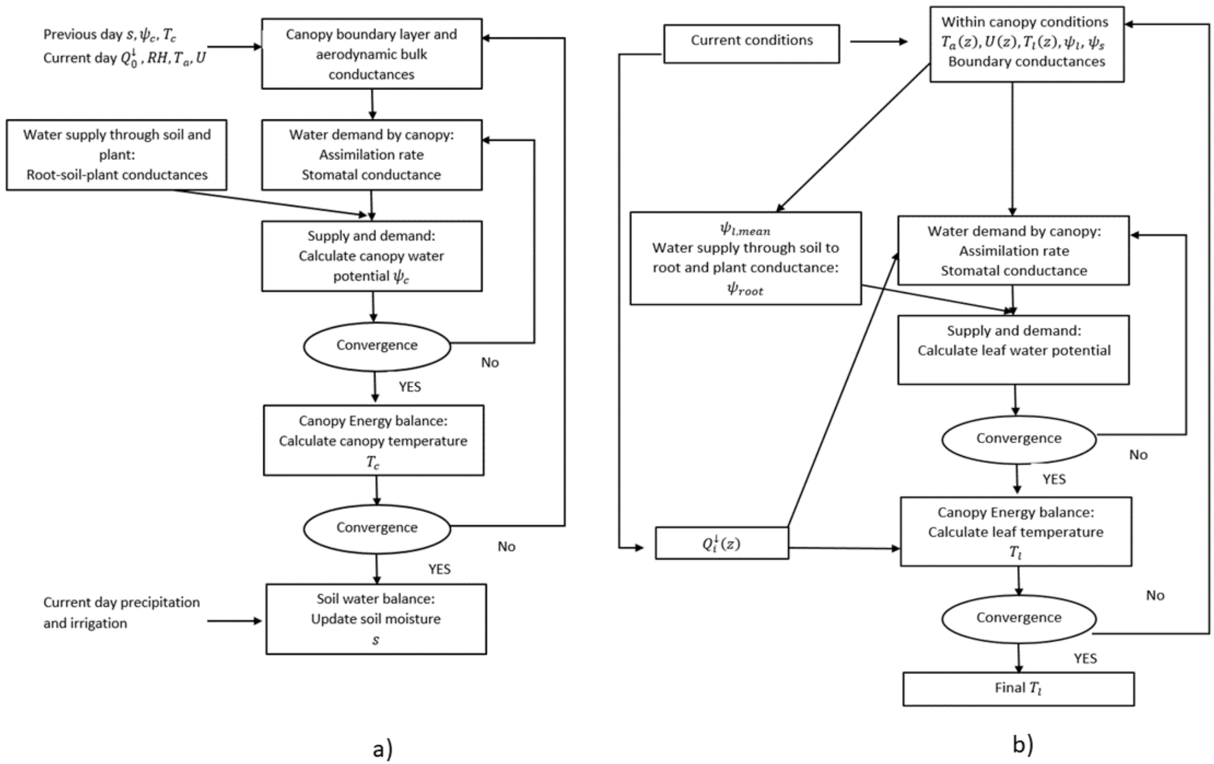

Figure 3. The schematic differences of canopy a) and leaf model b) structure for Paper I and II. Symbols in a) $s, \psi_c, T_c, Q_0^{\downarrow}, RH, T_a, U$ stand for soil saturation, canopy water potential, canopy temperature, incoming shortwave radiation, air relative humidity, air temperature, wind speed. Symbols in b) $T_a(z), U(z), T_l(z), Q_i^{\downarrow}(z), \psi_l, \psi_s, \psi_{l,mean}, \psi_{root}$ stand for air temperature, wind velocity, leaf temperature, radiation at canopy profile, with z being the height above the ground. Following symbols are leaf, soil water, mean leaf water, and root water potentials.

3.1.2 Using canopy temperature metrics for measuring crop heat stress

The results of Paper I were based on two metrics representing the potential heat stress for crops: (i) the mean T_c during the anthesis stage (21-day period around anthesis base on Mäkinen *et al.*, 2018), and (ii) P_{CHS}, the fraction of days in the period around anthesis during which T_c exceeded the crop-specific threshold (We defined threshold as 30 °C for wheat anthesis in Paper I based on Saini & Aspinall, 1982). P_{CHS} is thus a measure of the frequency and duration of the crop heat stress, while mean T_c quantifies the level of crop heat stress.

3.2 Statistical models: linear mixed models

Statistical models were established to analyze the compound effects of intra-seasonal and seasonal climatic conditions on crop yields at the county level in the U.S. We also assessed the efficacy of irrigation in mitigating detrimental climatic conditions, and determined the yield maximizing precipitation and its interaction with temperature.

3.2.1 Linear mixed model

We employed linear mixed model (LMM) for analyzing the county-level crop yield responses to compound events. LMM has a wide range of applicability in the cases where the data are clustered, and repeatedly recorded over time under different conditions (West *et al.*, 2014).

The selection of suitable statistical models is a balance of model flexibility and interpretability. Thus, the model selection depends on specific research questions. Compared to other statistical models, such as machine learning models, which are known for their strong predictive capacity, LMM owns better interpretability because of its explicit model structure that can use to account for different effects. Hence, we selected LMM as a tool to analyze climate-yield responses. The high degree of interpretability helps us to better associate the results with underlining crop physiological mechanisms. The mechanisms we interpreted from statistical models can be compared with their counterparts from mechanistic models.

For the rainfed cropping system, we established LMM that contained temperature and precipitation components respectively to account for temperature and precipitation individual effects on crop yield. In addition, the interaction term was included to consider the interactive (compound) effects of temperature and precipitation on crop yield. Time was included to consider other factors that bring the long-term yield change during the time window. For rainfed cropping, precipitation that falls into the intermediate range usually maximizes rainfed crop yields. Quadratic terms can be added to LMM to capture such precipitation-yield relationships (e.g. Paper IV). For mixed effects, location and time (here defined as a factorial variable) were adopted as random variables to consider the effects due to spatial heterogeneity and temporal covariates.

When data availability permitted, i.e. comparable irrigated yield data co-exist in the same time and location as the rainfed yield data (e.g. Paper III), we can further add irrigated cropping as a categorical variable on the top of rainfed cropping-based model structure to analyze the effects of irrigation on boosting yields and alleviating relevant climatic stresses. Details of these model structures were described in Paper III (Eq. 1) and IV (Eq. 1 and 2).

3.2.2 Data and climatic indices

Meteorological data with finer spatial and temporal resolution, in general, can improve the predictive power of statistical models. In particular, in the light of finer temporal meteorological data, we could further analyze the intra-seasonal climatic impacts on crop yields (Details of data are in the methods of Paper III and IV). In Paper III, both growing season climatic indices and intra-season indices were employed, while in Paper IV, we only adopted growing season indices alone. Growing season indices, mean temperature, T_{GS}, and precipitation totals, P_{GS} were selected to represent the overall climatic condition during the growing season. Shorter climatic stresses were captured by intra-seasonal indices, for which we adopted the longest dry spell during the growing season, which was defined as the longest period when daily precipitation <2mm, CDD_{GS}, and mean daily temperature during CDD_{GS}, T_{CDD}.

4. Results and discussion

4.1 Importance of compound effects of precipitation and temperature on crops

We found that precipitation evidently interacted with temperature in determining crop canopy and leaf temperature, the occurrence of potential crop heat stress (Paper I and II), and final yields (Paper III and IV). Despite the interaction of precipitation and temperature was complex in crop physiological processes, for wheat, T_c revealed a simple pattern to the compound effects of soil water availability and temperature. As soil moisture (soil saturation) was below a critical level 0.34 (-0.14 MPa), the difference of T_c and air temperature rapidly rose, and showed a non-linear pattern (Figure 4). Consequently, as low soil moisture coincided with high air temperature, T_c exceeded threshold (30 °C for wheat anthesis) temperature more frequently. As a result, we observed an increase of fractions of crop heat stress P_{CHS}. For both rainfed maize and soybean, their crop yields responded to precipitation, temperature, and their interactions (see Table 1 in Paper III): Soybean yields declined faster as low precipitation combined with high air temperature, while maize yields declined faster under high precipitation and air temperature conditions. For their yields in rainfed cropping, precipitation totals that maximize their yields interacted and increased with temperature (Paper IV). In addition, we found concord patterns of canopy temperature T_c and yield responses to climatic conditions: T_c changed from the highest to the lowest along the gradient of wet and cool to dry and hot environments (Figure 4). High T_c also translated into high yield losses, because we identified that the lowest yield to the highest also followed the same gradient as T_c (Figure 6, left).

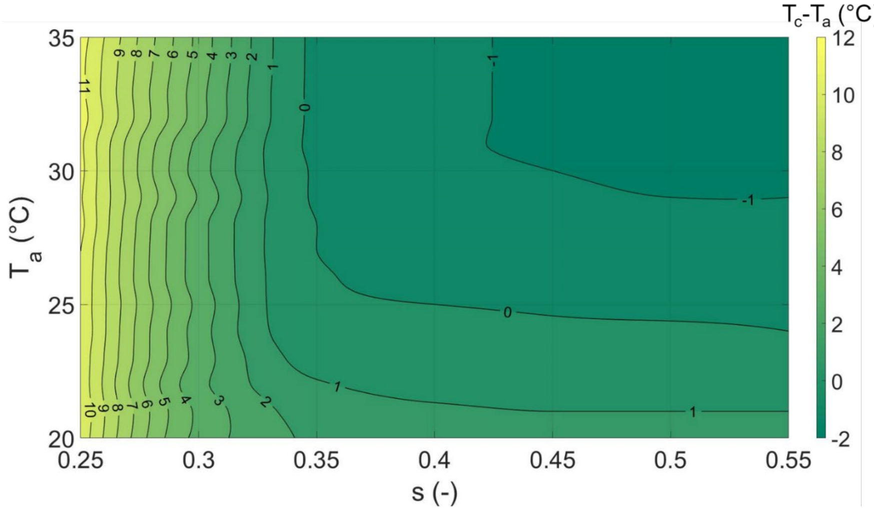

Figure 4. Canopy-air temperature difference, $T_c - T_a$ (colors and contour lines), as a function of soil moisture (s; x-axis) and air temperature (T_a; y-axis) for sandy loam.

4.2 Rainfed crop responses to mean climatic conditions during growing seasons

Long-term average air temperature increased the medians and variability of mean T_c. Conversely, precipitation totals decreased mean T_c, but showed no effect on T_c variability (Figure 5). In addition, marginal cooling effect of precipitation totals was identified: under the same long-term average air temperature, mean T_c had a larger decrease at low precipitation totals; while precipitation totals exceeded 900 mm, mean $T_c$was not evidently cooled by additional increase of precipitation.

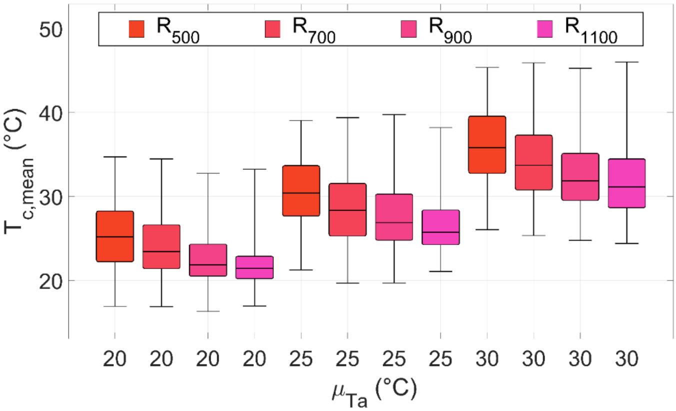

Figure 5. Mean canopy temperatures during anthesis, $T_{c,mean}$ (i.e. mean T_c), for four average annual precipitation totals (500, 700, 900, 1110 mm; colors) and three long-term average air temperatures μ_{T_a} (20, 25 and 30 °C; x-axis). Average precipitation depth was kept at 15 mm, while the average precipitation frequency changed within each group of 4 boxes, from 0.091 to 0.137, 0.183, and 0.228 d^{-1} (left to right), leading to increasing average annual precipitation totals (subscripts in the legend). For each climatic scenario, 500 21-day simulations were run. The horizontal black lines are the median values; the boxes extend from the first to the third quartile; whiskers cover the whole range.

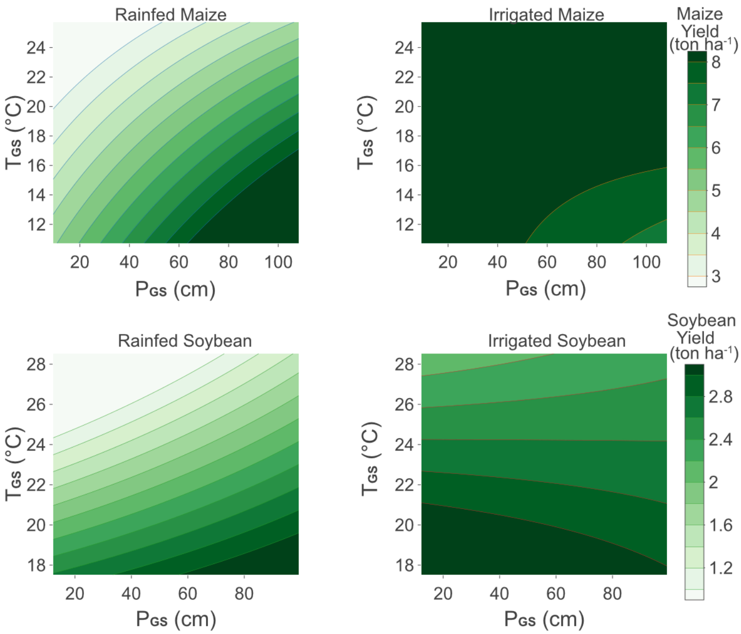

Figure 6. Crop yields as a function of temperature- and precipitation-related climatic indices for whole growing season total precipitation (P_{GS}) and mean daily temperature (T_{GS}). The contour plots are based on the fixed part of the statistical model (Eq 1 in Paper III), with coefficient estimates for maize and soybean (Table 1 in Paper III), and are relative to rainfed (left) and irrigated (right) cropping. Yields refer to year 1991, i.e., the middle-point of the period considered.

Likewise, our statistical-based results confirmed the negative effects of rising mean growing season temperature and precipitation totals on actual yield losses (Paper III, Table 1). We found T_{GS} decreased for both maize and soybean yields. As for precipitation totals, the decreasing precipitation totals only depressed maize yields, while had no marked effect on soybean yields.

In summary, we found deficit precipitation or rising temperature led to high mean T_c, and sometimes to yield losses. These two directions of climatic changes corresponded to potential heat and water stress for crop growth and development. We found similar patterns from the results of T_c and yield responses to compound event, this illustrated that crop heat stress, to a certain extent, can explain yield losses under compound events. The reasons for high T_c can translate into yield losses can be mainly attributed to two physiological mechanisms: one mechanism was the occurrence of T_c exceeding the threshold temperature, especially during critical developmental period (Paper I), can lead to severe losses. This agreed with most field experiments and model simulation results (Hlaváčová *et al.*, 2018; Marcela *et al.*, 2017; Liu *et al.*, 2016). Another mechanism is that the mean T_c can be driven away from the optimal range for crop growth and development. However, the variation of T_c is not always detrimental to crops. In the cases where crop grew at the cooler side of sub-optimal temperature range, the increase in T_c may shift crop growing at optimal temperature conditions.

4.3 Role of climatic variability and intra-season climatic conditions

To explore the effect of climatic variability on mean T_c and P_{CHS} during anthesis, we compared temperature and precipitation under constant mean conditions, but varied in their variability parameters. For temperature, we simulated temperature regimes under the same long-term mean temperature, but varied in temperature variances. Results showed that the change of temperature variance had no evident influence on the medians or variance of mean T_c and median P_{CHS} for rainfed cropping (Figure S6 in SI of Paper I). In contrast, the change of intra-seasonal precipitation conditions, as expressed by precipitation intermittency, impacted the mean T_c: under the same level of precipitation total, precipitation regimes with lower precipitation frequencies, i.e. more intermittent but intense precipitation, increased both medians and variances of mean T_c (Figure 5 in Paper I). Meanwhile, we observed a higher risk of P_{CHS} under intermittent precipitation regime (Figure 5 in Paper I).

To understand the effect of intra-seasonal climatic conditions on crop yields, we considered CDD_{GS} and T_{CDD} as explanatory variable for maize and soybean yields. The intra-seasonal indices explained yields as good as seasonal indices based on R^2 value (Table 1 in Paper III). More intermittent precipitation regimes potentially rendered a more uneven distribution of soil water availability within the growing season. As a result, under the same precipitation totals, low precipitation frequencies could lengthen CDD_{GS}. For both maize and soybean, prolonged CDD_{GS} reduced crop yields (Figure 1b in Paper III). In addition, increasing T_{CDD} also had negative effects on crop yields for both crops. Higher CDD_{GS} and T_{CDD} together had a compound effect, which resulted in more yield losses for maize and soybean.

To summarize, our results highlight the importance of considering not only seasonal precipitation totals but also their intra-seasonal pattern. Based on the results from both models (Figure 5 in Paper I, and Figure 1b in Paper III), crop responded to intra-seasonal climatic conditions, with interactions of the longest dry spells and temperature during the dry spells. Results suggested more intermittent precipitation was detrimental to crops. More intermittent precipitation regimes can increase the chance of intensive precipitation events and long dry spells. During heavy rainfalls, the chance of soil water losses via runoff and percolation is increased. With unaltered precipitation totals, this would, on average, reduce soil water availability during growing season and increases the risk of water stress. Dry spells, if they are long enough, or coincide with high water demand driven by high temperature during which, can also form water stress to crops. Consequently, the risk of water stress is increased under intermittent precipitation. Indeed, reducing rainy days during the growing season has already dampened crop yield, and could even reverse the benefits of increased total precipitation (Ram, 2016). Although our results showed temperature variability had no marked effect on mean T_c and P_{CHS}, and we did not employ temperature-related indices within growing season, such as maximum three-day temperature, to mimic the effect of heatwaves on yield losses. In reality, heatwaves can cause leaf senescence (Lobell *et al.*, 2012), and shorten crop growth cycle (Rashid *et al.*, 2019). Considering these aspects, heatwaves could induce additional yield losses. By our mechanistic modeling approach, we have not simulated but expected that, as temperature variability increased, the P_{CHS} of exceeding lethal temperature threshold would increase. Under such condition, crop cannot survive and harvest no yields. Besides, previous statistical-based result tells us that using temperature intra-seasonal indices also had good explanatory power in explaining yield responses to climatic extreme events (Troy *et al.*, 2015).

4.4 Yield maximizing precipitation for rainfed cropping

We showed in Paper I and III that deficit precipitation can lead to higher risk of T_c, P_{CHS} and larger yield losses. Conversely, model results suggested larger precipitation reduced T_c (Paper I) and crop yields (Paper III) and had marginal effects on stress alleviation. However, excessive precipitation can result in water excess. In paper III, this factor was not accounted because of few data pertain to excessive precipitation. To account for the negative effects of water excess, we further allowed our statistical model to capture yield losses in both water stress and excess conditions. We assumed an intermediate precipitation total emerged at which suitable soil water condition is met, and consequently yields reached their maximums (i.e. yield maximizing precipitation). In addition, how yield maximizing precipitation was altered by temperature is of our interest. This information is crucial for rainfed crops to make adaptive strategies in the face of climate change.

As expected, maize and soybean yields both showed non-linear dependence on P_{GS}, crop yields peaked at intermediate P_{GS} and declined towards both high and low levels of P_{GS}, which corresponded to likely water excess- and stress conditions (Figure 7). Yet, maize and soybean showed different sensitivities to high and low levels of P_{GS}. For maize, the parabolic curve was skewed to the upper-right and displayed asymmetric yield changing rates between high and low P_{GS}, especially at high T_{GS} (Figure 7 left, and Table S2 in Paper IV). It illustrated that maize yield was reduced faster at low P_{GS} compared to high P_{GS}. While for soybean, we found no apparent difference in yield changing rate between high and low P_{GS}. In addition, we found maize showed greater sensitivity to T_{GS} compared with soybean.

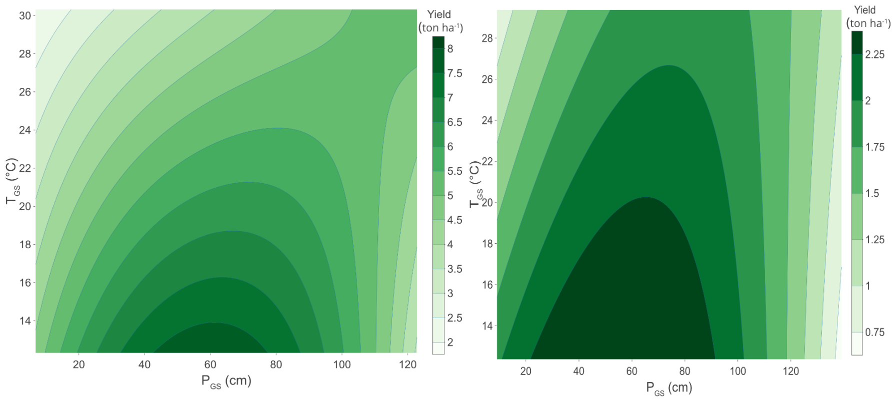

Figure 7 Crop yields as a function of growing season precipitation and temperature (Only plotted fixed effect), for maize (left) and soybean (right).

Significant interactions of P_{GS} with T_{GS} were observed for maize, but not for soybean (Paper IV, Table 1). For both maize and soybean, yield maximizing precipitations were increased with temperature (Figure 2 in Paper IV). The relationship of yield maximizing precipitation and temperature indicated that at low T_{GS}, soybean needed more precipitation with increasing temperature to meet growth requirement compared with maize. While at high T_{GS}, the opposite was true.

Maize yield declined faster at low precipitation compared with high precipitation, while for soybean low and high precipitation appeared equally damaging to yields. This is in accord with previous findings that maize was more sensitive to drought (Borgomeo *et al.*, 2020), while soybean was more negatively affected by water excess due to the water logging (Rhine *et al.*, 2010). In the future, the temperature will continue to increase in the U.S., together with diverging changes in precipitation amount depending on location (Wuebbles *et al.*, 2017). The yield maximizing precipitation and its relation with temperature based on our model indicated that current water excess can become less damaging and even beneficial to crop yields under rising temperature conditions, as long as the increased evapotranspiration due to rising temperature can effectively utilize the excess soil water. In contrast, in locations where precipitation is currently close to the yield maximizing level for the local temperature, warming can reduce yields, and lead to more severe yield losses if combined with less precipitation because it imposes the compound effects on crops.

4.5 Crop response to climatic conditions under irrigation

4.5.1 Irrigation mitigating effects on crops sensitivity to average climatic conditions

The dependence of precipitation pattern on T_c was reduced by irrigation. Across all levels of long-term air temperature, we found irrigation reduced both the median and variance of mean T_c (Figure 5 in Paper I), relative to the rainfed scenarios with the same climatic conditions. Nevertheless, the median and variance of mean T_c also slightly increased with air temperature under irrigated conditions. In addition, the mitigating effects of irrigation became less effective when air temperature increased (Table 1 in Paper I).

Crop yields reflected a similar pattern of irrigation mitigating effect as canopy temperature results. Irrigation reduced the dependence of crop yields on both temperature and precipitation (Figure 6; Figure 3 in Paper III) and, in some cases even reverted the direction of response. For instance, irrigation reverted the effects of increased temperature on maize yields. In contrast, the negative dependence of soybean yields on increasing temperature was only reduced by irrigation.

In general, irrigated cropping gained more yields compared with rainfed cropping, except for the wettest and coolest climatic conditions (Figure 6). Under the wettest and coolest conditions, irrigated cropping showed no increase in yields compared with rainfed cropping. In contrast, under the hottest and driest conditions, i.e. the compound event, irrigation boosted two and a half times crop yields compared to rainfed cropping (Figure 2 in Paper III). This demonstrated that irrigation can sustain the needed soil water for necessary plant crop and development, as well as soil water for evaporative cooling against heat stress during growing season.

4.5.2 Irrigation mitigating effects on crops of intra-seasonal climatic conditions

Irrigation reduced the influence of precipitation frequency on mean T_c and its variance (Figure 5 in Paper I). In contrast, irrigation had no evident mitigating effect on the increasing variance of air temperature (Figure S6, Paper I). Under irrigated conditions, the variances of mean T_c still increased with temperature variances.

Irrigation enhanced the crop yields for maize and soybean across CDD_{GS} and T_{CDD} (Figure 1b in Paper III). Under conditions of large CDD_{GS} and T_{CDD}, irrigation resulted in two times higher crop yields compared with rainfed cropping, and boosted 50%-100% of yields under other climatic conditions (Figure 2 in Paper III). Likewise, irrigation also reduced or reverted the negative dependencies of yields on CDD_{GS} and T_{CDD} (Figure 3 in Paper III): the dependencies of maize were reverted, while for soybean were reduced.

Taken together, we found irrigation reduced but not eliminated the risks of crop damage induced by adverse climatic conditions, based on the results of both crop canopy temperature and yields. Irrigation reduced the negative effects on mean T_c and its variance induced by high temperatures and intermittent precipitations (Figure 5 in Paper I), and on yields (Figure 1 in Paper III). Meanwhile, irrigation also showed its limited efficacy in mitigating the negative climatic effects in certain circumstances (Figure S6 in Paper I, and Figure 3 in Paper III). Indeed, irrigation can directly or indirectly mitigate the effects of heatwaves if wide-spread used at the larger scale (van der Velde *et al.*, 2010). Despite we confirmed the efficacy of irrigation mitigating effect on crop heat stress, and its capacity to boost yields, it should be noted the caveat for expanding irrigation, it some cases, it is impractical due to the socio-economic factor or water resource shortage. In other cases, it can bring negative environmental impacts, as we aforementioned in section 1.5.

4.6 Different responses to compound events between annual and perennial wheat

Perennial and annual crops had higher leaf temperature differences under well-water conditions compared with water stress conditions (Figure 8). Under well-watered conditions, high leaf area index (LAI) perennial had the highest leaf temperature difference with annual crops, followed by perennial with low photosynthetic capacity and baseline perennial. In fact, baseline perennial had similar leaf temperature compared with the annual crop. Under the well-watered and high-temperature conditions, the difference of leaf temperature between perennial and annual remained unchanged, except for high LAI perennial, whose leaf temperature difference was slightly higher than the one at low temperature. Under water stress, the pattern of the leaf temperature difference between perennial and annual remained, yet the magnitude of leaf temperature difference became smaller. Also, high and low temperatures showed similar leaf temperature differences under water stress. The same pattern of leaf temperature difference was found among ideotypes when the wind velocity was reduced (right column in Figure 8), only the magnitude of leaf temperature difference was larger across the soil water potentials and temperatures that we tested.

Canopy transpiration differences between all ideotypes of perennial and annual crops were less than 5%, except for the high LAI perennial under water stress and high-temperature conditions, at which canopy transpiration was 15% lower than annual crop. Instantaneous water use efficiency (WUE) at the canopy level showed a consistent pattern, which was independent of climatic conditions that we tested. Regardless of the levels of soil water potentials, air temperatures, and wind speeds, baseline perennial had the highest WUE compared with annual, followed by low photosynthetic capacity perennial and high LAI perennial. Among these perennial crops, high LAI was the only one that had marked and lower WUE compared with annual crops. Water stress and high temperature exacerbated the reduction of WUE in high LAI perennial compared with annual crops.

Based on our results, perennial ideotypes did not differ as a group from annual wheat in their leaf temperature, canopy transpiration, and canopy WUE among environmental conditions. Rather, the traits of perennial crops played a key role in determining crop sensitivity to water and heat stress. According to our simulations, LAI affected perennial crop responses to abiotic stressors.

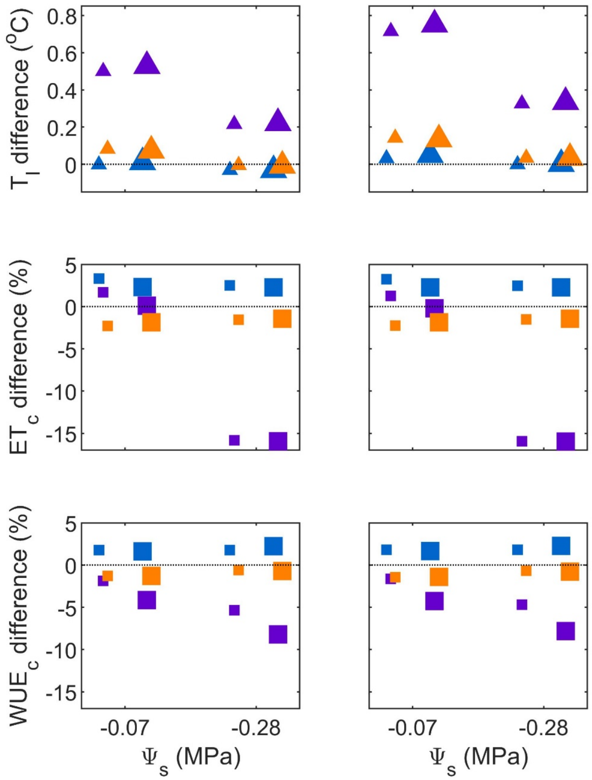

Figure 8. Differences in leaf temperature T_l (top), canopy transpiration ET_c (middle) and water use efficiency WUE_c (bottom), between each perennial ideotypes and the annual wheat. Differences are reported as percentage changes for ET_c and WUE_c. Conditions are well-watered conditions and medium stress (x-axis), low (small symbols) and higher (large symbols) reference air temperature (small symbols, 25 °C; large symbols, 30 °C), and decreasing wind speed (left column: 4 m s^{-1}; right column: 2 m s^{-1}). Colors refer to the perennial ideotypes: baseline perennial (blue), high L_{AI} (violet), and low photosynthetic capacity (orange). The dotted horizontal lines represent no difference between the perennial and annual.

4.7 Implications of results under a changing climate

Towards future changing climate, wherein rising average and altered precipitation regimes co-exist, assessing compound effects of temperature and precipitation on crop growth and yield become challenging yet crucial for ensuring food security. In fact, future climatic impacts on crop damage depend on the local climatic conditions, and how these conditions, especially the precipitation regimes, co-evolve in their average and variability.

The increasing average temperature will mostly cause negative effects on crops, because it could lead to the increase of average canopy temperature and its variability, which are closely associated with yield losses. However, to the regions subject to increasing precipitation, the negative effect of rising temperature could be at least partially counterbalanced. Apart from that, regions with current temperatures lower than the optimal temperature for the crop will also benefit from rising temperatures. For instance, some regions like northern Europe and China (Xiong *et al.*, 2014; Olesen *et al.*, 2011). Rising temperature and precipitation led to diverging responses in canopy temperature (e.g. Figure 5). Hence the net effect is determined by the balances of the magnitude of rising temperature and precipitation. Likewise, the responses of crop yields to changing climate depend on the covariant precipitation and temperature. As noted in section 4.4, the existing yield maximizing precipitation and yield losses along water stress and excess inform us that, in regions that are currently subject to harmful water excess, this condition can become less damaging or might benefit from temperature rises if precipitation totals remain unchanged. For those regions that will have both wetter and hotter climate, the yield will be increased or maintained when the increase in precipitation balances the increase in evapotranspiration demands. In contrast, in the locations where precipitation is currently near the yield maximizing level under present temperature, warming would reduce the yields if precipitation is unchanged, and even more so with decreasing precipitation.

In the future, the regions that are subject to the negative effects of intra-seasonal climatic conditions will face an extra burden to stabilize crop yield. We found more intermittent precipitation regimes can result in higher mean canopy temperature and its variability (Paper I), and longer CDD_{GS} reduced the crop yields (Paper III). Under the warming future, this would increase the risk of crop damage in the locations where precipitation totals remain unchanged, and exacerbate the risk of yield losses in the locations where will face deficit precipitation. Moderate excessive precipitation has the potential to buffer the negative intra-seasonal effects, which is similar to the effects provided by irrigation.

In the light of already over-used irrigation across many regions, we advocate practicing irrigation in a sustainable manner, especially save the irrigation for the most stressful climatic periods, for instance, the compound event. During the compound event, its negative effects can be maximally counteracted by irrigation. Meanwhile, the sustainable use of irrigation would also minimize the negative impacts on salt content and nearby water body. Hence, sustainable irrigation strategy, if well considered these factors should be advised as adaptation.

5. Conclusions and future research

5.1 Conclusions

In the light of the established mechanistic and statistical models, we quantified the effects on crop canopy temperature and yields of stressing climatic conditions, compounded or occurring in isolation. We also determine the potential of adaptation strategies, such as irrigation and crop species and varieties.

We highlighted the importance of considering precipitation and temperature compound events in determining the canopy temperature and yields. Canopy temperature increased and yields decreased from wet-cool to dry-hot conditions, which corresponds to the increased risk of crop heat and water stress. Moreover, two modeling approaches both found the compound effects of hot and dry conditions on crops. When soil saturation dropped below 0.34 (corresponding to a soil water potential of -0.14 MPa), canopy temperature rapidly rose. Consequently, canopy temperature was synergistically increased under compound events. Likewise, our statistical model confirmed several significant interactions of precipitation and air temperature. The compound effects on crop yield were also identified: under dry and hot conditions, maize and soybean yield synergistically declined.

As we expected, our model results suggested that decreasing precipitation totals and higher air temperature can enhance crop canopy temperature, crop heat stress, and yield losses. Conversely, increasing precipitation totals and cool air temperature created the less harmful environment to crops. However, when soil water availability ensures near well-watered conditions, increasing precipitation showed marginal benefits on crop canopy temperature. Beyond certain precipitation levels, further increases were detrimental to crops, which suggests potential water excess. Hence, not only suitable temperature range, but also the precipitation range is crucial for crops.

We found the climatic conditions within the growing season were equally good in explaining crops compared with growing season mean conditions. More intermittent precipitation can lead to more variable soil water availability and longer dry spells. Crops under intermittent precipitation regimes and longer dry spell showed both higher risk of crop heat stress and yield losses.

Irrigation mitigated compound effects, regardless the adverse conditions are seasonal or intra-seasonal. As a result, lower canopy temperature and the risk of crop heat stress, and higher yields were observed under irrigation conditions. Meanwhile, we also identified the limited efficacy of irrigation mitigating effects under high air temperatures. High canopy temperatures were not completely cooled down by irrigation under high air temperature levels. Our statistical-based results suggested that although irrigation can reduce or even revert crop dependences on climatic indices, the negative impacts of temperature remained under irrigated scenarios.

Perennial crops emerges as a promising crop to adapt to climate change because of the beneficial effects it brings to the environment. However, its sensitivity to abiotic stressors, such as water stress, heat, and their combinations largely remained unquantified. Our results suggested the specific traits of perennial crops defined crop responses to abiotic stressors. Leaf area index was found as an important trait in shaping the crop responses to abiotic stressors.

5.2 Future research

Our mechanistic and statistical models provided a benchmark for quantifying the risks of compound effects on crop temperature and yield. The models were parameterized within certain crop species, variety, traits, developmental stage, and geographical areas. Yet, both modeling approaches have the potential to be generalized other circumstances with caution.

5.2.1 A third interactive abiotic factor, elevated air CO_2 concentration

Climate change is not only characterized by changes in precipitation and temperature, but also elevated concentration of atmospheric carbon dioxide

(eCO_2). Air CO_2 concentration affects crop growth and yield. For crops, eCO_2 can stimulate their growth, photosynthesis, and can have fertilization effects on leaf activity and ultimately yields. Yet, the fertilization effects vary among crop species and growing conditions (Kimball, 2016). eCO_2 is more beneficial to C3 species under ample water, and nutrients conditions (Kimball, 1983), and crop yields for C3 species are generally increased by 10%-30% under eCO_2 conditions (Toreti *et al.*, 2020). In contrast, the fertilization effects on C4 species (e.g. maize) are either small or not evident in increasing crop yields.

We have not directly accounted for this fertilization effect stemming from eCO_2. Our statistical models have not considered the concentration of CO_2 as a variable for explaining crop yield. Because eCO_2 has been increasing chronically, inter-annual yield changes due to the fertilization effect are not evident. As such, fitting CO_2 in models could not detect a direct impact based on historical surveyed data. However, since we had a time variable (year) to account for the overall yield trend in time, chronic fertilization is indirectly considered in our model, although its effects are undistinguishable from those of technological improvements and trends in climatic conditions. For crop canopy temperature models, under eCO_2 conditions, crop stomatal conductance was reduced by 19% to 22%, which in turn reduced crop evapotranspiration by 10% (Toreti *et al.*, 2020). From crop physiological perspective, eCO_2 can increase crop canopy temperature by limiting crop transpiration, which can potentially aggravate crop heat stress. However, the reduction of evapotranspiration due to eCO_2 also slows down the rate of soil water depletion and, with that, the risk of water stress, all the rest being the same. Ultimately, the net effects of eCO_2 on canopy temperature and yields, considering the interactions with temperature and precipitation deserve further exploration. Our canopy temperature model is capable of considering the eCO_2 on relevant physiological mechanisms. Experiments that integrate variations of eCO_2, soil water conditions, temperature regimes, as well as crop parameters, can lend us support for model calibration and validation, which enables the simulations that integrate soil water, temperature, and eCO_2 altogether. There are few approaches suggested by Lobell and Asseng (2017) on how to incorporate the effect eCO_2 into statistical-based analysis. The most feasible one is taking not temperature, rather vapor pressure deficit, as a proxy of temperature (Urban *et al.*, 2015). As such, the predictor can be modified under different levels of eCO_2, and the modified vapor pressure deficit can absorb the effect stemming from eCO_2.

5.2.2 Crop phenological response to the compound event

Crops have changing sensitivities to heat and water stress at different developmental stages (Daryanto *et al.*, 2017; Sanchez *et al.*, 2014; Porter & Gawith, 1999). In general, crop reproductive stage is more vulnerable to these stresses compared with the vegetative stage. For our canopy temperature model, the effects of crop changing sensitivities are considered by adapting to stage-specific thresholds. For instance, in Paper I, we simulated the crop canopy temperatures for wheat during the flowering stage, because it is the most vulnerable stage to heat stress. For other developmental stages, our mechanistic model can also be utilized to assess crop heat stress by setting corresponding crop parameters and threshold temperatures. For our statistical models, since long-term information of crop developmental stages at a large spatial scale is not available, we could not account for this factor, for example splitting the growing season into different periods based on the crop phenological stage. In addition, warming can hasten crop development and result in faster maturity. Access to phenology data will also assist in the analyses of crop fast development. However, at the field scale where such information is available from long-term experiments, analyzing crop yields response to climatic conditions by stage (Carter *et al.*, 2018) can tell which stage is more vulnerable to the compound effect. We would expect a similar model improvement as did by Carter *et al.* (2018), if phenology data were available at the regional scale.

5.2.3 Management, with the main focus on limited role of irrigation.

Our mechanistic model governs irrigation scheme by setting target and intervention levels of soil moisture, which can minimize high canopy temperatures. Application of the model with site-specific parameters can inform choice of the irrigation strategy by which crops can be mostly grown at optimal temperature range, meanwhile minimizing the risk of crop heat stress and irrigation water requirements.

For our statistical models, now at regional-level, only irrigated and rainfed cropping is differentiated. We can only utilize that information as a categorical variable in our model. In reality, other irrigation attributes such as the frequency, and amount of irrigation, which also determine the magnitude of the mitigation effect. Such information on irrigation is not available at regional scale, but can be indirectly detected based on remote sensing data (Chen *et al.*, 2018). Specific attributes of irrigation, can be used as model explanatory variables, to not only disentangle irrigated and rainfed cropping, but also further decipher their impact on yields.

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Popular science summary

Climate change threatens global food security, because climatic conditions are increasingly adverse to cropping systems. Under changing climate, many key agricultural regions are and will be exposed to increasing risks of hot and dry conditions, occurring in isolation or in combination – the synergistic result of rising temperatures and altered precipitation patterns. Crops are vulnerable to hot and dry conditions, and even more so if these conditions occur together. But exactly how much are crops damaged by hot and dry conditions? And can we manage crops so as to reduce the potential for damage? In this thesis, we used two modeling approaches to simulate crop responses to hot and dry conditions under different climatic and management scenarios.

To this aim, we developed mechanistic models, based on crop physiological principles, and statistical models, exploiting data to explore the relationship between climatic conditions and crop yields. This two-pronged approaches allowed gaining a thorough understanding of crop responses to hot and dry conditions, from the leaf- to the field-level. The mechanistic model can be used for predicting crop canopy temperatures, which is a good indicator of what the crop senses in terms of temperatures under various environmental conditions. Crop with high canopy temperature can be damaging, with potentially severe yield losses. Conversely, statistical models can directly tell how large the yield losses were under hot and dry conditions. Furthermore, we aimed to assess if irrigation or choice of specific crop species and varieties can reduce the effects of hot and dry conditions.

Our results suggested that hot and dry conditions interacted with each other, leading to higher canopy temperatures and lower yields than the same conditions occurring in isolation. Mean climatic conditions and how the climatic conditions varied within the growing season were equally important in explaining the crop yields under hot and dry conditions. More intermittent precipitation, which corresponds to longer periods without rain, can negatively affect canopy temperature and yields even under unchanged mean climatic conditions. Yields of rainfed crops were highest at intermediate precipitation levels and declined towards both higher and lower precipitation levels – a clear indication that also excess of precipitation can be detrimental. The precipitation leading to the highest yields increased with air temperature.

In short, the expected future conditions can be damaging to crops and their yields in many regions. But can we adapt to these new conditions, with management choices that make the crops less vulnerable? Irrigation could alleviate but not cancel the negative effects of hot and dry conditions. Its use can thus help to ensure yields are not suppressed. But irrigation applications should focus on the cases where the benefits are substantial and overcome issues related to local factors, such as socio-economic, water resource availability, and potential negative environmental effects of irrigation. Also crop choice matters. Perennial grain crops which can survive for several seasons, have been suggested as an adaptation to climate change. We found that whether perennial grain crops could be better adapted than annual species to the projected future conditions depends on the specific plant characteristics. Breeding of perennial grain crops should focus not only on grain yields but also on the traits that allow adaptation to future conditions.

Populärvetenskaplig sammanfattning

Klimatförändringar är ett hot mot den globala livsmedelssäkerheten då extremväder påverkar våra odlingssystem negativt. Med ett förändrat klimat är och kommer många viktiga jordbruksregioner att utsättas för ökad risk för varma och torra förhållanden, som isolerade händelser eller i kombination - det synergistiska resultatet av stigande temperaturer och förändrade nederbördsmönster. Grödor är känsliga för varma och torra förhållanden, och än mer om dessa förhållanden uppträder tillsammans. Men exakt hur mycket skadas grödorna av varma och torra förhållanden? Och ser risken annorlunda ut när olika odlingsmetoder används? I denna avhandling använde vi två modelleringsmetoder för att simulera grödors respons på varma och torra förhållanden i scenarier med olika klimat och odlingsmetoder.

För detta ändamål utvecklade vi mekanistiska modeller, baserade på fysiologiska principer för grödor och statistiska modeller, där vi använde data för att utforska förhållandet mellan klimatförhållanden och grödor. Kombinationen av mekanistiska och statistiska modeller gjorde det möjligt att få en grundlig förståelse för grödans svar på varma och torra förhållanden, från blad- till fältnivå. Den mekanistiska modellen kan användas för att förutsäga bladtemperaturen, vilken är en bra indikator på vad grödan känner av under olika miljöförhållanden. Höga bladtemperaturer kan vara skadliga, och leda till väsentligt lägre avkastning. De statistiska modellerna ger dock en mer säker bild av hur stora avkastningsförlusterna faktiskt var under varma och torra förhållanden. Dessutom syftade vi till att bedöma om bevattning eller val av specifika växtarter och sorter kan minska effekterna av varma och torra förhållanden.

Våra resultat indikerade att varma och torra förhållanden interagerade med varandra, vilket ledde till högre bladtemperaturer och lägre skördar än om värme eller torkaförekom var och en för sig. Även genomsnittliga klimatförhållanden och hur klimatförhållandena varierade under växtsäsongen var viktiga för att förklara grödans avkastning under varma och torra förhållanden. Mer periodisk nederbörd, som motsvarar längre perioder utan regn, kan påverka bladtemperaturen och avkastningen negativt även under oförändrade klimatförhållanden. Grödor som inte bevattnats gav högst avkastning om nederbördsnivåerna var medelstora, och minskade vid både högre och lägre nederbördsnivåer - en tydlig indikation på att för mycket nederbörd kan vara skadligt. När temperaturen ökade uppnåddes dock den högsta avkastningen när även nederbörden ökade.

Kort sagt kan de klimatförhållanden som förväntas i framtiden vara skadliga för grödor och påverka avkastningen negativt i många regioner. Men kan vi anpassa oss till dessa nya förhållanden, med val av odlingsmetoder som gör grödorna mindre påverkade? Bevattning kan lindra men inte eliminera de negativa effekterna av varma och torra förhållanden på grödorna. Bevattning kan således bidra till att säkerställa att avkastningen inte minskar. Användandet av bevattning bör dock fokuseras på de fall där fördelarna är stora, och andra lokala faktorer, såsom socioekonomiska förhållanden, tillgång till vattenresurser och potentiella negativa miljöeffekter av bevattning. Även grödval är viktigt. Fleråriga spannmålsgrödor växer under flera säsonger har föreslagits som en anpassning till klimatförändringen. Vi fann att om fleråriga spannmålsgrödor skulle kunna anpassas bättre än ettåriga arter till de beräknade framtida förhållandena beror på de specifika växtegenskaperna. Förädling av fleråriga spannmålsgrödor bör inte bara fokusera på avkastningen utan också på egenskaper som möjliggör anpassning till framtida förhållanden.

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Hydrology and Earth System Sciences

Canopy temperature and heat stress are increased by compound high air temperature and water stress and reduced by irrigation – a modeling analysis

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Abstract. Crop yield is reduced by heat and water stress and even more when these conditions co-occur. Yet, compound effects of air temperature and water availability on crop heat stress are poorly quantified. Existing crop models, by relying at least partially on empirical functions, cannot account for the feedbacks of plant traits and response to heat and water stress on canopy temperature. We developed a fully mechanistic model, coupling crop energy and water balances, to determine canopy temperature as a function of plant traits, stochastic environmental conditions, and irrigation applications. While general, the model was parameterized for wheat. Canopy temperature largely followed air temperature under well-watered conditions. But, when soil water potential was more negative than −0.14 MPa, further reductions in soil water availability led to a rapid rise in canopy temperature – up to 10 °C warmer than air at soil water potential of −0.62 MPa. More intermittent precipitation led to higher canopy temperatures and longer periods of potentially damaging crop canopy temperatures. Irrigation applications aimed at keeping crops under well-watered conditions could reduce canopy temperature but in most cases were unable to maintain it below the threshold temperature for potential heat damage; the benefits of irrigation in terms of reduction of canopy temperature decreased as average air temperature increased. Hence, irrigation is only a partial solution to adapt to warmer and drier climates.

1 Introduction

High and stable crop yield requires suitable climatic conditions throughout the growing season. Abiotic stressors, like water scarcity and high temperatures, can adversely affect crop growth, development, and yield, as shown by controlled-condition and field experiments, large-scale surveys, and crop model applications (e.g., Zampieri et al., 2017; Daryanto et al., 2017; Kimball et al., 2016; Ray et al., 2015; Asseng et al., 2015). Both water and heat stress impair photosynthesis (Way and Yamori, 2014; Lawlor and Tezara, 2009), undermine crop growth (Hsiao, 1973; Hatfield and Prueger, 2015) and reproduction (Prasad et al., 2011), and hasten crop development and leaf senescence (Lobell et al., 2012), although the physiological mechanisms can differ (Fahad et al., 2017). Heat and water stress do not only act independently but also have compound effects on plant phenology and physiology, so heat stress is more detrimental if co-occurring with water stress (Mahrookashani et al., 2017; Prasad et al., 2011; Suzuki et al., 2014; Cohen et al., 2021). Yet, these compound effects of heat and water stress are seldom considered experimentally or via models (Rötter et al., 2018).

Climate change is projected to increase air temperature and, in many regions, decrease growing season precipitation or lengthen dry spells (IPCC, 2013). Hot and dry summers are becoming more common (Zscheischler and Seneviratne, 2017; Alizadeh et al., 2020), and changes in climate are already reducing and will likely further reduce crop yield and its stability and, ultimately, global food security (e.g., Challinor et al., 2014; Masson-Delmotte et al., 2018; Moore and Lobell, 2015; Rosenzweig et al., 2014). The frequency and severity of crop heat and water stress are directly affected by air temperature and soil water availability and indirectly driven by evapotranspiration, which is enhanced by warm temperatures. Nevertheless, how air temperature and precipitation and their variability interact in defining the occurrence, extent, and duration of crop heat and water stress has not been investigated in detail.

Canopy temperature allows more accurate estimates of the consequences of heat stress on the crop and its yield than air temperature (Gabaldón-Leal et al., 2016; Siebert et al., 2014; Rezaei et al., 2015). Canopy temperature can deviate from air temperature under field conditions because of the interplay among plant traits, plant water availability, air temperature and humidity, solar radiation, wind velocity, and the ensuing canopy microclimate (Michaletz et al., 2016; Schymanski et al., 2013). Considering canopy instead of air temperature is particularly important when characterizing the effects of compound heat and water stress and the mitigating potential of irrigation against heat stress because canopy temperature can be substantially higher than air temperature under water stress (e.g., Siebert et al., 2014).

Heat stress and damage are the result of complex and interacting plant physiological processes, depending on the temperature reached by the specific organ and the duration of the stress. Crop response to temperature is nonlinear (Porter and Gawith, 1999; Sanchez et al., 2014). Exceeding crop- and developmental-stage-specific thresholds can lead to plant tissue damage and halted physiological processes, although the plant can still survive. Also, the duration of exposure to high temperatures affects the outcome. For example, the accumulation of high temperature days negatively affected yield in rainfed systems (Schlenker and Roberts, 2009). In the face of increasing variability in the climatic conditions, we need to determine how stochastic precipitation and air temperature combine in determining canopy temperature. Average canopy temperatures and duration of periods above the threshold for damage can provide indications on the exposure of crops to potential heat stress.

Irrigation can buffer some aspects of climatic variability and extremes imposed on crop production (Tack et al., 2017; Zhang et al., 2015; Li and Troy, 2018; Vogel et al., 2019). Irrigation directly alleviates water stress by supplementing precipitation. Furthermore, by sustaining the plant's evaporative cooling, irrigation can reduce canopy temperature and, hence, the consequences of high air temperature (Vogel et al., 2019; Siebert et al., 2017). In other words, by removing water stress, irrigation can also diminish the occurrence of heat stress. Nevertheless, we lack a quantification of how much irrigation can reduce the effects of unfavorable air temperature and precipitation and the occurrence of crop heat stress and compound heat and water stress.

Canopy temperature is difficult to measure directly, although it can be estimated indirectly based on thermal imagery (e.g., Still et al., 2019). Models are a powerful tool for exploring how canopy temperature changes with growing conditions and plant traits beyond what is feasible via direct observations in specific experiments. Existing crop canopy temperature models either link canopy to growing conditions via simple empirical relations (e.g., Shao et al., 2019; Neukam et al., 2016) or explicitly model the leaf or canopy energy balance (Webber et al., 2016, 2017; Fang et al., 2014). But, so far, the role of plant water availability has been included only via semi-empirical corrections – even in mechanistic models. For example, actual canopy temperature was calculated based on canopy temperatures under maximum and zero stomatal conductances and a crop water stress index (for a review of approaches and their performance, see Webber et al., 2017, 2018). Mechanistic models fully representing plant physiology can estimate crop canopy temperature that better reflects soil water and weather dynamics and how plants respond to environmental conditions. Such models are currently lacking but are necessary for quantifying the effects of joint changes in air temperature and precipitation patterns and the benefits of irrigation.

We developed a mechanistic model to estimate crop canopy temperature as a function of crop physiology, soil features, and (stochastic) climatic conditions, coupling the canopy energy balance and the water transport through the soil–plant–atmosphere continuum (SPAC), with stomatal conductance based on an optimality principle. We used the model in a case study – wheat grown in a temperate climate – to answer the following questions:

- What are the compound effects of soil water availability and air temperature on crop canopy temperature?
- How does the precipitation pattern influence canopy temperature and its variability and the duration of potentially damaging canopy temperatures?
- How effective is irrigation in reducing canopy temperature and the duration of potentially damaging canopy temperatures, depending on the climatic regime?

2 Methods

2.1 Model description

To quantify the compound effects of air temperature and precipitation regimes on canopy temperature and the potential of irrigation to reduce the occurrence of crop heat stress, we developed a mechanistic model describing the coupled canopy energy and water balances and their interactions with the water balance of the rooting zone (see the model structure in Fig. 1 and the Supplement for details and symbols). The model allows us to explore how plant traits and physiological responses to growing conditions interact with air temperature and soil water availability in defining canopy temperature, while relying on parameters with clear physiological meanings (Table S2 in the Supplement).

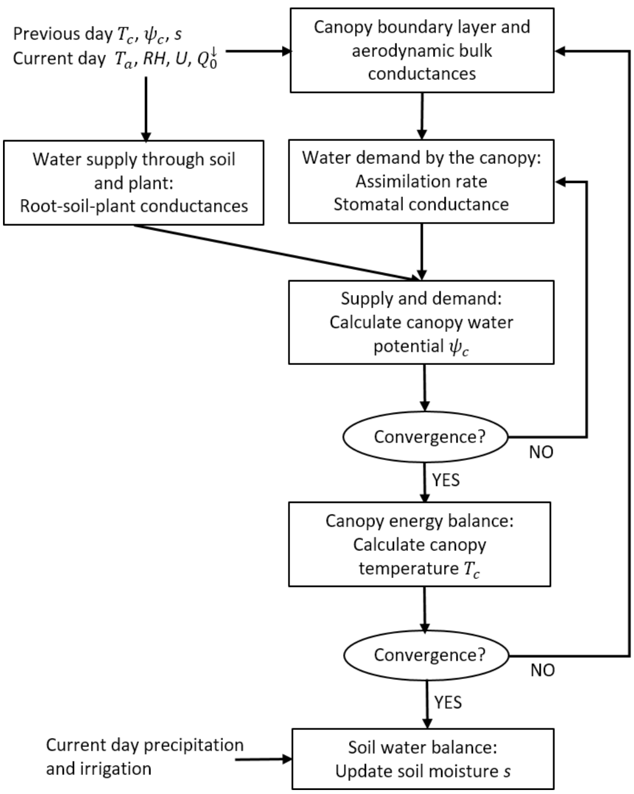

Figure 1. Flow diagram of the determination of canopy temperature and soil moisture dynamics.

To limit parameter and computational requirements, a minimalist approach was used, lumping the canopy in a big leaf model (Amthor, 1994; Jarvis and McNaughton, 1986; Bonan, 2019) and the soil water dynamics in a bucket-filling model, with instantaneous losses via runoff and percolation below the rooting zone (e.g., Milly, 1994; Rodriguez-Iturbe et al., 1999). These simplifications are expected to have minor repercussions on our conclusions (see Sect. S5 in the Supplement).

As detailed in the Supplement, combining the canopy water and energy balance, the canopy temperature, T_c, can be obtained as follows:

$$T_c = T_a + \frac{Q^{\downarrow} + B^{\downarrow}_{n,\,ref} - \lambda g_{v,\,c} D}{c_p g_{H,\,c} + \lambda g_{v,\,c} s_s + 4\varepsilon_c \sigma T_a^3 \left[1 - \exp\left(-K_{bl,d}\, L_{AI}\right)\right]}, \quad (1)$$

where T_a is the air temperature, $Q^{\downarrow}$ is the net absorbed shortwave radiation, $B^{\downarrow}_{n,\,ref}$ is the net absorbed longwave radiation at T_a (isothermal radiation), and D is the atmospheric vapor pressure deficit. $g_{v,\,c}$ and $g_{H,\,c}$ are the total canopy conductances to water vapor and heat, respectively, which include stomatal and aerodynamic conductances, λ, c_p, ε_c, σ, and $K_{bl,d}$ are constants (Table S1), s_s is the slope of the vapor pressure vs. temperature curve, dependent on T_a, and L_{AI} is the leaf area index.

We explicitly included the dependence of stomatal conductance on environmental conditions and plant physiology, exploiting an optimality principle, namely that plants are assumed to maximize carbon uptake over a given period, subject to limited water availability (Mäkelä et al., 1996; Eqs. S9–S11 in the Supplement). We chose this approach because it is simple, yet based on an evolutionary principle, and has led to promising results (Buckley et al., 2017; Eller et al., 2020). Many stomatal optimization models based on water use efficiency assume that photosynthesis is limited either by RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) or electron transport rate. To avoid this a priori assumption, we approximated the original Farquhar et al. (1980) model for the photosynthetic rate with a hyperbolic function that includes both limitations while retaining the same physiological parameters (Vico et al., 2013). This model was further developed here to account for the effects of the leaf boundary layer conductance and day respiration in addition to the key stomatal and non-stomatal effects of limited water availability on marginal water use efficiency and metabolic activity (Zhou et al., 2013; Manzoni et al., 2011; Vico and Porporato, 2008; see Sect. S1.2.1 for details). The results obtained with an alternative, empirical model of canopy conductance parameterized with eddy covariance data (Eqs. S30–S32; Novick et al., 2016) further support our mechanistic approach. But, they also highlight the need to explicitly represent canopy gas exchanges to capture the dependence of canopy temperature on air temperature, unless site-specific and crop-specific data are available to determine the canopy conductance empirically (Fig. S9). Finally, aerodynamic conductances to heat and vapor were determined based on wind velocity, U, and leaf width via well-established, semi-empirical relations describing heat and mass transport inside the leaf boundary layer and to the bulk atmosphere (Sects. S1.2.2 and S1.2.3).

The canopy conductances affect and are affected by the soil water balance and water transport along the SPAC. On the one hand, soil water potential influences leaf water potential and, hence, leaf physiological activities (stomatal conductance, metabolic rates, and marginal water use efficiency). On the other hand, stomatal conductance and atmospheric water demand drive the rate of canopy water losses and, hence, the decline of soil water content. We represented the soil water content as soil saturation, s ($0 \le s \le 1$; hereafter soil moisture), linked to soil water potential, ψ_s, via texture-dependent soil water retention curves (Eq. S24). A bucket-filling model was used to describe the soil moisture dynamics, with precipitation and irrigation as input and evapotranspiration, deep percolation below the rooting zone and surface runoff as losses but neglecting the root structure, the time needed for the water to be redistributed within the soil, and lateral soil water movements (Sect. S1.3.1; Vico and Porporato, 2010). The soil water balance was coupled to a minimalist description of water transport through the SPAC to determine the leaf water potential. The SPAC was modeled as a series of conductances from the soil, through the plant, to the atmosphere (Sect. S1.3.2; Manzoni et al., 2013).

These model components provide conductances and boundary conditions to apply Eq. (1) and quantify how canopy temperature, T_c, changes with environmental conditions and management, namely air temperature and humidity, wind velocity, incoming solar radiation, precipitation and irrigation applications, if any. The model needs to be solved iteratively (Fig. 1). At each time step (1 d; see Sect. 2.3), the model considers the previous soil moisture and current atmospheric conditions. The previous canopy temperature and water potential are used as initial guesses for the numerical integration. First, the model determines the canopy boundary layer and aerodynamic bulk conductances and water supply and demand. Then, the canopy water potential ψ_c is determined iteratively by equating water supply and demand. After convergence is reached on ψ_c, the canopy energy balance is used to determine T_c iteratively. Finally, the soil water balance is updated with inputs and losses cumulated over the time step.

2.2 Metrics of potential heat stress damage

Based on T_c, we derived the following two metrics representing the potential for heat stress damage: (i) $T_{c,\,mean}$, the mean canopy temperature during a specific period (anthesis; see Sect. 2.3), and (ii) P_{CHS}, the fraction of days during such a period when T_c exceeded the crop-specific threshold T_{th}, above which detrimental effects of crop heat stress are likely. P_{CHS} is thus a measure of the duration of the detrimental conditions, while $T_{c,\,mean}$ quantifies the level of detrimental conditions.

2.3 Case study

While the model is of general applicability, we focused on the case of wheat (*Triticum aestivum*) – a staple crop with relatively low tolerance to high temperatures when compared with other crops (Sanchez et al., 2014) – grown at 45° N. All the model parameters are summarized in Table S2.

We restricted our analyses to anthesis, when wheat is most vulnerable to heat (Porter and Gawith, 1999) and water (Daryanto et al., 2017) stress. Anthesis was assumed to last 21 d (Mäkinen et al., 2018), starting on day 140 of the year, i.e., 20 May (in line with observations and simulations at the latitude selected; Semenov et al., 2014; Bogard et al., 2011). For simplicity, the timing and length of anthesis were kept constant under all climatic scenarios, regardless of irrigation applications.

The model is capable of simulating the diurnal course of the key variables, but, for simplicity, we focused on the central part of the day, when incoming shortwave radiation at the top of the canopy $Q_0^{\downarrow}$ and air temperature T_a are at or near their daily maxima and T_c is expected to peak. Wind velocity U was assumed to be at the lowest end of its realistic range, and $Q_0^{\downarrow}$ to be that of clear sky conditions, thus providing the maximum expected T_c and a conservative estimate of the frequency of occurrence of potentially damaging temperatures.

Measured environmental conditions relative to a specific location could be used to force the model. Yet, here we employed synthetically generated environmental conditions, varying their parameters to systematically explore several climate scenarios. Daily precipitation was idealized as a marked Poisson process (Rodriguez-Iturbe et al., 1999), i.e., exponentially distributed interarrival times, with average frequency λ_p. Event depth was also assumed to be exponentially distributed, with average α_p (Sect. S1.4.2). The variability of T_a around its long-term average μ_{T_a} was described via an Ornstein–Uhlenbeck process (Sect. S1.4.3; Benth and Benth, 2007). In line with the focus on the warmest part of the day, T_a is interpreted as the maximum daily air temperature. Finally, U, $Q_0^{\downarrow}$, and RH (relative humidity) were assumed to be constant during the simulations (Table S2), whereas air water vapor pressure, e_a, and vapor pressure deficit, D, were calculated based on T_a (Campbell and Norman, 1998).

As baseline pedoclimatic conditions, we considered a sandy loam soil, an average precipitation frequency λ_p of $0.2\,d^{-1}$, an average event depth α_p of 8.2 mm (corresponding to an average annual precipitation total of 600 mm), a long-term average air temperature μ_{T_a} of 25 °C, an air temperature standard deviation of 3.6 °C, an air relative humidity RH of 40 %, a wind velocity U of $4\,m\,s^{-1}$, and a net incoming shortwave radiation $Q_0^{\downarrow}$ of $800\,W\,m^{-2}$. We also explored additional pedoclimatic conditions. Specifically, we considered more extreme precipitation scenarios, comprising increasing precipitation from increasing precipitation frequency, and a constant average annual precipitation total, but with more intermittent precipitation, with a reduced average precipitation frequency ($\lambda_p = 0.07\,d^{-1}$) and increased average event depth ($\alpha_p = 23.5$ mm). Long-term average air temperatures μ_{T_a} of 20 and 30 °C were also explored. Separate sensitivity analyses were run for the standard deviation of air temperature (Fig. S6), soil texture (Fig. S7), and U, $Q_0^{\downarrow}$, and RH (Fig. S8).

For the irrigated case, a demand-based (water) stress-avoidance irrigation was considered whereby an irrigation application is triggered whenever soil water potential reached the intervention point, $\tilde{\psi}_s$ (Vico and Porporato, 2011). To ensure well-watered conditions, $\tilde{\psi}_s$ was set to −0.07 MPa, i.e., just above the incipient water stress for wheat (−0.1 MPa; Kalapos et al., 1996). Each irrigation application restored a preset target soil water potential, $\hat{\psi}_s$, set at −0.01 MPa. The difference between the intervention point and the target soil water potential is large enough to allow the use of a traditional irrigation technology (e.g., sprinkler systems or surface irrigation; see Vico and Porporato, 2011 and references therein).

Finally, the crop- and developmental-stage-specific temperature threshold above which detrimental effects of crop heat stress are likely, T_{th}, was set equal to the maximum baseline (i.e., cardinal) temperature during anthesis. T_{th} is a large source of large uncertainty when aiming at defining the occurrence of crop heat stress and its consequences on the crop and final yield (Siebert et al., 2017; Wanjura et al., 1992). Even within a specific developmental stage, there is a large variability in reported baseline and optimal temperatures because of differences in variety, growing conditions, and experimental approach. Furthermore, a crop's baseline and optimal temperatures are often defined based on air temperature, although plants respond to canopy or even organ temperature. As shown below, the differences between air and canopy temperatures can be large, particularly under limited plant water availability. To make the comparison between T_c and T_{th} meaningful, we considered a maximum baseline temperature obtained under well-watered conditions and low D and set T_{th} equal to 30 °C (Saini and Aspinall, 1982). This value is similar to those obtained in other experiments focusing on wheat (Porter and Gawith, 1999).

2.4 Statistical tests

The simulated canopy temperatures were not normally distributed, according to the Anderson–Darling test ($p < 0.05$). To test if median $T_{c,\,mean}$ and P_{CHS} differed across scenarios, we employed the Mood test. And, to test the difference in their variances, we used the Brown–Forsythe test. The test results are summarized in Tables S3–S8. Differences are commented on when $p < 0.05$.

3 Results

The stochasticity of air temperature, T_a, and precipitation occurrence was mirrored by the erratic variations in soil moisture, s, and canopy temperature, T_c, in the numerically simulated trajectories (exemplified in Fig. 2). T_c largely followed T_a, but s determined whether T_c was near or above T_a. Under well-watered conditions, when s ensured unconstrained transpiration, T_c was similar to or even occasionally lower than T_a, whereas, when s decreased, T_c became warmer than T_a (after approximately day 12 in Fig. 2). The evolution of T_c and other key physiological state variables, including stomatal conductance, photosynthesis, and canopy water potential, during a dry down is reported in Fig. S1.

Despite the complex mechanisms linking T_a and plant water availability to T_c, the resulting temperature difference $T_c - T_a$ followed a relatively simple pattern (Fig. 3). When s was above 0.34 (corresponding to $\psi_s = -0.14$ MPa for the soil chosen), T_c was within 1 to 2 °C of T_a, with $T_c < T_a$ for $T_a > 25\,°C$. Conversely, for $s < 0.34$, $T_c - T_a$ increased as s declined, with increasing slope, from 1 °C at $s = 0.34$ to 10 °C at $s = 0.25$ (corresponding to $\psi_s = -0.62$ MPa), and

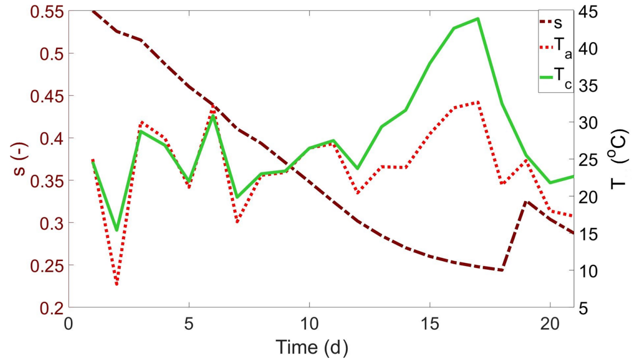

Figure 2. Example of numerically generated time series of soil moisture (s; dot-dashed burgundy line), air temperature (T_a; dotted red line), and canopy temperature (T_c; solid green line), for rainfed cropping. The left axis represents soil moisture and the right axis temperature. The model was run for 21 d with the baseline environmental conditions. Parameter values are listed in Table S2.

$T_c - T_a$ was independent of T_a (i.e., under water stress, $T_c - T_a$ is driven by soil water availability for evaporative cooling). Hence, high T_c could be caused by high T_a or low s or their combination. The dependence of the plant's physiological state variable on s is reported in Fig. S2 for set T_a.

Temperature and precipitation patterns interacted to define the mean canopy temperature during anthesis, $T_{c,\,mean}$. Increasing average precipitation totals decreased median $T_{c,\,mean}$ (colors in Fig. 4; Tables S3 and S4), particularly at lower precipitation totals (red in Fig. 4) and higher long-term average air temperature μ_{T_a} (red hues in Fig. 4). $T_{c,\,mean}$ was less affected by annual average precipitation totals larger than 900 mm and μ_{T_a} at 20 °C. $T_{c,\,mean}$ variability increased with μ_{T_a} and, to a lesser extent, with decreasing average precipitation totals (Tables S3 and S4).

Precipitation regime affected median of $T_{c,\,mean}$ and its variability even when considering the same precipitation total but different average precipitation frequencies, λ_p (and, hence, event depths, α_p; Fig. 5a). When compared with the baseline precipitation scenario (red bars), larger but more intermittent events (i.e., lower λ_p and higher α_p; violet bars) resulted in higher $T_{c,\,mean}$ median and variability in rainfed cropping (Table S5). The median of $T_{c,\,mean}$ increased with μ_{T_a} regardless of rainfall pattern, whereas the variance was not significantly affected (Table S6).

Irrigation reduced the median and variance of T_c with respect to rainfed cropping under the same climatic scenario (red vs. blue hues in Fig. 5a). Also, the dependence of T_c on the precipitation pattern was reduced with irrigation (Table S5). Yet, despite the irrigation, median and variability of T_c increased with μ_{T_a} (Table S6), although the increase in median T_c was less marked than that under rainfed cropping.

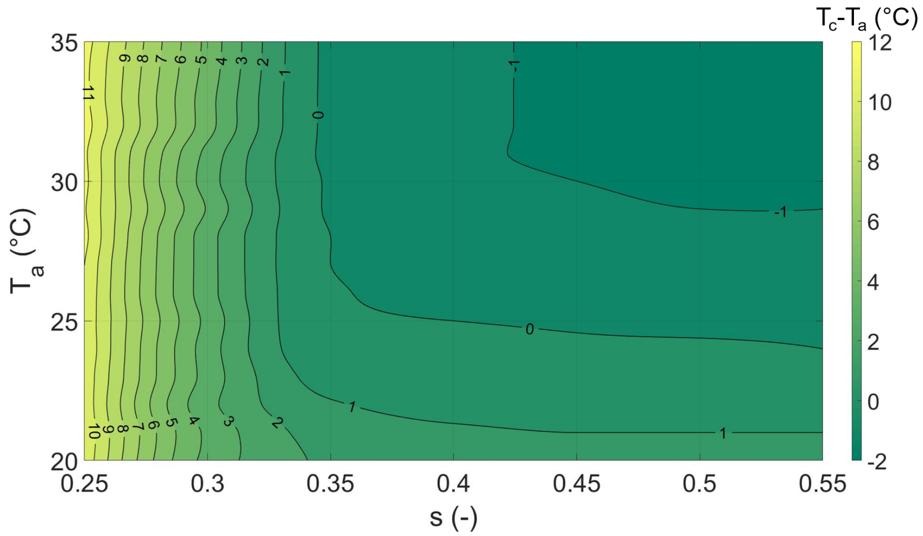

Figure 3. Canopy air temperature difference, $T_c - T_a$ (colors and contour lines), as a function of soil moisture (s; x axis) and air temperature (T_a; y axis) for a sandy loam. All other parameters are summarized in Table S2.

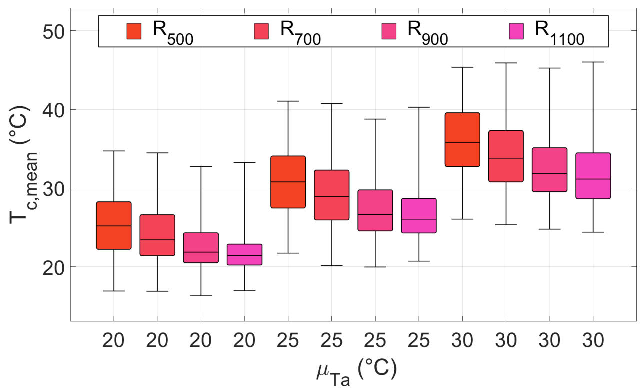

Figure 4. Distribution of mean canopy temperatures during anthesis, $T_{c,\,mean}$, for four average annual precipitation totals (500, 700, 900, and 1110 mm; colors) and three long-term average air temperatures μ_{T_a} (20, 25, and 30 °C; x axis). Average precipitation depth α_p was kept at 15 mm, while average precipitation frequency λ_p changed within each group of four bars, left to right, from 0.091 to 0.137, 0.183, and 0.228 d^{-1}, leading to increasing average annual precipitation totals (subscripts in the legend). For each climatic scenario, 500 simulations of 21 d each were run. The horizontal black lines are the median values. The boxes extend from the first to the third quartile; whiskers cover the whole range.

Irrigation applications reduced the fraction of days during which T_c was above the threshold temperature for potential heat damage, T_{th}, that is, of likely crop heat stress (P_{CHS}; Fig. 5b). But, it could not completely prevent this occurrence (i.e., median $P_{CHS} > 0$), except for $\mu_{T_a} = 20$ °C. Among the climatic scenarios considered, the largest median reduction in P_{CHS} (100 %) occurred at $\mu_{T_a} = 20$ °C and the smallest (between 53 % and 58 %) at $\mu_{T_a} = 30$ °C (Table 1).

Table 1. Reduction in the potential for heat stress by irrigation, as summarized by the median reductions in P_{CHS} from rainfed cropping to stress avoidance irrigation, using rainfed as reference.

μ_{T_a} (°C)	Baseline precipitation regime ($\alpha_p = 8.2$ mm; $\lambda_p = 0.2\,d^{-1}$)	More intermittent precipitation ($\alpha_p = 23.5$ mm; $\lambda_p = 0.07\,d^{-1}$)
20	100 %	100 %
25	78 %	80 %
30	53 %	58 %

Increasing air temperature variability left the median and variance of $T_{c,\,mean}$ unaltered in rainfed cropping but increased them in irrigated cropping (Fig. S6, top, and Table S7). There, the removal of water stress via irrigation made the resulting canopy temperature more sensitive to the air temperature regime. The median of and variance in P_{CHS} increased with temperature variability in the irrigated cropping (Fig. S6, bottom, and Table S7). Also, incoming shortwave radiation, $Q_0^{\downarrow}$, wind velocity, U, and air relative humidity RH affected T_c (Fig. S8). An increase in $Q_0^{\downarrow}$ increased T_c, particularly at $s < 0.35$. Decreasing U enhanced T_c for $s < 0.35$ but did not affect it when $s > 0.35$. In contrast, T_c slightly increased with RH for $s > 0.35$ but showed no response to it when $s < 0.35$. Finer soil texture did not affect $T_{c,\,mean}$ and P_{CHS}, although the difference between rainfall scenarios remained (Fig. S7 and Table S8). Also, rooting depth Z_r could affect $T_{c,\,mean}$ and P_{CHS}. Yet, when considering a range of Z_r compatible with observations for wheat (and annual crops in general; Jackson et al., 1996), the effects on $T_{c,\,mean}$ of reduced losses via deep percolation and runoff and stabilized

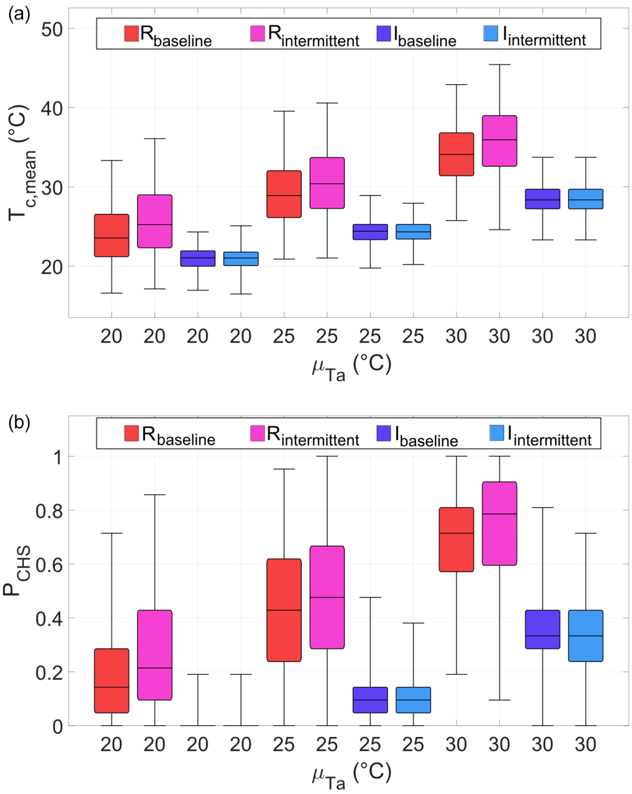

Figure 5. Distribution of mean canopy temperature during anthesis ($T_{\mathrm{c,\,mean}}$; **(a)**) and percentage of days during which T_c is above the threshold temperature for potential heat damage, T_th (P_CHS; **(b)**), under three long-term average air temperatures μ_{T_a} (x axis) and different precipitation and irrigation scenarios (colors). In each group of four boxes, from left to right, R_baseline and $R_\mathrm{intermittent}$ represent rainfed cropping, respectively, under baseline precipitation ($\alpha_\mathrm{p} = 8.2\,\mathrm{mm}$; $\lambda_\mathrm{p} = 0.2\,\mathrm{d}^{-1}$) and more intermittent precipitation ($\alpha_\mathrm{p} = 23.5\,\mathrm{mm}$; $\lambda_\mathrm{p} = 0.07\,\mathrm{d}^{-1}$). I_baseline and $I_\mathrm{intermittent}$ refer to stress avoidance irrigation under the same precipitation regime of the corresponding rainfed cases. For each climatic scenario, 500 simulations of 21 d each were run. The horizontal black lines are the median values. The boxes extend from the first to the third quartile; whiskers cover the whole range.

soil moisture with deepening roots (Laio et al., 2001) were negligible (not shown).

4 Discussion

4.1 Soil water availability and air temperature jointly affect canopy temperature

We quantified the compound effect on canopy temperature from the following environmental conditions: air temperature, soil water availability, incoming shortwave radiation, wind velocity, relative humidity, soil texture, and irrigation. Our model is an improvement with respect to existing approaches which simulate canopy temperature in agricultural systems and rely on empirical corrections of values determined by means of the energy balance under extreme conditions (Fang et al., 2014; Webber et al., 2016). Lacking adequate modeling tools has limited our ability to effectively quantify the likelihood and extent of potential heat damage to crops and the potential improvements by irrigation.

The role of environmental conditions is mediated by plant physiology and its response to conditions. Indeed, losses via evapotranspiration dominated the soil water balance in all the climatic scenarios explored (see Sect. S3.1). But, despite the complex mechanisms behind canopy temperature, the resulting pattern was relatively simple. Canopy temperature increased from cooler temperatures and wetter soils to warmer and drier conditions (Fig. 3). Under well-watered conditions, some thermoregulation occurred, cooling down or warming up the canopy, depending on air temperature, to maintain the canopy near-optimal temperature for photosynthesis (Michaletz et al., 2016). This thermoregulation capability was lost when low water availability limited evaporative cooling. The differences in canopy and air temperatures provided by the model are in line with experimental observations and other model results, thus lending support to our approach. In wheat, for example, field observations and model results showed that daily maximum or mid-day canopy temperature was 2 to 10 °C warmer than air under water stress and from 1 to 2 °C warmer to up to 6 °C cooler than air temperature under well-watered conditions (Pinter et al., 1990; Rashid et al., 1999; Jensen et al., 1990; Howell et al., 1986; Ehrler et al., 1978; Balota et al., 2008; Neukam et al., 2016; Webber et al., 2016; Schittenhelm et al., 2014; Webber et al., 2018; Mon et al., 2016). Our simulations led to canopies being 2 to 10 °C warmer than air under water stress and to a cooling effect of 1 to 2 °C under warm but well-watered conditions. Differences between model results and observations can be ascribed to cultivar-specific traits, specific approach to measuring canopy temperature, measurement timing and position (within or just above the canopy), and environmental conditions (e.g., solar radiation and soil texture). Some of these aspects can be accounted for by the model, by adjusting the parameters to the specific crop and variety, and environmental conditions.

The difference between canopy and air temperature was higher than, and independent of, air temperature when soil water potential was below a critical value (Fig. 3). This threshold-like response mirrors that of stomatal closure and plant transpiration reduction with water stress (for wheat; e.g., Sadras and Milroy, 1996; Shen et al., 2002; Wang et al., 2008; Wu et al., 2011; Kalapos et al., 1996). Yet, no threshold for stomatal closure was imposed a priori in the model. The emerging threshold of soil water potential (−0.14 MPa) is comparable with the soil water potential corresponding to incipient stomatal closure in some experiments (−0.1 MPa; Kalapos et al., 1996) but higher than those of others (between −0.27 and −0.35 MPa, depending on the cultivar; Wang et al., 2008) and lower than the value often assumed to correspond to well-watered conditions (−0.03 MPa; Ali et al., 1999; Laio et al., 2001).

4.2 More intermittent precipitation and higher air temperature increase canopy temperature

Climate change is expected to alter both air temperature and precipitation regimes, with further increases in average and extremely high air temperatures and, in some regions, scarcer or more intermittent precipitation, i.e., longer dry spells (IPCC, 2013). Co-occurring dry and hot extremes are becoming increasingly frequent (Alizadeh et al., 2020; Zscheischler and Seneviratne, 2017). We showed that these compound changes can increase canopy temperature and its variability (Figs. 4 and 5).

For set air temperature conditions, even with same average precipitation totals, less frequent but larger precipitation events increased the median of and variance in canopy temperature, and the fraction of days during which the temperature threshold for potential heat damage was exceeded (Fig. 5). Larger, less frequent precipitation events result in enhanced losses via runoff and percolation below the rooting zone, thus reducing plant water availability. The ensuing (longer) dry down can lead to lower soil moisture levels, potentially enhancing canopy temperature. It is thus important to consider not only seasonal precipitation totals but also their timing. Indeed, reductions in the number of rainy days have already reduced crop yield and could even override the benefits of increased total precipitation (Ram, 2016). For a set precipitation regime, an increase in long-term average air temperature resulted not only in a higher mean canopy temperature during anthesis, as expected (Eq. 1), but also in a larger variability in such a mean (Figs. 4 and 5). These complex, compound effects show that it is necessary to explicitly consider not just the means but also the timing of and variability in air temperature and precipitation, and their joint effects, when quantifying the potential of climate change to cause crop heat stress. Hence, models accounting in full for the stochasticity of environmental conditions are needed.

Crops are also faced with increasing air carbon dioxide (CO_2) concentration. While this aspect of global change was not explored here, an increase in air CO_2 concentration could reduce stomatal conductance and, thus, enhance canopy temperature when all the other conditions are the same. But, reduced stomatal conductance can also reduce the rate of soil water storage depletion and, thus, the maximum canopy temperature reached during a dry down. The net result of an increase in air CO_2 concentration is expected to be small. Indeed, an air CO_2 concentration of 200 to 220 ppm (parts per million) above ambient conditions increased canopy temperature only up to 1 °C in free air CO_2 enrichment experiments and model simulations (Webber et al., 2018), and a weak reduction in yield loss to heat with enhanced CO_2 is expected (Schauberger et al., 2017).

4.3 Irrigation reduces but does not cancel the risk of heat stress

By reducing the occurrence and extent of water stress, irrigation could lower canopy temperature, and its variability, and the frequency of it exceeding the threshold for potential heat damage (Fig. 5). Irrigation can have positive effects on yields, not only by reducing water stress but also by reducing heat stress. Indeed, the canopy-to-air temperature difference is well correlated with the final yield (e.g., Blum, 1996; Reynolds et al., 1994; Thapa et al., 2018), except under extremely dry conditions (Schittenhelm et al., 2014). This temperature difference is often used for cultivar selection (Graß et al., 2020; Munns et al., 2010).

The extent of the reduction in canopy temperature and, hence, of the occurrence of potential heat stress even under stress-avoidance irrigation depended on the precipitation regime and long-term average air temperature. Irrigation was particularly effective in reducing canopy temperature and the duration of potentially damaging conditions at lower long-term average air temperature. And, for a set long-term average air temperature, irrigation was slightly more effective under more intermittent precipitation (Table 1). Yet, irrigation aiming at maintaining the plants under well-watered conditions could not completely remove the possibility that canopy temperature exceeded the temperature threshold for potential heat damage, except under the coolest air temperature scenario. Furthermore, the benefits of irrigation became smaller as air temperature increased. Irrigation could also have indirect effects on canopy temperature. At the regional scale, irrigation, by enhancing evaporation, can further reduce air temperature (e.g., Sacks et al., 2009; Lobell et al., 2008a) and canopy temperature, while lengthening developmental stages. These effects could be included by altering the air temperature regime (see Figs. 3 and 4 and Table 1 for the effects of average air temperature) and the duration of the anthesis.

The risk of canopy temperature exceeding the temperature threshold for potential heat damage under (water) stress avoidance irrigation can be interpreted as the potential heat stress attributable only to air temperature. This is because no limitation on evaporative cooling is expected under the imposed irrigation scenario, where the soil water potential triggering an irrigation application was less negative than the critical soil water potential emerging from Fig. 3. The reduction in the fraction of time in which canopy temperature is above the threshold for potential heat damage obtained via irrigation (Table 1) is a measure of the relative importance of air temperature and water stress in defining high canopy temperatures. In addition, for the most effective use of the available water resources against heat stress, the emerging threshold of soil water potential that limits water-stress-induced high canopy temperatures (Fig. 3) could be used to define a crop-specific irrigation intervention point for irrigation. Maintaining the soil water potential above that threshold would require additional water resources, while leading to marginal further cooling effects, i.e., little advantage in staving off heat stress.

Irrigation could not fully eliminate the negative effects of heatwaves and the warmer conditions expected in the future, but a widespread use of irrigation could directly or indirectly mitigate the effects of heatwaves (van der Velde et al., 2010). Nevertheless, even for air temperatures for which irrigation can reduce the potential for heat stress damage, and considering these regional effects, expanding irrigation to mitigate the effects of high canopy temperatures can be unadvisable or impossible due to physical or economic water scarcity (Rosa et al., 2020), already unsustainable exploitation of water resources (Wada et al., 2010), or the negative impacts of irrigation on soil salt content and nearby water bodies (Daliakopoulos et al., 2016; Scanlon et al., 2007). Other management approaches are, thus, needed to limit the potential for crop heat stress, particularly under high average air temperatures (Deryng et al., 2011; Lobell et al., 2008b). Examples are shifting to more heat-tolerant cultivars and species (Tack et al., 2016), altering the sowing date (Lobell et al., 2014; Mourtzinis et al., 2019), or migrating crops (Sloat et al., 2020) so that anthesis occurs when air temperature is, on average, lower.

5 Conclusions

Longer dry spells and high air temperatures are expected to become even more frequent in the future, with potential negative and compound effects on crop development and yield. Exploring the occurrence and severity of crop heat stress requires quantifying canopy temperature and considering under which conditions it exceeds the temperature threshold known to create appreciable damage. We developed a mechanistic model to determine canopy temperature, based on the explicit coupling of the soil water dynamics with the canopy energy balance, and an optimality principle for stomatal functioning, mechanistically accounting for plant physiology and its response to (stochastic) environmental conditions.

Using wheat as a case study, we explored how canopy temperature and its variability changed with stochastic air temperatures and precipitation in rainfed and irrigated cropping. When soil water potential was less negative than -0.14 MPa, the additional benefit of an increase in soil water availability and, hence, potential evaporative cooling became marginal, and thermoregulation ensured semi-optimal leaf temperature. However, canopy temperature rose rapidly above air temperature when soil water potential was less than -0.14 MPa, due to lowered evaporative cooling.

Less frequent and more intense precipitation caused more variable soil water contents, leading to higher and more variable canopy temperatures, and a higher fraction of days on which the temperature threshold for potential heat stress damage was exceeded. Larger precipitation totals and irrigation applications could reduce the occurrence of high canopy temperature and the potential for heat damage. Yet, irrigation could not completely remove the risk of crop heat stress when long-term average air temperature was 25 °C or higher, calling for alternative management solutions.

Accurate estimates of canopy temperature are necessary to assess the role of precipitation and air temperature patterns in defining the risk of crop heat stress and to evaluate the mitigation potential of irrigation. Mechanistic models explicitly linking plant physiology to environmental conditions also allow the exploration of the effects of plant traits on the occurrence and extent of water and heat stress. As such, these models can support management decisions, from using the most beneficial irrigation applications to identifying crops able to avoid heat stress.

Code availability. The MATLAB 2018a code of the model is available at https://doi.org/10.5281/zenodo.4540738 (Vico and Luan, 2021).

Data availability. Data for model parameterization are available in the cited literature.

Supplement. The supplement related to this article is available online at: https://doi.org/10.5194/hess-25-1411-2021-supplement.

Author contributions. GV conceived the idea. XL and GV developed the codes of the model. XL performed the analyses and created the figures. XL and GV wrote the paper. GV revised the paper.

Competing interests. The authors declare that they have no conflict of interest.

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Combined heat and drought suppress rainfed maize and soybean yields and modify irrigation benefits in the USA

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Abstract

Heat and water stress can drastically reduce crop yields, particularly when they co-occur, but their combined effects and the mitigating potential of irrigation have not been simultaneously assessed at the regional scale. We quantified the combined effects of temperature and precipitation on county-level maize and soybean yields from irrigated and rainfed cropping in the USA in 1970–2010, and estimated the yield changes due to expected future changes in temperature and precipitation. We hypothesized that yield reductions would be induced jointly by water and heat stress during the growing season, caused by low total precipitation (P_{GS}) and high mean temperatures (T_{GS}) over the whole growing season, or by many consecutive dry days (CDD_{GS}) and high mean temperature during such dry spells (T_{CDD}) within the season. Whole growing season (T_{GS}, P_{GS}) and intra-seasonal climatic indices (T_{CDD}, CDD_{GS}) had comparable explanatory power. Rainfed maize and soybean yielded least under warm and dry conditions over the season, and with longer dry spells and higher dry spell temperature. Yields were lost faster by warming under dry conditions, and by lengthening dry spells under warm conditions. For whole season climatic indices, maize yield loss per degree increase in temperature was larger in wet compared with dry conditions, and the benefit of increased precipitation greater under cooler conditions. The reverse was true for soybean. An increase of 2 °C in T_{GS} and no change in precipitation gave a predicted mean yield reduction across counties of 15.2% for maize and 27.6% for soybean. Irrigation alleviated both water and heat stresses, in maize even reverting the response to changes in temperature, but dependencies on temperature and precipitation remained. We provide carefully parameterized statistical models including interaction terms between temperature and precipitation to improve predictions of climate change effects on crop yield and context-dependent benefits of irrigation.

1. Introduction

The harvest we reap from our crop fields depend to large extent on the climatic conditions and their fluctuation (Porter and Semenov 2005). Temperature and precipitation explain one-third of global yield variation (Ray *et al* 2015). Climate change is expected to put pressure on crop production (IPCC 2019) and has already caused yield losses (Lobell *et al* 2011). Increased frequency of co-occurring high temperatures and low precipitation (Mazdiyasni and AghaKouchak 2015, Alizadeh *et al* 2020) suppresses crop yields by causing heat and water stress in the crop plants (Lesk *et al* 2016, Zscheischler *et al* 2017). Carefully parameterized yield models that include interaction terms between temperature and precipitation hold potential to improve predictions of climate change impacts on crop yield (Carter *et al* 2018).

Plant physiology and small-scale field and controlled-environment experiments tell us that stress combinations can have synergistic effects on yield formation (Suzuki *et al* 2014). Reduced water availability limits the plant's ability to regulate its temperature via evaporative cooling, thereby increasing its vulnerability to high temperatures (Siebert *et al* 2014, Neukam *et al* 2016). Experiments demonstrate how yields are more suppressed when heat and water stresses are combined than their summed effects when occurring in isolation (Prasad *et al* 2011, Mahrookashani *et al* 2017, Cohen *et al* 2021). Analyses of yields from arable fields with detailed climatic data show that interactive effects of precipitation and temperature or precipitation and vapor pressure deficit are needed to explain yield variation (Urban *et al* 2015, Carter *et al* 2018). Yet, the combined effects of heat and water stress on yields have often been overlooked in field-scale experiments and modeling (Rötter *et al* 2018).

The combined effects of precipitation and temperature have been examined for national crop yields. Yields across Europe were better explained with the bivariate return period of warm or cold temperatures and high or low precipitation total, compared with models relying only on temperature and precipitation (Zscheischler *et al* 2017). National maize and soybean yield losses were exacerbated in hot and dry seasons globally, in the USA and India (Matiu *et al* 2017), the American Midwest (Carter *et al* 2018, Kukal and Irmak 2018), and France (Hawkins *et al* 2013). But aggregating yields over vast geographical areas, such as with national data, can mask and average out adverse climatic conditions that often have more limited geographic range (Matiu *et al* 2017).

Crops respond to both seasonal average conditions and unfavorable conditions of shorter duration. Climatic conditions integrated over the growing season, such as precipitation totals and temperature means, are well correlated with crop yield across nations and regions (Lobell *et al* 2011, Osborne and Wheeler 2013, Challinor *et al* 2014, Zhao *et al* 2017). But averaging over the growing season can mask short-term but potentially damaging conditions, which can cause substantial yield losses (Lobell *et al* 2012, 2013, Troy *et al* 2015, Lesk *et al* 2016, Vogel *et al* 2019) depending on timing, duration, and intensity of the unfavorable conditions (Tack *et al* 2017). Analyses with a finer spatial and temporal resolution across large geographic areas and long time series, with climatic indices based on knowledge of plant physiological response to environmental stressors, could improve our understanding and predictions of climate impacts on yield.

Although crops are exposed to the same climatic conditions, yield can be differently affected under irrigated and rainfed cropping (Siebert *et al* 2017). Irrigation can, at least partially, mitigate negative effects from adverse climatic conditions on crop yields (Troy *et al* 2015, Leng 2017, Li and Troy 2018, Zhu *et al* 2019), directly by alleviating crop water stress (Zipper *et al* 2016) and indirectly by reducing heat stress through evaporative cooling (Siebert *et al* 2017, Tack *et al* 2017, Luan and Vico 2021). However, yield data collected across nations and regions are usually not separated into irrigated and rainfed yields. And, even where these data are available (as in parts of the USA), there is a lack of large-scale analysis of the interactive effects of temperature and precipitation on yield, explicitly considering the role of irrigated or rainfed cropping. Analyzing irrigated and rainfed crop yields from the same geographic location will elucidate the mitigating effects of irrigation on yields and how these effects might be linked to temperature and precipitation.

We explored the interactive effects of temperature and precipitation and the role of irrigation on fine-resolution (i.e. county-level) crop yields from the USA 1970–2010. We combined, for the first time, all of these factors in the same analysis, using county-level data, distinguishing irrigated and rainfed yields, and considering the interactive effects of temperature- and precipitation-related climatic indices. We considered two sets of climatic indices to capture different physiological mechanisms: (a) mean climatic conditions during the whole growing season (subscript GS), i.e. growing season precipitation total, P_{GS}, and mean air temperature, T_{GS}, and (b) shorter-term intra-seasonal conditions, as represented by maximum number of consecutive days with precipitation <2 mm during the growing season, CDD_{GS}, and mean daily air temperature during this dry period, T_{CDD}. We hypothesized that (a) there are compounded damaging impacts of combined high temperature and reduced water availability, which correspond to potential negative effects of heat and water stress, (b) irrigation reduces negative impacts of the two climatic stresses, both when occurring separately and when combined, and (c) measures of within-season conditions explain crop responses to heat and water stress at least as well as the whole season indices.

2. Materials and methods

2.1. Crop yields

We selected two staple crops, soybean and maize, grown both rainfed and irrigated, with a wide geographical distribution in the USA (supplementary information, SI, figure S1 (available online at stacks.iop.org/ERL/16/064023/mmedia)). County-level grain yield data for the period 1970–2010, separated for rainfed and irrigated cropping, were obtained from the US Department of Agriculture National Agricultural Statistical Service (Quick Stats; for details see SI S1.1).

2.2. Climatic indices and their calculations

We selected four climatic indices as candidate explanatory variables for crop yields to represent variation in air temperature and plant soil water availability during the growing season. The growing season was defined as the period between the local mean planting and harvesting dates (SI S1.3).

Two climatic indices were chosen to reflect air temperature and soil water availability during the whole growing season (subscript GS): mean daily air temperature averaged over the growing season (T_{GS}), and total precipitation over the growing season (P_{GS}), reflecting the input to the soil water balance.

Two climatic indices were chosen to represent conditions of shorter duration but linked to potential water and heat stresses within the growing season. The maximum number of consecutive dry days with daily precipitation less than 2 mm within the growing season (CDD_{GS}) reflects the length of each season's longest dry spell, during which soil water availability is gradually reduced: the longer the period, the more likely the occurrence of water stress. The second intra-seasonal index was the mean daily air temperature during CDD_{GS} (T_{CDD}). While CDD_{GS} can also fall in periods other than the warmest part of the growing season, CDD_{GS} and T_{CDD} describe conditions occurring at the same time, including the combination of potentially damaging heat and water stress. We repeated analyses described below also setting as threshold for a dry day daily precipitation of 0 and 1 mm, reaching similar conclusions.

To calculate the climatic indices, we used daily gridded data of precipitation and air temperature at 1/8° spatial resolution (Maurer *et al* 2002) and information on the timing and duration of the growing season at spatial resolution of 1/2° (Sacks *et al* 2010). These data were spatially aggregated at the county scale, before calculating the seasonal and intra-seasonal climatic indices (SI S1.2).

2.3. Statistical analyses and model predictions

We explored how crop yields varies with selected climatic indices and management (i.e. irrigated or rainfed cropping), via mixed effects statistical models explicitly including interactions of these drivers (e.g. Gałecki and Burzykowski 2013).

For each crop, the seasonal and intra-seasonal indices were analyzed in two separate statistical models, with yield (either maize or soybean yield) as dependent variable. Yields and climatic indices were not de-trended prior to analysis. Instead, the effect of likely trends from climate change and technological advances were considered by including time as the continuous variable t, as years elapsed from 1969. The fixed factors also included the precipitation-related index P_{GS} for the seasonal and CDD_{GS} for the intra-seasonal analysis, and the temperature-related index T_{GS} for the seasonal and T_{CDD} for the intra-seasonal analysis. Management M was included as categorical variable, for either irrigation or rainfed cropping. The two- and three-way interactions among the factors temperature, precipitation and management were added as fixed parts to the model. The resulting fixed part of the model reads:

$$\begin{aligned}\text{Yield} = {} & \beta_0 + \beta_P\, x_P + \beta_T\, x_T + \beta_t\, t \\ & + \beta_{PT}\, x_P\, x_T + \Delta_0\, M + \Delta_P\, M\, x_P \\ & + \Delta_T\, M\, x_T + \Delta_{PT}\, M\, x_P\, x_T \end{aligned} \qquad (1)$$

where t is years elapsed from 1969, M is the management ($M = 0$ for rainfed and $M = 1$ for irrigated), and $x_P = P_{GS}$ and $x_T = T_{GS}$ for the seasonal statistical model and $x_P = CDD_{GS}$ and $x_T = T_{CDD}$ for the intra-seasonal one, i.e. two models were fitted for each crop. Regarding the coefficients, β_0 is the model intercept and Δ_0 the change in intercept from a shift from rainfed to irrigated cropping. Further, β_i and Δ_i are the slopes describing the changes in yield explained by precipitation- and temperature-related indices ($i = P$ or T respectively) and their interactions ($i = PT$), for rainfed cropping (β_i) and how these slopes are changed by a shift from rainfed to irrigated cropping (Δ_i). To these models, we added as random factors the interaction between county and management M, to allow for different responses to irrigation and rainfed cropping in each county. We also added year as categorical variable to the random part of the model, to account for the covariance across large geographic areas in climatic conditions within a year. The model was fitted to the data across all counties, as detailed in SI, S2.1. No model simplification was done, because treatment interactions were an inherent part of this study.

The model estimates in table 1 enable calculations of yield outcomes under any temperature and precipitation within the explored range of climatic indices (SI S2.2). Below, we first explored the sensitivity of yield to changes in temperature- and precipitation-related indices. Second, we showed how the model can be used to predict impacts on yield from changes of climatic conditions in line with climate change projections. We show results for a 2 °C increase in both temperature indices, accompanied by reduced, unchanged or increased precipitation indices. We used currently observed climatic conditions each year and county as baseline. The percentage change was averaged over the years within each county.

3. Results

As expected, increasing temperature reduced rainfed yields (negative coefficient for T_{GS} in table 1(a)). Precipitation increased yields in both crops, but more so in maize than soybean (table 1, figure 1). Irrigated crops yielded consistently more than rainfed crops (figure 2). There were also several significant two- and three-way interactions among management, precipitation and temperature, for both whole season and intra-seasonal climatic indices (table 1). Hence,

Table 1. Model estimates, their standard errors (SE) and significance (p) from the linear mixed effects model for maize and soybean, for (a) whole growing season and (b) intra-seasonal indices, where M is water management and t is years elapsed from 1969. The model estimates (equation (1)) are presented with rainfed cropping as the baseline level for the categorical variable of management M. The marginal and conditional R^2 give information on the goodness of fit of the model to data, i.e. the variation explained by the fixed factors alone and by the entire model including fixed and random factors, respectively.

		Maize			Soybean		
Predictor	Symbol in equation (1) (units)	Estimate	SE	p	Estimate	SE	p
(a) Whole growing season results where $x_P = P_{\mathrm{GS}}$ and $x_T = T_{\mathrm{GS}}$							
Intercept	β_0 (ton ha^{-1})	4.184	5.912×10^{-1}	<0.001	6.214	3.134×10^{-1}	<0.001
x_P	β_P (ton ha^{-1} cm^{-1})	7.772×10^{-2}	1.055×10^{-2}	<0.001	-3.908×10^{-3}	6.188×10^{-3}	0.528
x_T	β_T (ton ha^{-1} °C^{-1})	-1.921×10^{-1}	2.720×10^{-2}	<0.001	-2.463×10^{-1}	1.348×10^{-2}	<0.001
t	β_t (ton ha^{-1} yr^{-1})	1.057×10^{-1}	8.030×10^{-3}	<0.001	2.788×10^{-2}	2.486×10^{-3}	<0.001
M	Δ_0 (ton ha^{-1})	2.612	7.201×10^{-1}	<0.001	-9.421×10^{-1}	3.696×10^{-1}	0.0108
$x_P \times M$	Δ_P (ton ha^{-1} cm^{-1})	-1.082×10^{-1}	1.431×10^{-2}	<0.001	-1.355×10^{-2}	8.076×10^{-3}	0.0935
$x_T \times M$	Δ_T (ton ha^{-1} °C^{-1})	1.551×10^{-1}	3.473×10^{-2}	<0.001	1.108×10^{-1}	1.618×10^{-2}	<0.001
$x_P \times x_T$	β_{PT} (ton ha^{-1} cm^{-1} °C^{-1})	-1.925×10^{-3}	5.051×10^{-4}	<0.001	7.125×10^{-4}	2.724×10^{-4}	0.00892
$x_P \times x_T \times M$	Δ_{PT} (ton ha^{-1} cm^{-1} °C^{-1})	3.575×10^{-3}	6.884×10^{-4}	<0.001	4.751×10^{-6}	3.580×10^{-4}	0.989
Number of observations		15 580			10 148		
Marginal R^2		0.723			0.657		
Conditional R^2		0.883			0.829		

		Maize			Soybean		
Predictor	Symbol in equation (1) (units)	Estimate	SE	p	Estimate	SE	p
(b) Intra-seasonal results where $x_P = CDD_{\mathrm{GS}}$ and $x_T = T_{\mathrm{CDD.}}$							
Intercept	β_0 (ton ha^{-1})	2.575	2.526×10^{-1}	<0.001	1.662	1.052×10^{-1}	<0.001
x_P	β_P (ton ha^{-1} d^{-1})	-9.323×10^{-3}	4.923×10^{-3}	0.0583	-7.997×10^{-3}	3.871×10^{-3}	0.0389
x_T	β_T (ton ha^{-1} °C^{-1})	-1.660×10^{-2}	6.535×10^{-3}	0.0111	-8.702×10^{-3}	3.660×10^{-3}	0.0174
t	β_t (ton ha^{-1} yr^{-1})	1.087×10^{-1}	8.606×10^{-3}	<0.001	2.836×10^{-2}	2.410×10^{-3}	<0.001
M	Δ_0 (ton ha^{-1})	4.296	1.992×10^{-1}	<0.001	7.095×10^{-1}	1.184×10^{-1}	<0.001
$x_P \times M$	Δ_P (ton ha^{-1} d^{-1})	-2.323×10^{-2}	6.731×10^{-3}	<0.001	2.198×10^{-3}	5.179×10^{-3}	0.671
$x_T \times M$	Δ_T (ton ha^{-1} °C^{-1})	-1.754×10^{-2}	9.048×10^{-3}	0.0525	6.161×10^{-4}	4.978×10^{-3}	0.902
$x_P \times x_T$	β_{PT} (ton ha^{-1} d^{-1} °C^{-1})	-3.342×10^{-4}	2.559×10^{-4}	0.192	-3.523×10^{-4}	1.672×10^{-4}	0.0352
$x_P \times x_T \times M$	Δ_{PT} (ton ha^{-1} d^{-1} °C^{-1})	1.807×10^{-3}	3.519×10^{-4}	<0.001	5.607×10^{-4}	2.252×10^{-4}	0.0128
Number of observations		15 580			10 148		
Marginal R^2		0.695			0.577		
Conditional R^2		0.874			0.794		

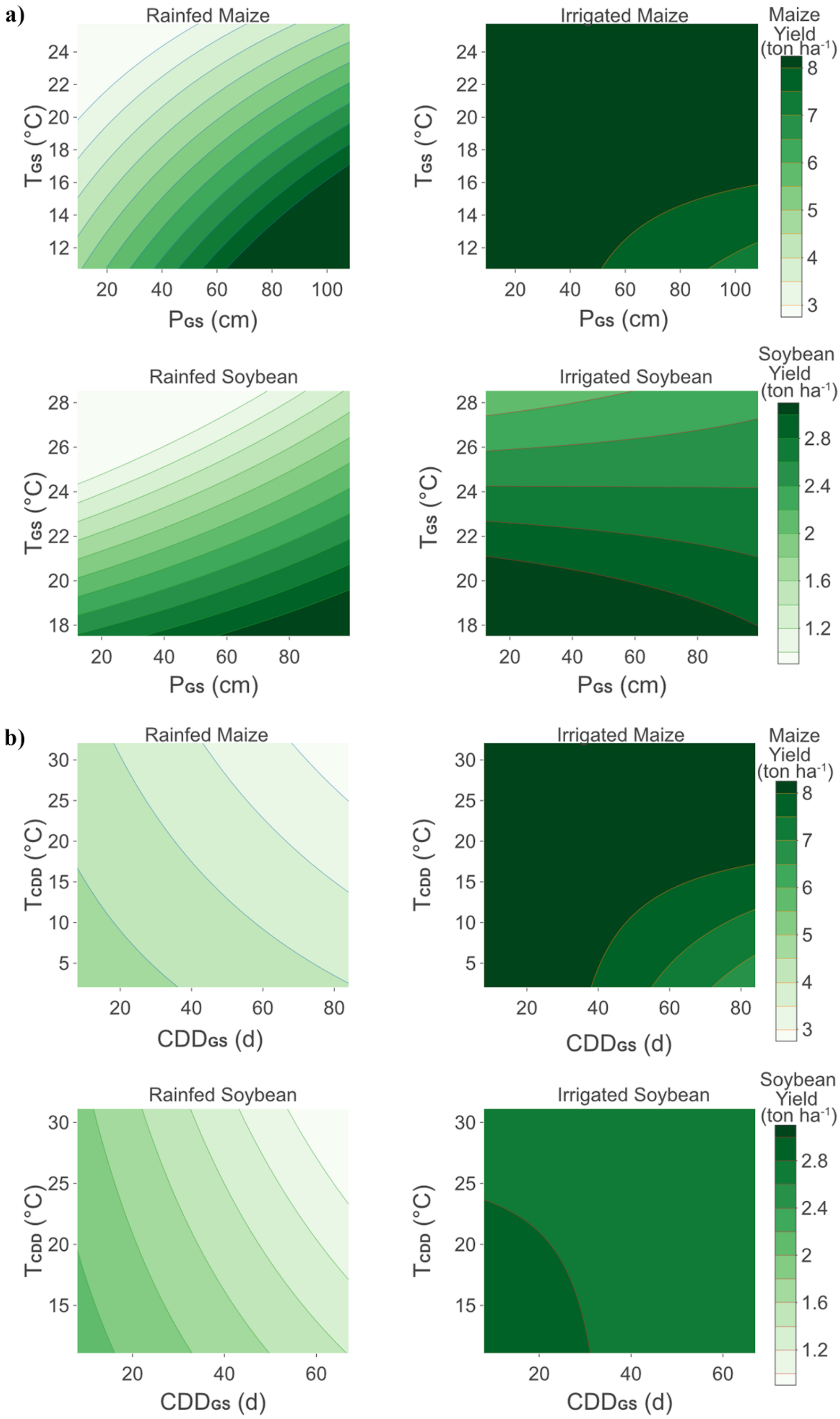

Figure 1. Crop yields as a function of temperature- and precipitation-related climatic indices for (a) whole growing season total precipitation (P_{GS}) and mean daily temperature (T_{GS}), and (b) for intra-seasonal largest number of consecutive dry days (CDD_{GS}) and mean daily temperature during this period (T_{CDD}). The contour plots are based on the fixed part of the statistical model (equation (1)), with coefficient estimates for maize and soybean (table 1), and are relative to rainfed (left) and irrigated (right) cropping. Yields refer to year 1991, i.e. the middle-point of the period considered. The ranges of the climatic indices correspond to those of the observations (SI, figure S3).

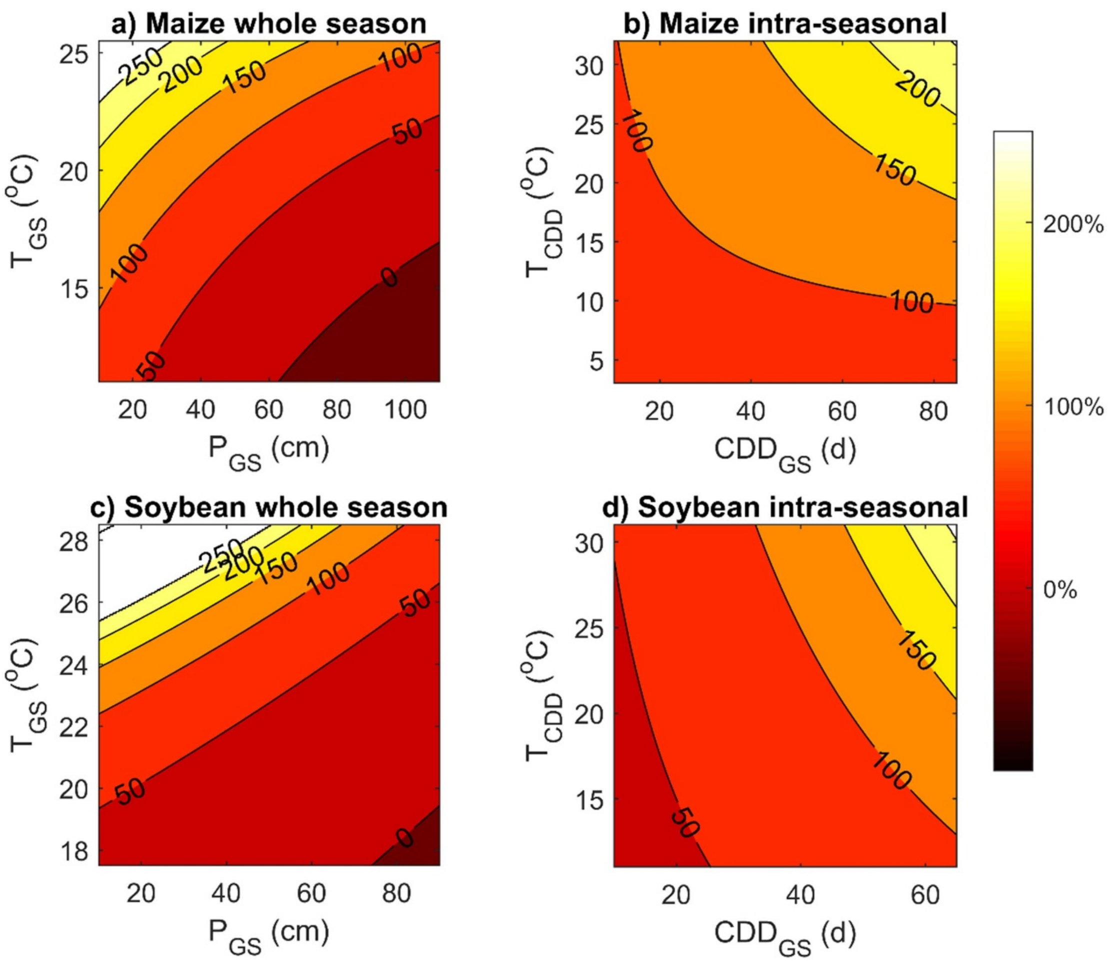

Figure 2. Crop yield gain by irrigation, i.e. percent change in crop yield with irrigation, using rainfed yield obtained under the same climatic conditions as baseline, as a function of seasonal (left) and intra-seasonal (right) climatic indices, for maize (top) and soybean (bottom). The contour plots are based on the fixed part of the statistical model (equation (1), estimates in table 1), calculated for irrigated ($M = 1$) and rainfed ($M = 0$) cropping, for the year 1991. The white area in the top left corner of (c) depicts conditions for which rainfed yield was very low (figure 1), leading to increases in yields with irrigation greater than 250%.

yields depended on the combination of temperature and precipitation, which also altered the benefit from irrigation (figures 3 and S7 in the SI). Yields increased over the years (positive coefficient for t in table 1). The explanatory powers of the whole season and intra-seasonal models were similar, although models based on whole season climatic indices explained somewhat more of the yield variation (marginal R^2 in table 1).

3.1. Rainfed yield responses to whole growing season climatic conditions

The mean seasonal daily temperature (T_{GS}) and seasonal accumulated precipitation (P_{GS}) affected rainfed yields in both maize and soybean (table 1(a)), where high temperature and low precipitation gave the lowest yields (table 1(a), figure 1(a)). The interaction $x_P \times x_T$ was significant, i.e. the effects on yield of temperature and precipitation were not equal across their respective ranges (table 1(a), figure 3). For instance, at a seasonal precipitation of 280 mm there was a loss of 0.25 ton ha^{-1} of maize per °C rise in temperature, while at 490 mm precipitation the loss increased to 0.29 tons ha^{-1} °C^{-1} (solid green arrows in figure 3(a)). Hence, a 1 °C rise in temperature had a larger negative impact on maize yields at higher precipitation totals. The reverse was true for soybean. At 280 mm precipitation 0.23 ton ha^{-1} soybean were lost for °C increase in temperature, but at 490 mm precipitation the loss was 0.21 ton ha^{-1} °C^{-1} (dotted green arrows in figure 3(a)).

Precipitation increased maize yields more at low than at high temperatures: a 10 mm increase in precipitation at 19 °C increased maize yield by 0.041 ton ha^{-1}, while the same precipitation increase at 23 °C increased the yield by 0.033 ton ha^{-1} (solid green arrows in figure 3(b)). Again, the reverse was true for soybean, where 10 mm more precipitation increased yield only by 0.0096 ton ha^{-1} at a low temperature, but 0.012 ton ha^{-1} at a high temperature. The difference between maize and soybean can also be seen in the curvature in the surface plots, convex in maize and concave in soybean (figure 1(a)).

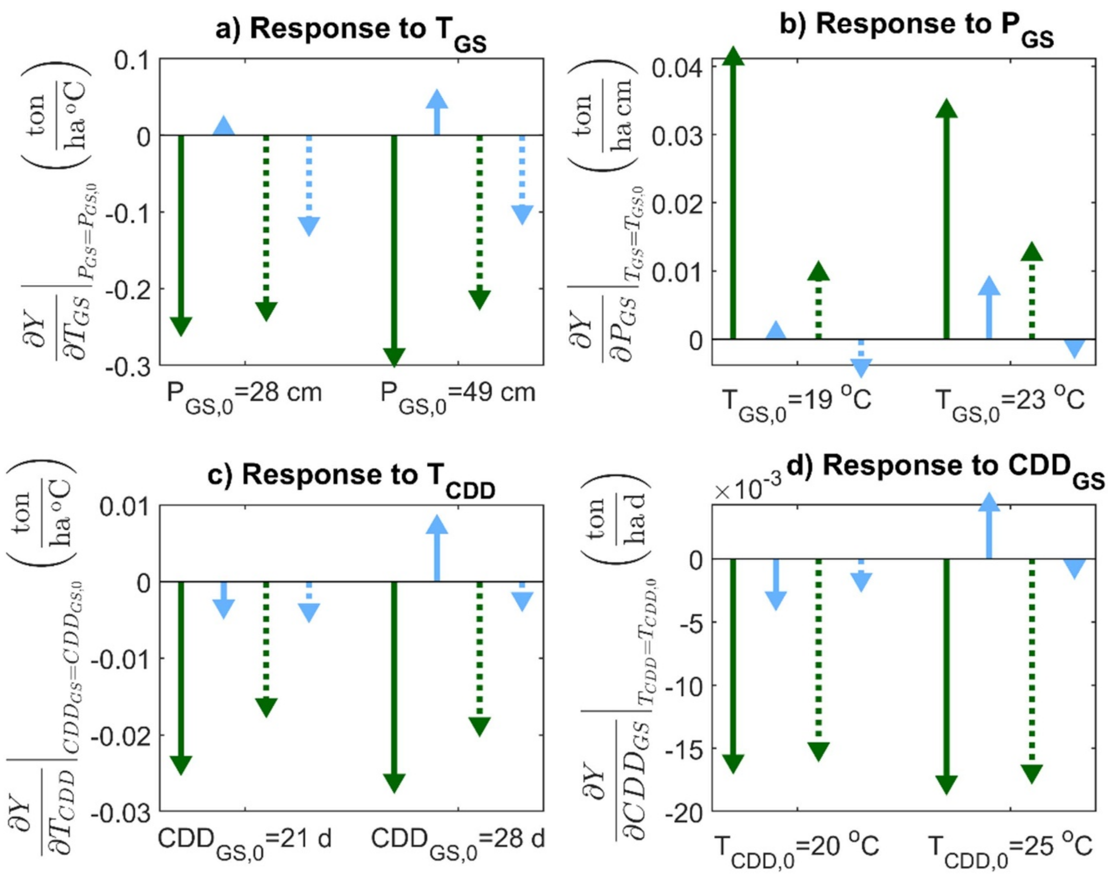

Figure 3. Response of crop yield Y to a unitary change in (a) whole seasonal mean daily temperature (T_{GS}), (b) total growing season precipitation (P_{GS}), (c) mean temperature during the longest dry spell within the season (T_{CDD}), and (d) duration of the longest dry spell within the season (CDD_{GS}), for maize (solid arrows) and soybean (dotted arrows), and for rainfed (dark green) and irrigated (light blue) cropping, as predicted by the fixed effects of the model (equation (1)) table 1; see also SI, equations S1 and S2). For each climatic index, i.e. in each panel, the response is calculated at two values of the other climatic index included in the model (denoted with subscript 0): these values correspond to the 20th (left four arrows) and 80th (right four arrows) percentiles of the values of the climatic index in the data, averaged between maize and soybean. Other choices of percentiles lead to similar patterns, albeit not identical arrow lengths due to the interactions of precipitation and temperature indices.

3.2. Rainfed yield responses to intra-seasonal climatic conditions

Long dry spells (high CDD_{GS}) and high mean temperatures during the dry spell (high T_{CDD}) reduced yields in both soybean and maize (table 1(b), figure 1(b)). For each °C rise during dry spell, yields were reduced more during longer dry spells for soybean, but not significantly so for maize (table 1(b), green arrows in figure 3(c)).

A lengthening of the dry spell by 1 d reduced yields at both low and high temperatures (green solid arrow figure 3(d)), but yields were slightly more reduced per day of dry spell lengthening at high compared with low temperatures during the dry spell for maize, but not significantly so for soybean ($x_P \times x_T$ in table 1(b), green dotted arrow figure 3(d)).

3.3. Irrigated yield responses to whole growing season climatic conditions

Irrigation increased both maize and soybean yields (figures 1 and 2, table 1(a)), except under the lowest and wettest conditions (dark red area figure 2). Irrigation dampened and sometimes reversed the effects of temperature and precipitation changes on yield, but the interactive effects of temperature and precipitation remained for maize, but not for soybeans ($x_P \times x_T \times M$ in table 1(a); figures 2 and 3). For instance, at a seasonal precipitation of 280 mm there was an increase of 0.0092 ton ha^{-1} of irrigated maize per °C rise in temperature, but a 0.044 ton ha^{-1} °C^{-1} increase at 490 mm precipitation (solid blue arrows in figure 3(a)). Hence, irrigation reverted negative impacts of high temperature in rainfed maize. Irrigated soybean continued to lose yield with increasing temperature, but less so compared with rainfed cropping. Irrigation benefits were larger at high precipitation (figure 2(b), dotted blue arrows in figure 3(a)).

Irrigation reduced the effects of precipitation changes. A 10 mm increase in precipitation resulted in a maize yield increase smaller than in rainfed cropping, and the increase was higher at warmer temperatures (solid blue arrows in figure 3(b)). Irrigated soybean yields instead declined by 0.0038 ton ha^{-1} at low and 0.00096 ton ha^{-1} at high temperatures per 10 mm added precipitation (dotted blue arrows in figure 3(b)).

3.4. Irrigated yield responses to intra-seasonal climatic conditions

Irrigation enhanced yields in both maize and soybean across dry spell lengths and temperatures (table 1(b), figure 2), and dampened and sometimes reversed effects of changes in dry spell length and temperature on yield, with significant three-way ($x_P \times x_T \times M$) interactions in both crops (table 1(b), figure 3). In maize, irrigation increased yields with a rise in temperature during longer, but not shorter, dry spells (blue solid arrows in figure 3(c)). Irrigation reduced soybean yield loss per °C increase during the dry spell slightly more at long compared with short dry spells (blue dotted arrows in figure 3(c)). The patterns were the same for a lengthening of the dry spell, at low or high dry spell temperatures (figure 3(d)).

4. Discussion

Based on detailed crop yield information from counties across the USA, in which rainfed and irrigated cropping co-exist, we provide climatic models that explain up to 72% and 66% of maize and soybean yield variability. This is an improvement compared with other analyses (e.g. Ray *et al* 2015, Zampieri *et al* 2017, Zhu *et al* 2019), we believe at least partially thanks to the use of county-level data, separately observed rainfed and irrigated yields, and explicitly including the interactions between precipitation- and air temperature-related climatic indices. As expected, high temperatures reduced rainfed maize and soybean yields (Schlenker and Roberts 2009, Schauberger *et al* 2017). These declines were accelerated by low precipitation (Lobell and Field 2007, Zscheischler *et al* 2017, Feng and Hao 2020). Maize and soybean yields decreased particularly under warm and dry weather. In addition, interaction terms between whole season temperature and precipitation indices were significant for rainfed yields, except for soybean yields explained by intra-seasonal climatic indices (table 1). This was in agreement with previous results in four states in the USA (Carter *et al* 2018), but not with an analysis based on national yield data, where interactions were found for some crops and nations, but not for soybean and maize in the USA (Matiu *et al* 2017). The interaction terms signify that the yield change due to rising temperature or precipitation differs depending on how warm and dry the conditions are (figure 3). For instance, rainfed soybean yields declined faster with rising temperature in dry conditions and benefitted more by precipitation increase under warmer conditions.

Compared with soybean, maize has higher total evapotranspiration (Suyker and Verma 2009) and optimal precipitation requirement (Dietzel *et al* 2016), but lower optimal temperature for grain filling and critical temperature for yield reduction (Schlenker and Roberts 2009, Hoffman *et al* 2020). Soybean yield was indeed less responsive than maize to an increase in growing season temperature and precipitation (figures 3(a) and (b)), but responses were similar for changes in intra-seasonal indices (figures 3(c) and (d)). In relative terms, the mean yield reduction for the USA per degree warming has been estimated to 10.3% for maize and 6.8% for soybean (Zhao *et al* 2017). Other analyses suggest losses up to 30% (Rose *et al* 2017) and extreme variability across states (Mourtzinis *et al* 2015). For maize, the first set of estimates fits well our predicted mean yield reduction across counties of 15.2% with a 2 °C temperature increase given no change in precipitation (figure 4 gray boxes). However, the corresponding relative loss in rainfed soybean amounted to 27.6%. This loss is larger than the estimates mentioned above, but our estimation does not account for the potential mitigation from enhanced air CO_2 concentration, which will be greater in C3 species, such as soybean, than in C4 species (Makowski *et al* 2020). For both crops, the losses due to an increase in temperature were exacerbated by a concurrent reduction in precipitation or lengthening of dry spells (figure 4 orange boxes). The exact mechanism for the different sensitivities to combined changes in temperature and precipitation are complex and mediated by the timing of heat and water stress, with some particularly sensitive crop phenological stages (Hoffman *et al* 2020).

The two analyses, based on whole growing season or intra-seasonal climatic indices, provide complementary information. The intra-seasonal model had high explanatory power, just slightly lower than the whole season model (70% vs 72% variation explained for maize and 58% vs 66% for soybean, table 1), showing that unfavorable conditions with short duration are important determinants of yield. The slightly lower performance can be partially explained by the larger role of soil moisture at the beginning of the longest dry spell compared with that at the beginning of the growing season. Further, the timing of the longest dry spell was spread during the growing season, i.e. the longest dry spell did not necessarily co-occur with the warmest seasonal temperatures (SI, figure S4). Considering the timing and shift in timing of dry spells (Breinl *et al* 2020) might improve predictions and support management decisions (Zipper *et al* 2016).

The choice of whether to irrigate or not has large impacts on crop yields and their dependence on climatic conditions, underlining the importance of explicitly evaluating the outcomes of rainfed and irrigated agriculture when assessing the role of climatic conditions. In general, irrigation increases yields by reducing the negative effects of dry and hot weather conditions or both (Zhang *et al* 2015, Leng 2017, Tack *et al* 2017, Li and Troy 2018). Here, irrigation was most effective in enhancing yields under conditions of low precipitation or extended dry spells and high temperatures (figure 2), when water shortage is most likely and extreme and rainfed yields

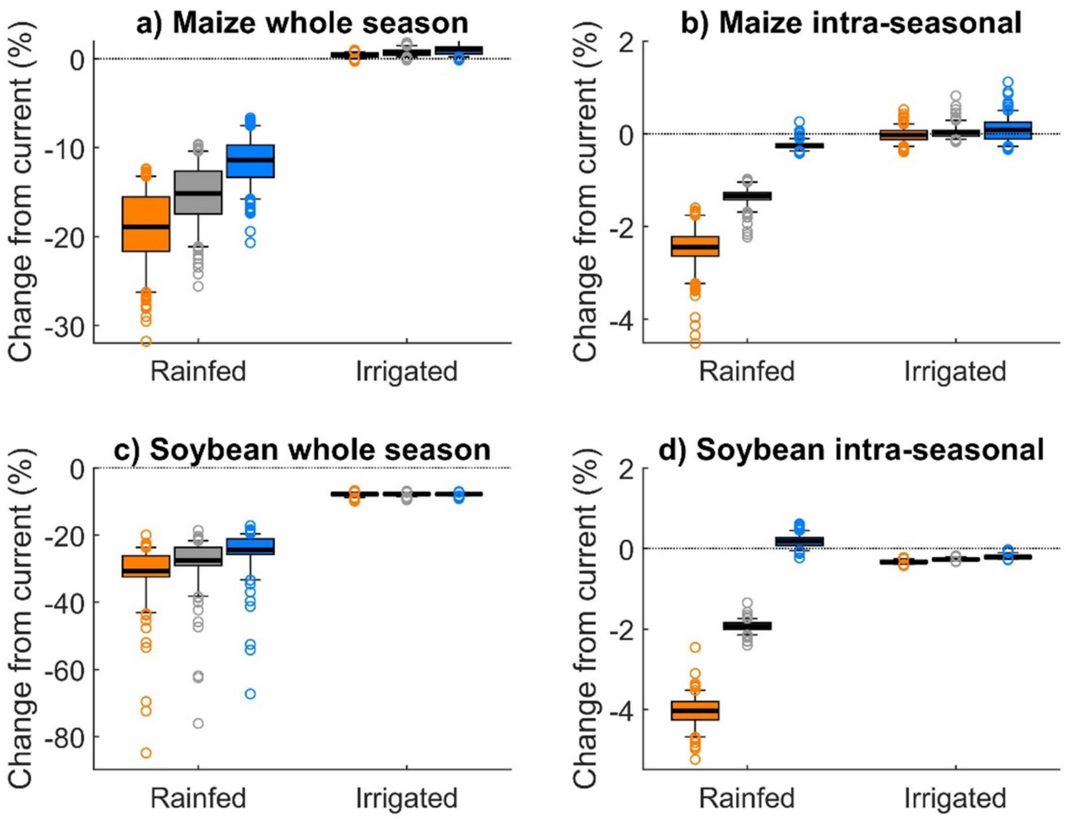

Figure 4. Distribution of county-average percent changes in yield, as calculated based on the fixed part of the statistical model (equation (1), estimates in table 1) for three expected effects of climate change on temperature and precipitation for maize (top) and soybean (bottom), based on climatic indices describing growing season (left, P_{GS} and T_{GS}) and intra-seasonal (right, CDD_{GS} and T_{CDD}) conditions. We present yield changes predicted by the statistical model in equation (1) from a 2 °C increase in temperature-related indices (T_{GS} in the left column and T_{CDD} in the right column). To this warming, we superimpose three shifts in precipitation: (a) a 10% reduction in P_{GS} and increase in CDD_{GS} (orange box, left), (b) unaltered P_{GS} and CDD_{GS} (gray box, center), and (c) a 10% increase in P_{GS} and reduction in CDD_{GS} (blue box, right). In all cases, the relative change in yield is calculated using as baseline the yield predicted by the model under currently observed climatic conditions in the same year and county. A single data point per county is included in the box plots, representing the percentage change averaged over all the years for which data are available. Horizontal bars are means, boxes extend from the 1st to the 3rd quartile, whiskers from the 5th to the 95th percentiles, and symbols are points outside this range.

were low (figure 1). In the central USA, irrigation was able to reduce the combined effects of precipitation and accumulated extreme temperatures in maize and soybean (Zhang *et al* 2015), as well as the effects of dry spells, precipitation totals and several types of temperature extremes in isolation (Troy *et al* 2015). In another analysis, the marginal gain of irrigation was reduced as seasonal precipitation increased in both maize and soybean, but temperature had a less definite effect (Li and Troy 2018).

Irrigation also reduced the dependence of crop yields on climatic conditions (shorter blue than green arrows in figure 3) and in some cases even reverted the direction of response. Irrigation mitigated and in the case of maize reverted the effects of increased temperature, pointing to the importance of water availability to alleviate also heat stress by supporting evaporative cooling. In the case of soybean, irrigation mitigated, but did not cancel the negative effects of increased temperature (figure 3(a)), in agreement with local and global analyses (Tack *et al* 2017, Agnolucci *et al* 2020). This underlines the importance of reducing water stress to increase the optimal temperature for crop yield and stave off the negative effects of high temperatures (Siebert *et al* 2017, Agnolucci *et al* 2020). Irrigation also reduced the positive effects of an increase in precipitation in maize, while a shift from positive to negative dependence of yields on precipitation when shifting from rainfed to irrigation cropping emerged in soybean (figure 3(b)). We speculate that maize, with its higher water demands and lower optimal temperature for grain filling, always benefited from enhanced water availability. Conversely, irrigation in soybean fulfilled its lower water demands and allowed it to exploit the additional sunshine provided by reduced precipitation (Zhang *et al* 2015).

Although being an effective adaptation strategy to increasingly dry and hot climates (figures 2–4), irrigation is in many regions unsustainable to expand or impossible to implement due to water scarcity (Wada *et al* 2012, Rosa *et al* 2020). In the American Midwest, for instance, irrigation relies on groundwater, which is already overexploited (Scanlon *et al* 2012). Irrigation can also lead to soil salinization and exacerbate pollution of surface- and ground-water via salt mobilization and nutrient leaching (Scanlon *et al* 2007). To avoid these issues, and with expected higher temperatures, more intermittent precipitation and reductions in summer precipitation totals, soil and crop management other than irrigation will be required to minimize the need for migration from exposed crop cultivation areas (Sloat *et al* 2020). Adaptation practices include growing drought- and heat-tolerant varieties and crops (Tack *et al* 2016), altering sowing dates (Lobell *et al* 2014, Mourtzinis *et al* 2019), enhancing soil water retention capacity through, for instance, conservation tillage, cover crops and organic soil amendments (e.g. Lal 2004, Pittelkow *et al* 2015, Kaye and Quemada 2017) and diversifying crop rotations (Bowles *et al* 2020, Marini *et al* 2020).

5. Conclusions

We confirm drastic yield reductions of maize and soybean under combined hot and dry conditions, which are likely to induce heat and water stress in the crops. Both maize and soybean yields declined with increased temperature and decreased precipitation. The interaction terms between temperature and precipitation in the statistical models showed that yield changes from increasing temperature or decreasing precipitation differed depending on climatic conditions, where rainfed yields were reduced more rapidly with warmer temperatures in dry conditions for soybean and wet conditions for maize. Irrigation increased and stabilized yields and alleviated both water deficit and high temperatures.

Data availability statement

No new data were created or analyzed in this study.

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