American Maize: Climate Change, Adaptation, and Spatio-Temporal Variation in Temperature Sensitivity

American Maize: Climate Change, Adaptation, and Spatio-Temporal Variation in Temperature Sensitivity

A DISSERTATION PRESENTED
BY
ETHAN E. BUTLER
TO
THE DEPARTMENT OF EARTH AND PLANETARY SCIENCES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN THE SUBJECT OF
EARTH AND PLANETARY SCIENCES

HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS
APRIL 2015

Thesis advisor: Professor Peter Huybers Ethan E. Butler

American Maize: Climate Change, Adaptation, and Spatio-Temporal Variation in Temperature Sensitivity

Abstract

Agricultural production is vulnerable to climate change. However, this vulnerability can be reduced by adapting food crops to a hotter climate. Many studies have ignored adaptation when quantifying the effect of climate change on crop yield, which has likely overestimated yield losses. Therefore, it is necessary to quantify agriculture's adaptive potential to climate change. Such work is challenging because there are no historical analogues to current or future warming. In place of such a precedent this work explores the varying sensitivity of maize yield to elevated temperatures through a suite of multiple linear regression models. These models use high resolution yield and crop development data available since 1981 in the United States to account for overlooked features of maize physiology and agricultural management. The results of these models substantially alter estimates of how crops will respond to a warming environment.

The studies here illustrate how finer scale details can be incorporated into broader regional models. Temperature sensitivity is found to vary with local climatology indicating that maize cultivars are adapted to their particular environment. Incorporating this historical adaptation into estimates of yield loss substantially reduces the effect of a modest warming. A physiological basis for spatial adaptation is apparent when maize development data are incorporated into the model – cooler regions accelerate through sensitive development phases faster than hotter areas. The development data also suggest that crop development has been adapted to the seasonal cycle and that a

non-trivial portion of the temporal trend in maize yield has resulted from management adjustments. Finally, the importance of spatio-temporal variation in temperature sensitivity is highlighted through case studies of recent years with record-setting yield losses. Spatial and/or temporal variation in temperature sensitivity is necessary to reduce bias in estimates of yield loss in these years.

This work builds from previous conclusions regarding the negative effects of hot temperatures, and suggests that while hotter temperatures will harm maize yields there are steps that farmers might take to manage and reduce these losses. Taken together these results quantify how extant adaptation may help to ameliorate yield losses in a hotter future.

Contents

Listing of figures

I dedicate this dissertation to my wife, Kaye Wierzbicki.

Acknowledgments

First I must thank my advisor, Peter Huybers for his tireless support and guidance. I would also like to thank my committee, Dan Schrag, Missy Holbrook, and Steve Wofsy for their dedication and feedback over the course of this project. Eli Tziperman has also been a constant source of encouragement and stimulating conversation.

I would also like to thank the administrators who have helped me through many of the bureaucratic hurdles of graduate school; Sarah Colgan and Sabinna Cappo are invaluable. I would also like to thank Chenoweth Moffat, Marjorie Grande, and Marjorie Grande for their work to keep everything going smoothly.

When I started in this program I was joined by two remarkable scholars: Andy Rhines and Nathan Arnold. Together we made the three climateers and I look forward to many many more years of exploring the natural world together.

Office mates and the Huyber's group have been a constant source of learning and enjoyment. Thank you Kathryn McKain, Karen McKinnon, Nathan Mueller, Marena Lin, Cristian Proistocescu, Martin Tingley and Zan Stine.

I have enjoyed greatly enjoyed the community within the department of Earth and Planetary Science, other Harvard departments from Astronomy to English, as well as the greater Cambridge academic community. I would like to particularly acknowledge the conversations and company of: Tom Laakso, Kristian Bergen, Clarissa Scholes, Sierra Petersen, Helen Amos, Patrick Kim, Jason Munster, Eileen Evans, Greg Santoni, Rick Kraus, Ian Eisenmann, Dorian Abbott, Laure Zanna, Tim Cronin, Martin Singh, Daniel Chavas, Bianca Levy, Nick Stone, Sarah Ruggheimer, Liz Brown, Alicia Breakey, Trisha Banerjee, Alexis Kellner Becker, David Weimer, John North Radway, Olivia Bailey.

I benefitted tremendously from the Plants and Climate journal club that I founded with Becca Neumann and the many presentations, conversations, and stimulating ideas generated there. I look forward to continuing to explore the ideas we touched on in this group far into the future. Thank you: Tom Powell, Abby Swann, Becca Neumann, Ke Zhang, Alex Antonarakis, Jade D Alpoim Guedes, Matthew Gilbert, Rick Wehr, Roisin Commane, Matt Hayek, Stephen Klosterman, Trevor Keenan, and Katie Dagon. This group led to many connections and in particular I would also like to thank Joshua Elliot from the University of Chicago for the high resolution Iowa data in chapter 4.

I have been blessed with many good friends across many walks of life and all of you have lent me support and comfort when I was away from academia. I look forward to many future adventures as we continue down the road of life: Abe Lateiner, Adan Martinez, Ben Morse, Matt Eaton, Jimmy Purvis, Bess Thaler, Sam Fentress, Inam Ahmed, Ian Hanks, Adam Hetland, David Jay, Jesse Delia, Steph Carlisle, Nick Pevzner, Hillary Eaton, Erika Ramos, Caitlin Lowans, Sam Jordan, Max Krafft, Kelsey Heebink, Michelle Mizner, Ian Russell, Ulysses Lateiner, Mattia Maurée, Sarah Grafman, Ben Abrams, Logan Wright, Andy Sponsler, Stefan Litwinczuk, Jonah Gordon, Alex Voves, John Matis, Scott Lund, Dan Peltzman, Sarah Sponsler, Jessica Burke, Seth Goodlaxson, Phil Rosenfield, Jason Gendler, David Favero, Greg Holdsworth, Tom Peteet, Shilpa Reddy, Joanna Solins.

I have benefitted from the guidance and support of several individuals a bit further along the road than I am and I'd like to thank Anis Ahmed, Jamie Gerber, and Diane Hill for their help along the way. I would also like to thank my physic's mentor, Brian Stewart, for his continued guidance as I pursued this research that differs so dramatically from the work we explored together in his laboratory.

My family have always been there for me. For all the years of support leading up to this and your constant belief that I would find my way through the complications of this path I thank my mother Phylis, my father Lin and my sister Breanna.

To my wife, Kaye, thanks can not express my gratitude for all that you bring to my life. You are a beacon to guide me home from my wandering way.

Corn (maize) is arguably man's first, and perhaps his greatest, feat of genetic engineering

Nina V. Fedoroff, Science, 2003

0

Introduction

Over the ten-thousand years of agricultural history, cultivated land – combining both agriculture and pasture – has become the dominant cover of Earth's land surface, claiming over 30% of total land area[124]. The growth of this managed land is one of the greatest signals of humanity's control over the natural world, and it has been accomplished with a surprisingly small selection of plants. The spread of agricultural land under a handful of crops is due, in part, to the adaptability of agriculturally useful plants to varied environments. In fact, many cultivars have become significantly more productive upon moving into novel environments from those within which they evolved[49]. The historical plasticity of agricultural plants stands in sharp contrast to much of the discussion surrounding the effect that anthropogenic global warming will have on crops[82,140]. Given the critical role that adaptation has played in the history of agriculture it must play an important role in predicting its future.

The lack of attention to adaptation in widely cited empirical work[82,86,140] is surprising. Every assessment of the Intergovernmental Panel on Climate Change regarding the impacts of climate change on agriculture has included an analysis of adaptation. The work presented here uses a similar strategy as these recent empirical studies, employing a linear regression framework to analyze the relationship between temperature and crop yield. The break with previous work is the incorporation of increasingly detailed variations in crop yield sensitivity across different spatial regions and temporally over the course of the growing season. By incorporating finer scale details of the relationships amongst crop production, weather, and climate, clear spatial patterns of local adaptation emerge. The program of this research has been to incorporate details from finer scale agronomic research while maintaining a regional area of study that covers a broader range of climate than agronomists generally explore. The result has been a middle path, which uses the modeling techniques of global and regional scale crop analyses, but which also incorporates critical details from agronomic studies. The importance of considering temperature sensitivity over time[149] and space[165] has been known for some time, but here we are able to bring these detailed analyses up to scales that have hitherto been unexplored. By doing so this research bridges some of the divide between critical adaptation research occuring at the field scale and the broad analyses which have highlighted the dangers of global warming to agriculture.

Before moving into the details of adaptation, it is necessary to explain some of the other relevant features of agriculture's global impact, how modern agriculture developed, and the non-climatic challenges facing twenty-first-century agricultural production. Beyond the massive areas of land dedicated to agricultural production mentioned above there are two other global perturbations worthy of note: the redistribution of fresh water towards agricultural land and massive additions to the global nitrogen cycle. In the modern world, water use is overwhelmingly dominated by agriculture, accounting for 70% of global water withdrawal[145]. This reshaping of global hydrology may not match the scale with which humans have reshaped the biomes of the planet, but the productivity of many agricultural regions is maintained through the drastic redistribution of water. Irrigation has a profound effect on productivity, and as we shall see in chapter 1, also offers some reduction in crop vulnerability to extremely hot condtions. Perhaps less perceptible but more profound than the redistribution of water is the degree to which agriculture has altered the biogeochemical cycling of nitrogen. The early 20$^{\text{th}}$ century development of the Haber-Bosch process through which atmospheric nitrogen is transformed into urea and then other nitrogenous compounds for application to soil and consumption by plants has had a profound impact on both crop productivity and the unmanaged environment[148]. Now, human production and application of nitrogen is equivalent to the entire unmanaged portion of the terrestrial biosphere[21]. This application of nitrogen, accompanied by the physiological and agronomic modifications of agriculture have enabled the explosive growth in crop yields over the course of the 20$^{\text{th}}$ century, in the so called "green revolution"[49].

Despite continuing improvements in productivity brought about through the diversion of land, water and chemical compounds into agriculture, as well as substantial managerial innovations, the rate of yield increase has been largely linear since improvement began. This is a challenge because a linear increase in yields produces a relatively smaller fractional increase relative to the local mean[25,26]. The slowing relative increase in yields, even in the absence of the biophysical challenge that twenty-first-century agriculture faces from global warming, will strain global production in the face of substantial social forces which will demand greater productivity. Historically, population growth and agricultural production are tightly linked, though the causation between production and population has been debated[15]. The most recent United Nations projections[162] suggest that even in a moderate population growth scenario there will be nearly 11 billion people on the planet by the end of the century, though the uncertainty around the value is a topic of open debate[58]. However, the generally accepted doubling required of global food production by mid-century is not primarily driven by population, but the economic demands of an increasingly affluent population[158]. Meeting these demands is a challenge that global warming will only exacerbate.

Despite these challenges, recent work has indicated the potential for agriculture to increase its productivity under current technological constraints while also potentially reducing the environmental impact of agriculture through optimization of nutrient use[108]. The challenge of feeding an increasingly large and affluent population even in the absence of climate change uncerscores the urgency of developing adequate methods of inferring how agriculture may adapt to an increasingly hot environment.

A strategy to adapt crops to a hotter world must not be seen as a substitute for continuing to work towards mitigating greenhouse gas emissions to contain the total amount of warming the planet ultimately experiences. However, recent estimates of global mean temperature all converge on warmer conditions regardless of the emissions trajectory, at least into mid-century[73]. Furthermore, even if we are able to curtail emissions and restrict warming to 2°C, we will be living in warmer conditions for quite some time[3]. That we are locked into a warmer world and that it will continue to be so beyond the foreseeable future underscores the critical importance of adapting agriculture to this warmer world. We must be able to thrive in hotter conditions because at this point we have no choice, and to do so we must develop methods by which we can understand crop adaptation.

Much agriculture and climate research has focused on the three crops that account for the majority of human caloric consumption: wheat, rice, and maize. It is impressive that of the 300,000 estimated species of plants on the planet these three have received such particular attention and so much land, though perhaps this is ultimately unsurprising as each crop has proven incredibly productive. However, the developments that have led to dramatic yield increases over the twentieth century vary significantly between these key species. Maize yield has increased by substantially increasing its planting density, with more plants able to share the same space – in other words, maize has become a better neighbor. In the United States the density of maize plant populations has increased by nearly 1000 plants per hectare every year since the 1930s[41]: that's nearly a tripling in population density in the most highly cultivated areas. Wheat has seen a substantial rise in its harvest index, the fraction of the plant's total biomass dedicated to grain[66]. While the duration for a rice crop to reach maturity has been shortened, which has allowed many regions to double and some even triple-crop within a single year[50,135]. Of note is that these three yield increasing strategies occupy such different spaces: maize has been optimized over space, rice over time, and wheat around the individual plant. Many of the optimization strategies have been combined to some degree. For example, rice has begun to receive more attention to the spatial arrangement of crop fields, a purely managerial adjustment, which has substantially increased yields[36].

The primacy of these three crops in global caloric consumption suggests that they deserve particular attention, but each crop has its own unique strategies which have allowed it to thrive. The level of detail required in assessing adaptability to a novel environment requires limiting the scope of the investigation. This was noted in the first IPCC report: "Because of the very wide array of potential adjustments, which will vary according to type of climate change, type of farming, and many other factors, it is not profitable (even if sufficient information on likely changes of climate were available) to generalise at length about them. More specific discussion is needed at the regional case study level..."[119]

Here, we will focus on maize, because of the wide range of environments for which high quality data are available. The adaptability of maize has its roots in the plant's earliest domestication, though its origin is still a topic of some contention[91]. The contours of the argument further highlight the longstanding relationship of adaptation between humankind and cultivated plants. One of the most likely candidates for the primogenitor of today's *Zea Mays* is teosinte. The small proto-cobs of teosinte bear almost no resemblance to the massive grain bearing corn cobs of modern American field corn, and there is no clear evolutionary pathway that leads from one to the other. So it has been proposed that this transformation is one that was driven almost entirely by human hands[9]. There is something fitting in a human origin of modern maize because the plant has since proved so amenable to continued development.

In terms of productivity the development of hybrid varieties of maize, in the early twentieth century, sparked a tremendous increase in yield that is ongoing to this day. This classic feat of breeding involves crossing distinct genetically pure lines to produce single cross hybrids or breeding together those single cross hybrids to produce double cross hybrids. The crossing of genetically pure lines unlocked the potential of combining optimal traits, so called hybrid vigor, and when coupled with improvements in fertilization, and a wide range of management adjustments, the average yield of maize has increased by nearly seven-fold since the United States began recordkeeping after the Civil War, fig. 1*. However, the optimism that this increase in production would seem to support must be countered by the drag that climate change may exert on these yield trends and the increasingly small fractional increase in yields from the generally linear yield trend, mentioned above[25,26]. Despite this concern, the historical adaptability of maize provides some hope that there will continue to be room for yield improvement even in the face of a changing climate.

The plasticity of maize is further evident in the range of condtions over which it is grown. Orgininally domesticated in southern Mexico, it is now grown from greater than 45°N down to 35°S, the most widespread cultivation of any crop in the world. This translation into novel habitats comes with a host of challenges and benefits. For example, an originally tropical crop like maize had to be adapted to the longer days of mid-latitude summers, but after the plant was adjusted to the novel environment it produced greater yields in mid-latitudes than in its native environment[49]. Given the degree to which maize has thrived outside of its region of original domestication, there is a strong precedent for the crop to flourish in novel conditions. The widespread cultivation of maize also suggests that there are extant cultivation techniques and/or varieties already being used in warmer environments that will provide insight into how currently highly productive but cooler environments may adjust their production to continue to thrive in a warmer world.

*A note on units. Agricultural productivity is generally expressed as a yield, mass per unit area, which in the United States Department of Agriculture/National Agriculture Statistics Service is presented as bushels per acre. The first chapter will present results in these units, and subsequent chapters, for easier international comparison will be converted to metric tons per hectare, under the assumption that a bushel of US maize is equivalent to 25.4 kilograms. This makes a straightforward conversion from bushels per acre to metric tonnes per hectare by multiplication of 0.0628 (t/ha)/(bushels/acre)

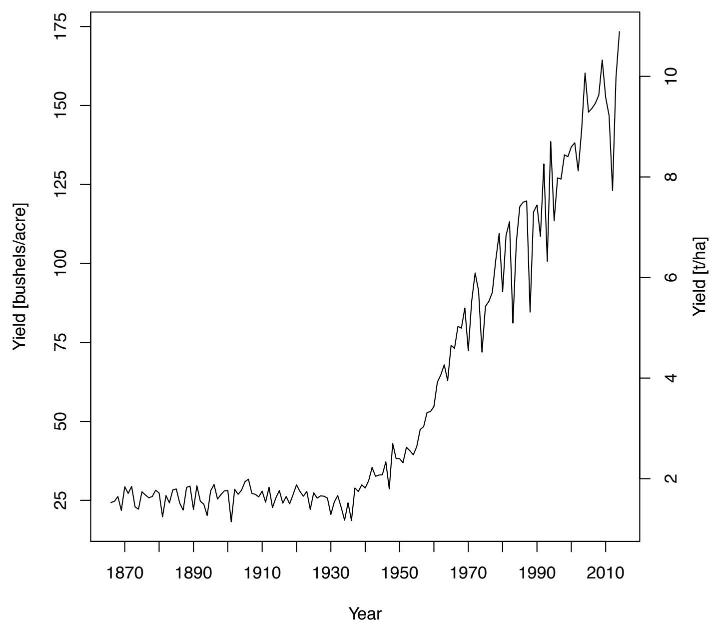


Figure 1: Average United States Maize Yield. Yields have steadily increased since the widespread adoption of hybrid varieties in the 1930s. Despite isolated events of severe yield drops, the trend has been towards consistent increase, resulting in a near septupling of yields over the course of this record. The left axis reports yields in standard US units of bushels per acre while the right axis is in international units of metric tons per hectare. Data are from the USDA/NASS[123].

The United States is the largest producer of maize in the world. Accounting, in 2013, for about a third of the world's total supply[163]. It is also the most widely grown crop in the United States, occupying nearly 30% of US farmland. As a result of its widespread cultivation maize is grown in a wide range of climates within the United States, all of which may be assumed to operate at near their optimal production capacity. As such, the US is an ideal region to investigate how the temperature sensitivity of maize varies across different environments. This is further supported by the wide range of publically available data from the United States Department of Agriculture / National Agriculture

Statistics Service (USDA/NASS), which provides relatively high spatial resolution data throughout much of the 20$^{\text{th}}$ century, with detailed management data beginning in the 1980s. It is such detailed data on both productivity and management that enable the studies presented here, which primarily detail how maize has been locally adapted to its environment through both cultivar selection and adjustments in the cropping calendar.

The available data have substantially shaped the structure of this project, which is briefly outlined below. The first chapter is a study of how maize yield sensitivity to temperature varies across space. Prior work has generally taken crop sensitivity to environmental variation to be spatially invariant, but this stands at odds with the local adaptation that has been a hallmark of cultivar development. This work is repeated, nearly verbatim, from Butler and Huybers (2013)[18]. The primary difference is that supplementary material has been incorporated directly into the body of the work, with references modified to match this presentation. The second chapter adds temporal variability to crop sensitivity, by incorporating detailed phenological data according to different developmental phases of the maize crop. This work is repeated from Butler and Huybers (2015)[20], though again has been modified to incorporate the supplemental material into the body of the text. The phenological data provide a more physiologically based hypothesis for the spatial variation in sensitivity observed in chapter 1. The third chapter continues the analysis of developmental sensitivity by further exploring how alterations in planting times and cultivar types have altered the climate to which the crop is exposed, and indicates that, for the most part farmers have altered their calendars to significantly improve their yields. The fourth and final chapter is a set of detailed case studies on the hottest and lowest yielding years in the recent record. Disturbingly, the empirical models used produce biased estimates across the hottest counties within these years. However, this bias may be eliminated when more spatially and temporally detailed development data are incorporated into the analysis. Taken together these results highlight how details matter when studying how agriculture has been and will continue to be affected by a changing climate.

Maize, despite what some may say, is not a homogeneous crop, and the effects of temperature on its yield vary substantially depending on when and where both damaging and beneficial events occur. The details presented here indicate that more nuance is called for when analyzing how crops will be affected by climate change, and provide further insight into strategies that may reduce the damages that an increaingly warm environment will inflict on a static production system. Fortunately, the historical evidence analyzed here suggests that farmers have steadily adjusted their cultivars and management strategies to their local environment, and there is every reason to believe this will continue into a warmer future. My hope is that by clearly illustrating the adaptations that have already been taken to optimize maize production in the current climate, the path will be smoother towards a highly productive maize agriculture in a warmer future.

1

Adaptation of US Maize to temperature variations

1.1 Abstract

High temperatures are associated with reduced crop yields[140,85], and predictions for future warming[98] have raised concerns regarding future productivity and food secu-

rity[139,82,43,8,81]. However, the extent to which adaptation can mitigate such heat-related losses remains unclear[130,164,99,45,141]. Here we empirically demonstrate how maize is locally adapted to hot temperatures across U.S. counties. Using this spatial adaptation as a surrogate for future adaptation, we find that losses to average U.S. maize yields from a two degree Celsius warming would be reduced from 14% to only 6% and that loss in net production is wholly averted. This result does not account for possible changes in temperature variability or water resources, nor does it account for all possible forms of adaptation[133,111,37,146,44], but it does show that adaptation is of first order importance for predicting future changes in yield. Further research should be undertaken regarding the ability to adapt to a changing climate, including analysis of other crops and regions, the application of more sophisticated models of crop development, and field trials employing artificially increased temperature.

1.2 Introduction

Global maize yields are forecast to decline in response to increasing temperature, particularly as the upper range of growing season temperatures become hotter[82,8,43,139,131,140,85]. The sensitivity of crop yields to increased temperature is often estimated through analysis of variability in annual yield and growing season temperature[139,131,140,85], but there is a potentially important distinction between year-to-year anomalies and changes in climate in that the latter can be more fully adapted to. For instance, U.S. corn hybrids have a product half-life of about 4 years[45], suggesting sufficiently rapid turnover to adapt to decadal changes in climate. To explore adaptability of maize production to long-term differences in climate, we analyze the sensitivity of extant crops growing in a range of different climate conditions and use this spatial variation to develop a functional form for future adaptation.

We explore yields within the U.S. because relatively high quality data and a highly adapted and managed agricultural demographic can be assumed. Yield data are available from over 1600 counties between 1981-2008 from the United States Department of Agriculture/National Agriculture Statistics Service[123] in the Eastern U.S., and daily temperature is estimated for each county using a network of 534 weather stations[101] for which daily minimum and maximum surface air temperature is available.

The influence of temperature upon yield is parameterized using Growing Degree Days (GDDs) and Killing Degree Days (KDDs). GDDs are a commonly used measure for the cumulative warmth a crop has experienced over the growing season[140,80,166,37], here defined as the sum of all daily average temperatures over the growing season in excess of 8°C. The threshold is in accord with previous studies[140,37], but we use a novel approach to define the growing season using average planting and harvest dates reported for each state on each year[123], with the average weighted according to the amount of planted or harvested crop. Daily temperature is computed by taking the average of the maximum and minimum temperature at the nearest available weather station. KDDs are defined similarly to GDDs, but summing maximum temperatures in excess of 29°C, consistent with previous studies[140,131,85]. Whereas GDDs are indicative of higher yields (e.g., by enabling a longer period of grain development), KDDs decrease yield (e.g., by accelerating the plant through grain development or directly damaging plant tissue or enzymes[169,49]). Note that although 29°C is a low threshold for the initiation of damage[31], stressed maize plants have been shown to experience higher temperatures than the air measured above the crop canopy[57].

1.3 Model Description

Time-series of GDD and KDD anomalies for each county are linearly combined along with a constant and time-trend term to represent yield for each county,

$$Y = \beta_0 + \beta_1 t + \beta_2 GDD' + \beta_3 KDD' + \epsilon. \tag{1.1}$$

A prime indicates that the sample mean is removed. The β coefficients are fit so as to maximize the variance explained in Y, subject to the condition that GDD contributions cannot be negative ($\beta_2 \geq 0$) and KDD contributions cannot be positive ($\beta_3 \leq 0$). The linear time term, t, accounts for technological and other steady changes over this time period and ϵ is the residual error. Uncertainty estimates are obtained for each of the parameters using a bootstrapping method.

Fitting the four adjustable parameters in Eq. 1.1 to each county results in an average squared cross-correlation between predictions and observations of R^2=0.65 (fig. 1.1a). For comparison, other recent empirical fits to maize data obtained an R^2 of 0.47 with four adjustable parameters[82] and 0.77 using about 20 adjustable parameters[140]. An F-test is then used to determine whether the full model of Eq. 1.1 performs significantly better ($P \leq 0.05$) than one containing only the mean and time trend. Counties with insignificant model fits are omitted, reducing our pool of counties from over 1600 to a subset of 1013 counties showing a statistically significant relationship with temperature variations (fig. 1.1b), though a similar result is obtained when using the full sample. See the methods section for further description of the model and the last section for a more detailed case study.

The sensitivity of yield to GDD has values of 0.15 (bushels/acre)/GDD in cool North-

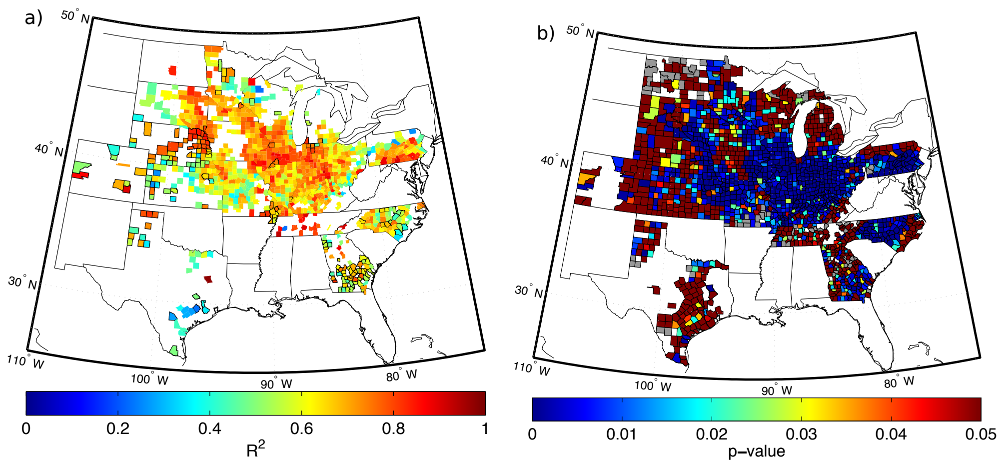


Figure 1.1: Model significance and squared cross correlation. (a) The squared cross-correlation for all significant counties. Irrigated counties are outlined in black. (b) P-values from an F-test comparing the full model to a reduced model including only an intercept and time trend for all 1666 counties, with the colorbar truncated at p=0.05. Omitted counties with p-values greater than 0.05 are in deep red and counties omitted for insufficient data are in gray. The final pool of counties is 1013. States not reporting planting and harvest times are shown in white. Note that a scatter plot of p-values and KDD sensitivity had no apparent structure.

western regions of the study domain and trends to values near zero in the hotter South-eastern regions (Fig. 1.2a). Yield sensitivity to KDDs (Fig. 1.2b) is nearly orthogonal to that of GDDs, trending from more negative than -0.5 (bushels/acre)/KDD in North-eastern regions toward less negative than -0.2 (bushels/acre)/KDD in Southwestern regions. Variations in the sensitivity to GDDs and KDDs is perhaps unsurprising, given that maize originated in the tropics and has been adapted to grow in colder climates[49].

Our focus will be on KDDs regional variation in sensitivity and the consequences of a warming climate. Field trials on cultivars planted in different regions of the U.S. have demonstrated a pattern of heat tolerance[130] consistent with our findings of lower sensitivity in hotter climates (Fig. 1b). Cultivars adapted to hot climates produce more heat-resistant proteins and control for moisture deficits through greater stomatal sensitivity,

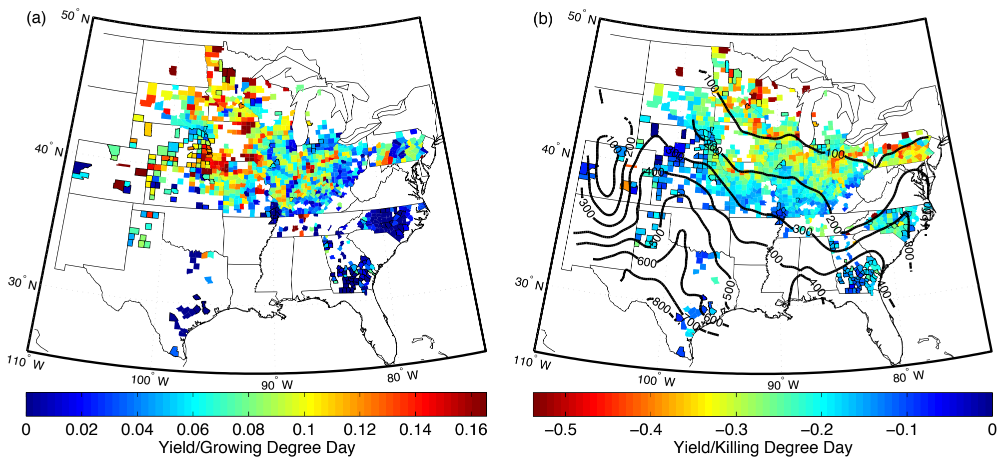


Figure 1.2: Sensitivity of maize yield to temperature variations. (a) Yield sensitivity to Growing Degree Days. (b) Yield sensitivity to Killing Degree Days (shading) and the climatological average of Killing Degree Days (contours). Counties with at least 10% of their crop area irrigated are indicated by black borders.

osmotic adjustment, and membrane structures that confer drought resistance[130,164,45]. While there are other management options that could reduce sensitivity to temperature, such as developing fields to increase water retention, the most likely candidate to explain the observed variation in KDD sensitivity is cultivar selection, and we seek to capture this effect in the form of a simple function. Note that although another study[140] reported lack of evidence for regional variations in yield sensitivity to high temperatures, further analysis using that study's approach gives results consistent with the above reported findings.

1.4 Causes of spatially variable sensitivities across the US

We interpret the varied spatial sensitivity to KDDs diagnosed across U.S counties as indicative of adaptability. Indeed, there exists a strong relationship between the climatology of KDDs and the sensitivity of yield to KDDs for both unirrigated (Fig. 1.3a) and

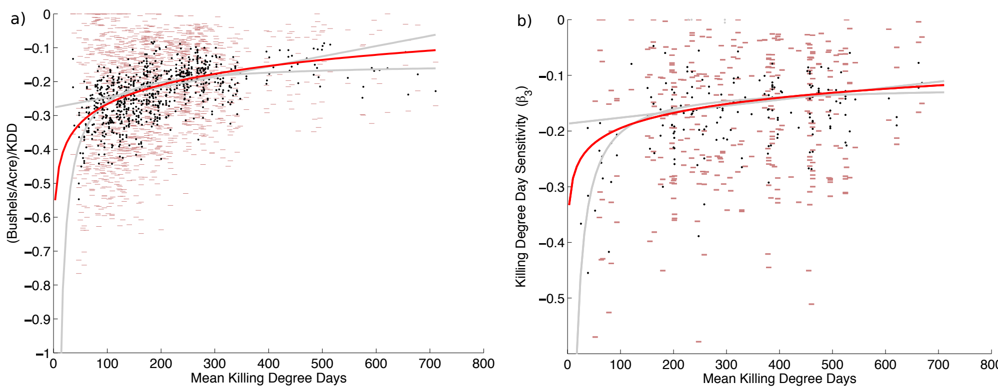


Figure 1.3: The climatological average Killing Degree Days (KDDs) versus the sensitivity of yield to KDDs for individual U.S. counties. (a) A logarithmic fit provides a functional relationship between climatology and sensitivity (red line, Eq. 1.2). For reference, linear and inverse fits are also included (gray lines) and would imply greater and lesser ability to adapt to warming, respectively. Red dashes represent bootstrap 95% confidence intervals. For visual clarity, data points with 95% confidence interval lengths greater than 0.5 (bushels/acre)/KDD are not shown as they have little influence upon the weighted fit. (b) The fit to irrigated counties is substantially weaker than for rainfed counties (linear (gray) $R^2 = 0.12$, logarithm (red) $R^2 = 0.21$, and inverse (gray) $R^2 = 0.25$) possibly because of the differing levels of irrigation between counties. For consistency, we use the logarithm of mean KDD to model the adaptation of irrigated counties.

irrigated crops (Fig. 1.3b) that can be approximated using a logarithmic relationship,

$$\beta_3 = \alpha_o + \alpha \ln(\overline{KDD}) + \eta. \tag{1.2}$$

Eq. 1.2 is fit to the data by minimizing the sum of η^2, where the sum is inversely weighted according to the bootstrapped variance estimates associated with each sensitivity, β_3. This gives a base sensitivity of $\alpha_o = -0.64$ (bushels/acre)/KDD (with a bootstrapped 95% confidence interval of -0.69 to -0.59) and adaptation factor of $\alpha = 0.08$ (bushels/acre)/(KDD ln(KDD)) for unirrigated crops (95% c.i., 0.07 to 0.09). For irrigated crops the base sensitivity is much lower, $\alpha_o = -0.38$ (95% c.i., -0.47 to -0.28), and adaptation is weaker, $\alpha = 0.04$ (95% c.i., 0.02 to 0.06).

Essentially, Eq. 1.2 states that hotter counties are less sensitive to yield losses from heat but that differences in sensitivity asymptote to zero toward hotter climatologies. This formulation has the advantage of indicating the greatest change in the most data rich regions and minimal change in the hottest regions, thereby limiting inferences based upon extrapolation. Furthermore, when we consider a 2°C warming scenario (Fig. 1.4), only 18 of the 837 unirrigated counties included in this study exceed the sampled range of the historical climatology, and even though those counties experience amongst the largest changes in KDD, their inferred adaptive change in sensitivity averages only 0.03 (Bushels/Acre)/KDD whereas the domain average is 0.05 (Bushels/Acre)/KDD. Exclusion of these 18 counties would have no influence on yield statistics at the reported precision level. Eq. 1.2 represents a moderate case relative to the greater and lesser adaptability respectively implied by linear and inverse relationships and provides a similar fit to the data: R^2=0.44, compared to R^2=0.23 for the linear and R^2=0.47 for the inverse forms. What adaptation function is most suitable remains something of an open question, but any of these would serve to qualitatively illustrate our basic point that plausible degrees of adaptation fundamentally change predictions of yield response to moderate warming.

1.5 Spatial Adaptation

To explore the implications of the observed spatial adaptation to KDDs for the sensitivity of yield to warming, we redefine β_3 in Eq. 1.1 to follow the adaptation function given by Eq. 1.2,

$$Y = \beta_0 + \beta_1 t + \beta_2 GDD' + (\alpha_o + \alpha \ln(\overline{KDD}) + \eta) KDD' + \epsilon. \tag{1.3}$$

In Eq. 1.3, as climatological KDDs increase with greater warming, fig. 1.4b, it is assumed that cultivar selection and management practices are adjusted in keeping with the extant adaptation observed across the U.S. Yield is solved for each county and each year using the β, ϵ, α, and η terms from Eqs. 1.1 and 1.2 such that, in the absence of any change in temperature, the original yield data is recovered.

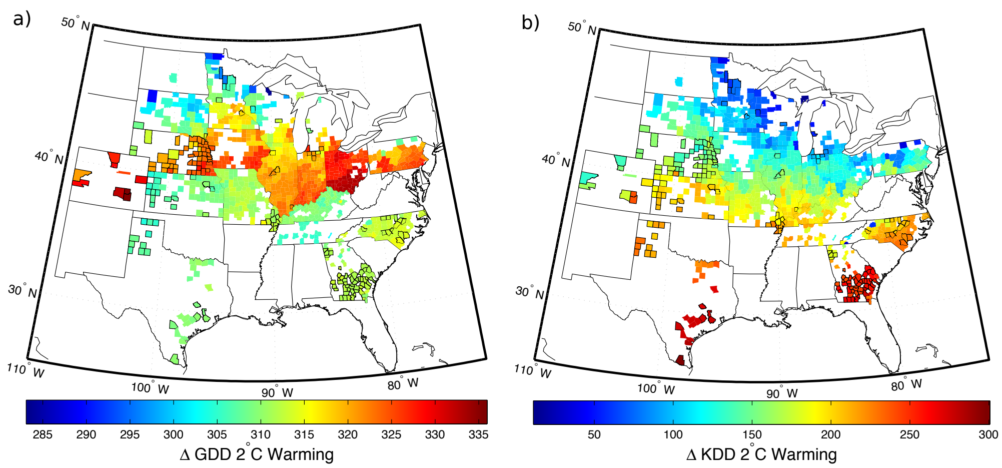


Figure 1.4: Increase in Growing and Killing Degree Days from a 2°C warming. (a) Changes in each counties Growing Degree Days correspond well with the growing season length of each county. The majority of days during the growing season are well above the minimum threshold for GDD accumulation so that changes in GDDs are essentially linear with changes in mean temperature. (b) Changes in each county's Killing Degree Days correspond with the local mean temperature in each region. Cold counties are generally below the 29°C threshold and accumulate few KDD with modest warming, while hot counties are already near or above the threshold and accumulate more KDDs. This helps explains why hot counties incur greater losses from the the warming, despite having a lower sensitivity. Irrigated counties are outlined in black.

To illustrate the differences between non-adapted (Eq. 1.1) and adapted (Eq. 1.3) yield responses, it is useful to consider a specific warming scenario, here taken to be a uniform 2°C warming, which is often considered the "safe" limit of warming[129]. Specifically, we add 2°C to all temperature records, recalculate the GDD and KDD terms from these warmer records but using the original sample means to get new anomaly terms, and calculate a new average yield for each county. Without adaptation, Northwestern regions broadly gain from warming because the benefits from increased GDDs outweigh the losses from KDDs, whereas some Southern regions sustain losses of more than 50% because increased KDDs reduce yield and low sensitivity to GDDs provides little compensatory gain (Fig. 1.5a). Also, warm regions will gain KDDs more rapidly in response to uniform warming because they have more days that already exceed the 29° threshold. The mean yield decrease for a 2°C warming without adaptation is 14%.

This result is generally consistent with foregoing estimates, though comparisons are limited by the fact that different spatial averages are considered. One study[82] found a 17% decline in global average yields in response to a 2°C warming. Another study[140] found a 15% decline in an area-weighted average of eastern U.S. yields. Our calculations indicate only a 5% decrease in area-weighted yields, but the lower value is expected because some of the hottest states in the southeastern U.S. are excluded from our study on account of data regarding planting and harvest times not being available. Note that all of these studies are essentially perturbation approaches to calculating yield anomalies, and that the accuracy of these estimates becomes increasingly questionable for larger changes in temperature.

When adaptation is included, the average yield response to a uniform 2°C warming is reduced from a 14% loss to one of 6% (Fig. 1.5b,c) (95% c.i. -5 to -7%). Minnesota now stands to increase yields by 11%; the yield losses from northern Ohio west to northern Missouri are nearly eliminated; and North Carolina, Georgia, and east Texas reduce losses from 49% without adaptation to 39% with. These latter regions are already well above the optimal temperature for current U.S. maize production, and although the indication is that adaptation can help, sizable losses are nonetheless incurred. Already, many of the southern states are relatively unproductive compared to the Corn Belt, and one consequence of increased temperature could be migration of maize production toward cooler latitudes. Another implication of low southern productivity is that area-weighted yields (equivalent to fractional changes in total production) go from a 5% decrease without adaptation to no change with adaptation because gains in the highly productive Corn Belt compensate for losses in the less productive South.

1.6 Discussion

The adaptation function that we have empirically estimated for a theoretical warming is consistent both with extant regional adapatation and field trials of differing cultivars[130], but this analysis omits other extenuating factors that may stymie or facilitate adaptation. For example, reducing sensitivity to heat may entail negative physiological trade-offs that reduce yields[146]. To further explore the issue of trade-offs, we extend Eq. 1.3 to include a reduction in the positive effects of GDDs with warming that mirrors the reduction in the negative effects of KDDs. A least-squares-linear fit indicates maladaptation for GDDs that average an order of magnitude smaller than the positive adaptation found for KDDs (Fig. 1.6). It follows that inclusion of GDD maladaptation in our model leads to relatively small changes, and we now obtain an 8% decline in average yield in response to a 2° warming, as opposed to a 6% decline when considering the basic KDD-only adaptation scenario. Inclusion of GDD maladaptation also broadens the 95% confidence interval to 6-11% because of the uncertainty in the GDD adaptation fit. This reduction in adaptability and increase in uncertainty does not change the conclusion that adaptation offers the potential to substantially reduce damages from a warming climate, but highlights how more work is needed to constrain the specific magnitudes of losses. Furthermore, there are also potential benefits to warming that we

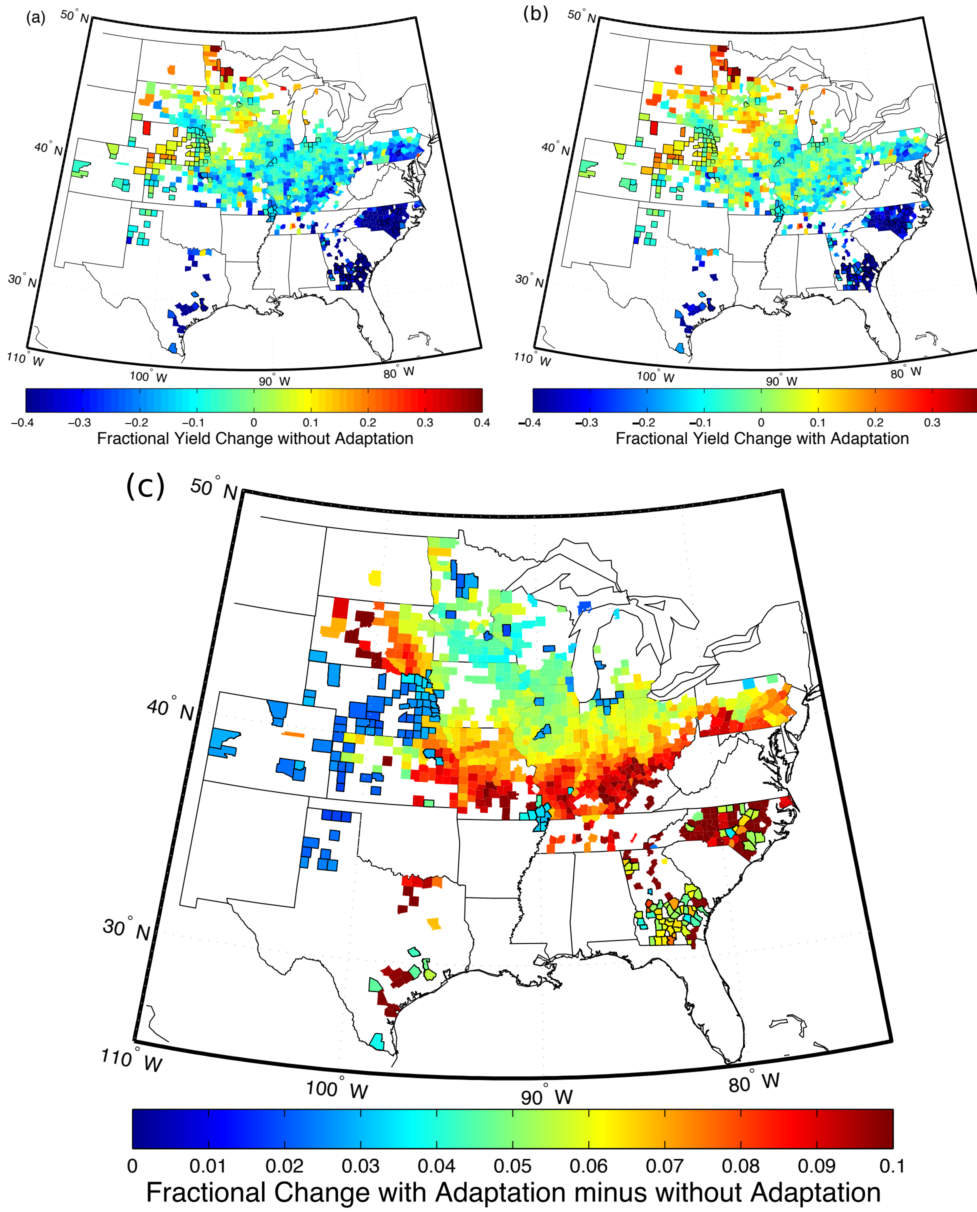


Figure 1.5: Changes in yield from a 2°C warming. (a) Without adaptation warming causes yield to decrease by 14% on average, though counties in the deep South lose more than 50% of their yield, whereas those in the Northwest increase by as much as 30%. The colorbar saturates at ±40% in order to highlight variation across the middle range of counties. **(b)** When adaptation is accounted for, warming is estimated to cause only a 6% average loss in yield. **(c)** The increase in yield brought about by adaptation relative to the no-adaptation scenario. The colorbar saturates at 10% to highlight variation across the majority of counties. Black borders indicate irrigated counties.

have not included in our model, such as greater flexibility in planting times[37], a longer growing season, and opportunities for cultivating new regions[125]. Finally, note that most, if not all, of these forms of adaptation can only be implemeneted in a warmer climate, explaining why farmers that we expect to benefit from adaptation have not yet made such changes.

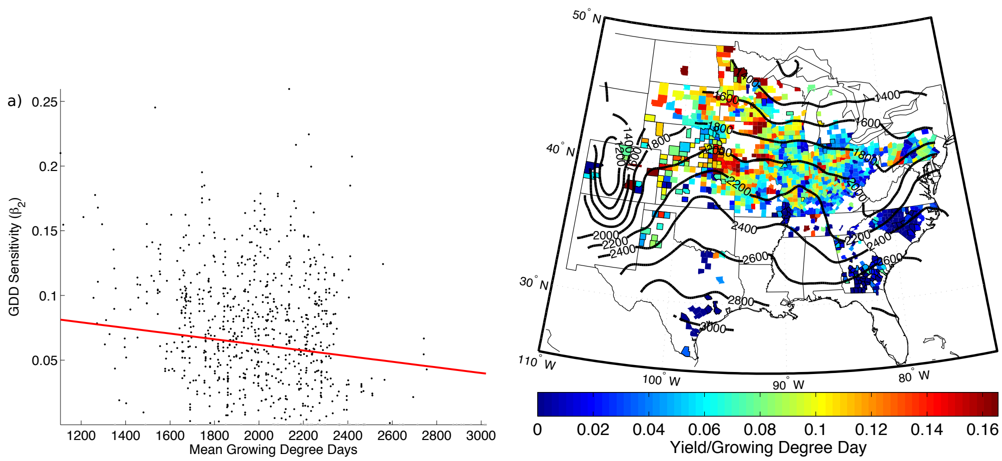


Figure 1.6: Climatological GDDs and GDD sensitivity. (a) There is a weak relationship between GDD climatology and GDD sensitivity. As with KDD, this fit was performed separately for irrigated counties. Counties with extremely low sensitivity to GDD (GDD sensitivity < 0.001) were omitted from this fit (shown in grey) and the regression was weighted by the inverse of the bootstrap variance estimate of the GDD sensitivity parameter. The net effect of reducing GDD sensitivity as GDD climatology warms is a mean yield loss of 8% from a 2°C warming, as opposed to a 6% loss when changes in GDD sensitivity are ignored. (b) Climatological GDDs (contours) are weakly negatively correlated with unirrigated GDD sensitivity (shading, r=-0.3). The regions with the shortest growing season tend to have the highest GDD sensitivity. In the North, where the growing season is potentially too short for the crops to reach maturity, yields respond well to seasons with above average GDD; whereas in the South, where GDDs are abundant, yield is largely insensitive to fluctuations in GDD.

Changes in water availability are another important consideration. Counties that irrigate more than 10% of their harvested area have an average sensitivity to KDDs that is 0.08 (bushels/acre)/KDD smaller than neighboring counties without irrigation, a difference that is highly significant ($P < 0.01$, using a one-sided t-test, see Fig. 1.2b) and is in qualitative agreement with other findings[133,111]. Prize winning yields from the 2010 and 2011 National Corn Yield Contest also point to the importance of irrigation. For unirrigated crops, the median prize-winning yields increase from 216 bushels/acre in the South, to 247 in the Center, and 266 in the North of the U.S. (regional groupings follow that of a previous study[140]). For irrigated crops, however, median southern yields are 260 bushels/acre, central yields are 267, and northern ones are 247. The highest yields come from Texas with 370 bushels/acre, showing that states with hot climatologies are capable of attaining high yields.

We experimented with including a representation of precipitation in the model, but it negligibly influences model skill, even when only non-irrigated crops are examined. The absence of significant improvement may reflect that variations in precipitation are less important for determining maize yield than temperature[87] but likely also results from a strong covariance between temperature and precipitation that makes inclusion of the latter partially redundant. Precipitation is negatively correlated with maximum daily temperatures everywhere in our study domain (Fig. 1.7), as may be expected from the effects of clouds and evaporable soil moisture. This anti-correlation reaches values of -0.8 in some Southern regions. The coincidence of high KDDs and reduced water availability underscores that the low sensitivity to KDDs found in Southern regions reflects substantial adaptation. It also suggests that our empirically fit adaptation function partially accounts for the expectation that warming will cause dry regions to become drier[68], though further explicit examination of the influences of water availability upon yield appears necessary.

Losses to U.S. maize yield from increased temperature is almost certainly overestimated if adaptation is not accounted for[139,140], and here we have shown that adaptation could decrease the average fractional losses in the Eastern U.S. by roughly a factor of

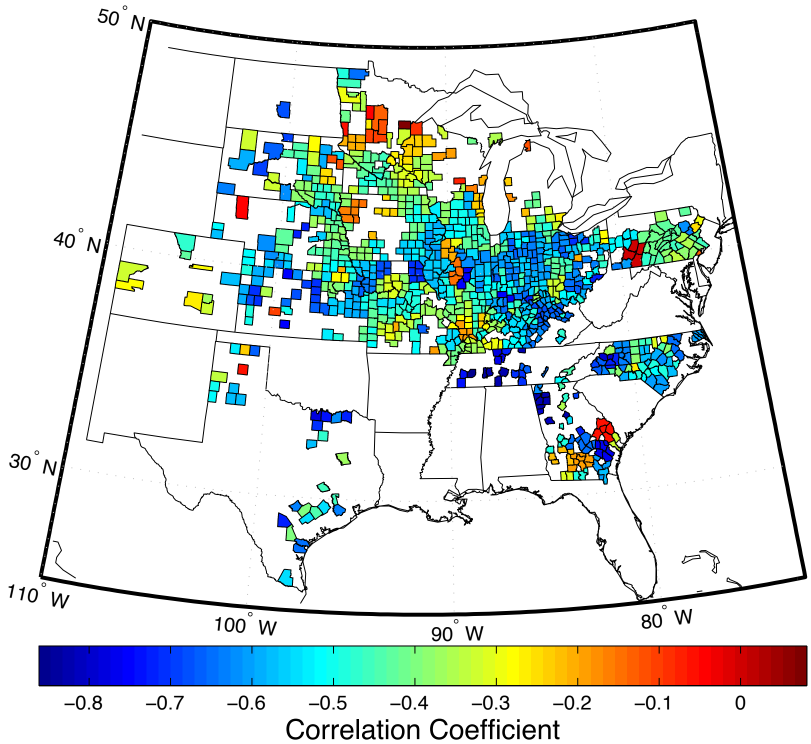


Figure 1.7: Correlation between mean KDD and mean precipitation. The correlation is almost everywhere negative between mean KDD and mean precipitation. The strong negative correlation in the south further supports that local adaptation accounts for the low sensitivity to KDD, as opposed to compensating meteorological factors. In general, years with high KDD are accompanied by low precipitation.

two and could negate losses with respect to total production, at least for a modest 2°C warming. The prospect that adaptation could have such a significant influence upon future yields provides impetus for further study. Trials growing crop varieties in different conditions of temperature and water availability, analysis of the sensitivity and adaptability of other major food crops and other growing regions, and the application of more complete biophysical models of crop interactions with environmental variations would all be prudent undertakings for adequately predicting the ecological response of crops to a changing climate.

1.7 Methods

The data included in this study are from states that report maize planting and harvest times for at least eight years, limiting the pool to 19 states in the Eastern United States. Temperature records are screened to include only those having fewer than eight consecutive days of missing temperature values, with the remaining gaps infilled using linear interpolation. Data from 78 counties are also omitted because yield or nearby weather station records have less than eight years of usable data.

Reported confidence intervals account for uncertainties in fitting a particular model to the observations, but do not account for uncertainties in model formulation itself. Some indication of model uncertainty is provided by the three functional forms discussed in regard to KDD sensitivity versus climatology (Fig. 1.3) and by the inclusion of GDD maladaptation. A range of alternative data selections and model configurations were also explored before those presented in the main text were selected for their simplicity and descriptive skill, and here we further describe the implications of those choices. Counties not significantly fit ($P < 0.05$) by Eq. 1.1 were omitted. Including all counties gave similar losses from a 2°C warming of 11% without adaptation and 4% with, where the slight reduction in sensitivity is consistent with Eq. 1.1 being less likely to obtain a significant fit with counties that have low sensitivity to weather variations.

A range of KDD thresholds between 25° and 35°C were also experimented with for each county, as well as thresholds based on the 90th percentile of temperatures in each county, but these also gave little improvement in fit (Fig. 1.8). We found no clear spatial pattern in optimal threshold values and, for consistency, selected the same threshold of

29°C used in previous studies[140,131]. Calculating GDDs after capping daily maximum temperatures at 29°C in order to exclude overlap with KDDs also had little overall effect.

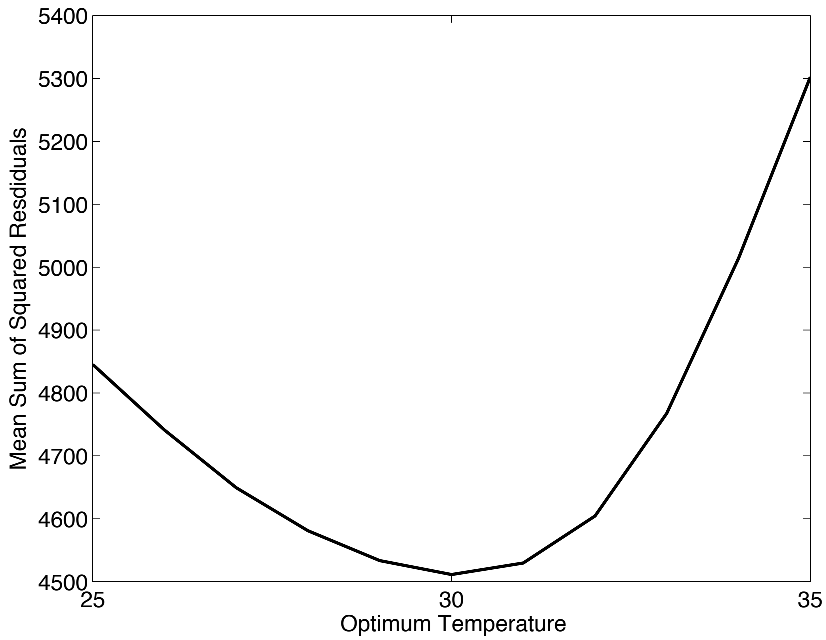


Figure 1.8: Goodness-of-fit for the temperature threshold above which killing degree days are computed. The goodness-of-fit is measured as the sum of the squared residuals when fitting Eq. 1.1 to the county-level yield data. The best fit is achieved with a temperature threshold of 30°C, but we use a threshold of 29°C throughout this study for consistency with previous work. Use of a 30°C threshold reduces the estimated losses from a 2°C warming to 11% without adaptation and 4% with adaptation. Note that although the magnitudes differ according to the threshold, the relative differences are comparable using either threshold, supporting our main conclusion that adaptation has major implications for forecasting the effects of climate change upon crop yield.

Inclusion of a freezing degree day term in Eq. 1.1 likewise gave negligible improvement in the ability of the model to predict yield variations, presumably because of the very few freezing days that occur during the growing season. Finally, inclusion of linear and quadratic precipitation terms were experimented with but gave negligible increases in the model fit, as discussed in the main text, and led to many more counties being rejected because of an insignificant fit as a result of the increased degrees of freedom.

Other studies used a logarithmic transformation of yield data, as opposed to magnitudes, in order to minimize influence from trends and regional differences in yield[140,85]. Repeating our analysis using logarithmically transformed yields gave a similar relationship between climatological KDDs and the sensitivity to KDDs (compare Fig. 1.9 and Fig. 1.3) and somewhat lower yield losses of 11% without adaptation and 2% with adaptation.

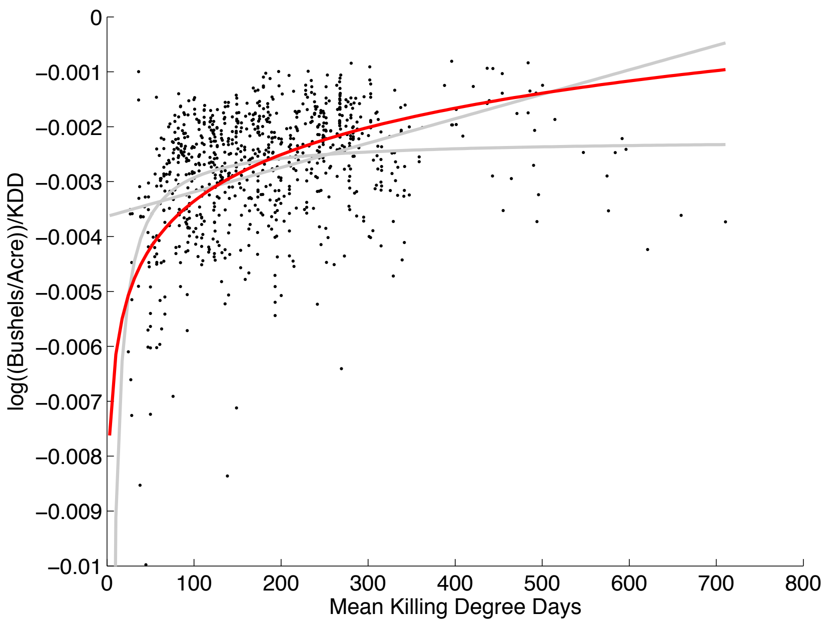


Figure 1.9: Alternative analysis using the logarithm of yield. Other studies (i.e. refs[140,85]) often use log(yield) instead of magnitude. The basic relationship between climatological KDD and log(yield) sensitivity is quite similar to that between climatological KDD and yield sensitivity (Fig. 1.3). The y-axis has been truncated for clarity at -0.01, omitting the four most sensitive values, all of which had very low mean KDDs, though the points were included in the fit.

The above modifications regarding data selection and model configuration that we explored lead to qualitatively consistent results, providing confidence that adaptation has significant potential to mitigate yield losses from moderate warming. Nonetheless, further research using alternative simple model formulations, more complete biophysical models, and field trials to test these models are all needed to better understand the effectiveness of and scope for adaptation.

1.8 Case Study: Butler County

It is useful to consider a specific case study as a means of illustrating the overall analysis process, and here we focus on Butler County, Ohio, at 39.4°N and 84.5°W. Butler County's mean yields are 118 bushels/acre relative to the average of 108 bushels/acre over all counties. Butler is one of the better modeled counties, with the model explaining 86% of the yield variability (in the 75^{th} percentile of variance explained, fig. 1.10a), but the results presented here are nonetheless generalizable to results from other counties.

An obvious relationship exists between peaks in KDD anomaly and troughs in annual yield from Butler (Fig. 1.10b). Furthermore, Butler serves to illustrate how GDD and KDD vary relatively independently. For example, the worst yields for Butler in this study occurred in 1983 (52.3 bushels/acre) with a GDD anomaly of +3.6 degree-days and a KDD anomaly of +200 degree-days. In 1985, a year with one more GDD but a KDD anomaly of -59.3 degree-days, the yields were over double those in 1983 (122.8 bushels/acre). This demonstrates the great sensitivity of yields in Butler to variations in KDD, and a central question for determining Butler's response to future warming is whether such large losses could be mitigated if higher levels of KDDs become the norm.

In the case of no adaptation, our model predicts that a 2°C warming would lead to a 19% reduction in yield from 118 to 96 bushels/acre (Fig. 1.10c) in Butler, whereas with adaptation, mean yields decline by 11%. Losses with and with-out adaptation are calculated by running the model with historical temperatures plus 2°C, giving a different time-history of GDDs and KDDs (Fig. 1.10d). For example, in year 10 our model gives a 3 bushels/acre greater loss without adaptation, relative to with adaptation, whereas in years 3 and 27 there is a 21 bushels/acre greater loss. (Years are reported generically under the warming scenario with year 1 corresponding to 1981 and year 28 corresponding to 2008 in the historic record.) All statistics that we report in the main manuscript are calculated by averaging across years for which historical data are available, which for the future warming scenario implicitly assumes that the distribution of temperatures around a given mean is unchanged.

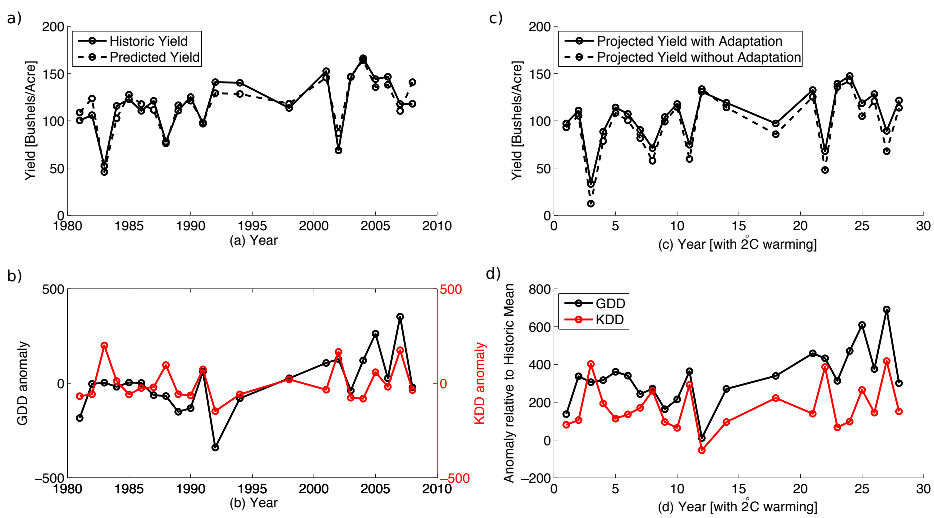


Figure 1.10: Case study for Butler, OH. (a) Butler, OH yields (black) and model fit (dashed). **(b)** Yearly variation in GDD and KDD anomaly. **(c)** Estimated yield without adaptation (dashed) for a 2°C warming and with adaptation (solid). Note that year 1 corresponds to 1981 and year 28 corresponds to 2008 from the historical record. **(d)**The comparable increase in GDD anomaly is not enough to offset the effects of increased KDDs, even with a reduced KDD sensitivity. Note that while anomalies increase by similar amounts, the fractional increase in KDD is substantially larger. There are missing data for Butler County in years 1993, 1995, 1996, 1997, 1999, and 2000 because of gaps greater than one week in the maximum temperature data obtained from station 121030 at 39.4°N and 85.0°W.

2

Variation in extreme temperature sensitivity by region and growth phase

2.1 Abstract

Maize yield is sensitive to high temperatures, and most large scale analyses have used a single, fixed sensitivity to represent this vulnerability over the course of a growing season.

Field scale studies, in contrast, highlight how temperature sensitivity varies over the course of development. Here we couple United States Department of Agriculture yield and development data from 1981-2012 with weather station data to resolve temperature sensitivity according to both region and growth interval. On average, temperature sensitivity peaks during silking and grain filling, but there are major regional variations. In Northern states grain filling phases are shorter when temperatures are higher, whereas Southern states show little yield sensitivity and have longer grain filling phases during hotter seasons. This pattern of grain filling sensitivity and duration accords with the whole-season temperature sensitivity in US maize identified in recent studies. Further exploration of grain filling duration and its response to high temperatures may be useful in determining the degree to which maize agriculture can be adapted to a hotter climate.

2.2 Introduction

Most large-scale empirical studies of the effects of extreme temperatures upon maize yield have employed a single, fixed sensitivity[157,24,139,82,140,65,18]. A more resolved analysis is useful, however, because sensitivity varies substantially across development phases, and accounting for these variations permits for better discernment of physiological controls and quantification of the relationship between weather and yield.

Early field-scale work[35] demonstrated that the sensitivity of maize yield to temperature peaks at a value approximately three times above the average around 90 days after planting, during silking. Since that time, many further field-scale studies have confirmed that maize yield is particularly sensitive to elevated temperatures during silking as well as grain filling[138]. Several large-scale empirical analyses have also analyzed sensitivity during portions of maize development. For example, moderate sensitivity to high temperatures prior to silking, exceptional sensitivity during silking, and increased yields with elevated temperatures after the silking period were demonstrated for sub-Saharan maize yields[85]. Similarly, sensitivity to high temperatures during early reproductive stages has been demonstrated for US Maize[115,116,10].

Complementary to temporal variation in sensitivity is to explore regional variations in sensitivity. Trials on various cultivars show that those planted in the South produce more heat shock proteins, lose less water, and have morphologies better adapted to hot environments relative to those typically planted in the North[130]. It has also been shown that temperate cultivars accelerate development in response to high temperatures more so than tropical varieties[127,126]. Consistent with these variations amongst cultivars, maize has been found to be more sensitive to high temperatures in the US North than South[18,142].

Also suggested is that the observed spatial variations in sensitivity may permit for inference of adaptability to future increases in temperature[18], though the appropriateness of such an inference depends on the basis for present spatial variations in sensitivity, and whether these qualities could be advantageously imported to new regions given warmer conditions[142,19,79]. Here we focus on identifying physiologic adaptations to high temperatures in rainfed maize that may underlie variations in spatial sensitivity.

2.3 Methods

We first characterize spatial variation in temperature sensitivity using a model with a single fixed sensitivity over the course of the entire growing season, similar to the approach in many previous studies[157,24,139,82,140,65,18], and then introduce a technique to incorporate developmental data into a regression model in order to explore how temperature sensitivity varies through the growing season.

As input to the regression model we use development data from the United States Department of Agriculture/National Agriculture Statistics Service[123] and temperature data from the United States Historical Climatology Network weather stations[101]. Development data are available for 17 states within the Eastern United States, all extending from 1981-2012 except for Georgia (1981-1999) and Texas (1985-2012). Virginia, Tennessee, and North Dakota also have development data but are omitted because less than 15 years of data makes reliable parameter estimation difficult. Temperature data are maximum daily temperature, denoted $T_{max,d}$, and minimum daily temperature, $T_{min,d}$. These daily temperature values are interpolated from a subset of 444 weather stations using a Delaunay Triangulation[12] to the center point associated with each county contained within the 17 states having sufficient development data

Heavily irrigated counties are excluded from our analysis because irrigation significantly reduces temperature sensitivity[18] and to ensure a more homogeneous sample. Specifically, irrigation data are averaged across three available census years (1997, 2002, 2007) and counties whose average irrigation exceeds 10% of its total harvested area are excluded. Colorado is removed entirely for having only a single unirrigated county with a sufficiently long record of maize planting, bringing the total number of states analyzed to 16.

We use growing degree days (GDD) as an estimate of the beneficial effects of temperature. GDDs are typically used as a measure of the thermal time required for a specific cultivar to develop, but in this aggregate analysis there are many maturity classes within any given state on any given year, and yearly GDDs help determine which of those cultivars are most successful. This approach is in keeping with previous aggregate statistical studies[85,38,18]. The daily heat unit, $\mathrm{GDD_d}$, is defined on each day,

d, using the representation of[1]:

$$\mathrm{GDD}_d = \frac{T^*_{min,d} + T^*_{max,d}}{2} - T_{low}, \tag{2.1}$$

where

$$T^*_{\mathrm{max,d}} = \begin{cases} T_{\mathrm{max,d}} & \text{if} \quad T_{\mathrm{low}} < T_{\mathrm{max,d}} < T_{\mathrm{high}}, \\ T_{\mathrm{low}} & \text{if} \quad T_{\mathrm{max,d}} \leq T_{\mathrm{low}}, \\ T_{\mathrm{high}} & \text{if} \quad T_{\mathrm{max,d}} \geq T_{\mathrm{high}}. \end{cases} \tag{2.2}$$

$T^*_{min,d}$ is defined with analogous bounds. Similarly, damaging heat units, killing degree days (KDDs), are used to quantify temperatures that may reduce yields, for example, through desiccation or accelerated development, and are defined as:

$$\mathrm{KDD}_d = \begin{cases} T_{\mathrm{max}} - T_{\mathrm{high}}, & \text{if} \;\; T_{\mathrm{max}} > T_{\mathrm{high}}, \\ 0, & \text{if} \;\; T_{\mathrm{max}} \leq T_{\mathrm{high}}. \end{cases} \tag{2.3}$$

In the above, T_{low} is set to 9°C and T_{high} to 29°C, similar to typical values for GDDs[1]. A T_{high} value of 29°C for damaging temperatures is consistent with previous statistical studies of the influence of high temperature on yield[24,140,85,18,65], though is notably cooler than thresholds established for protein denaturing (≈ 45°C)[156] or photosynthetic inhibition (≈ 38°C)[31]. This discrepancy can be explained in that KDDs represent many negative effects of high temperature, which begin to accrue at temperatures just above the optimum. It is also noteworthy that discrepancies can exist between ambient air temperature – for which data are widely available – and crop canopy temperature[57]. We also experimented with including freezing days, precipitation, and potential sunshine hours in the model but these were ultimately rejected for adding little explanatory power relative to the increased number of free parameters, particularly in that our focus is on variations in the sensitivity to temperature.

Summing GDD_d and KDD_d across each year's growing season and removing the sample mean across all years, y, gives anomalies in accumulated temperature measures, GDD'_y and KDD'_y, with which we formulate a panel regression model for the yield,

$$Y_{y,c} = \beta_{0,c} + \beta_{1,i}y + \beta_{2,i}\text{GDD}'_{y,c} + \beta_{3,i}\text{KDD}'_{y,c} + \epsilon_{y,c}. \tag{2.4}$$

$Y_{y,c}$ represents the yield in county c and year y expressed in metric tons per hectare (t/ha). The $\beta_{0,c}$ term is a county dependent intercept, whereas other β terms are uniform across each state, i. The inclusion of a state-wide linear time trend sensitivity, $\beta_{1,i}$, accounts for technological improvement over the study period, 1981-2012. Overall positive yield trends are a result of both cultivar and management improvement, with the greatest increase generally attributed to greater stand densities, which have increased by approximately 1000 plants per hectare per year[59,160,41]. In addition, kernel weight has increased over the course of plant breeding and contributes to the higher yields of modern varieties[66]. Although the estimated β_1, β_2, and β_3 would not change if the magnitude of GDD and KDD were used instead of anomalies, the value of β_0 would then not be interpretable as the mean county yield. This model is similar to that used in other recent studies[38,65], though here it is employed to estimate spatial variation in parameter estimates, as in[18].

Resolving temporal as well as spatial variations in yield sensitivity requires additional analysis. First, we develop and employ a technique to combine state-level development data with county-level yields and weather station temperatures. The United States Department of Agriculture/National Agriculture Statistics Service development data indicates when crops pass through six distinct developmental stages: planting, silking, doughing, dented, mature, and harvested. These stages are used to define four phases of maize development: (1) planting to silking is collectively referred to as the vegetative phase; (2) silking to doughing is the early grain filling phase, (3) doughing to mature is the late grain filling phase; and (4) mature to harvested is the drydown phase. Note that phase 3 encompasses passage through the dented developmental stage, making the early and late grain filling phases of similar duration. Although yield is largely biologically insensitive to most environmental stresses during phase 4, the model is ultimately constrained by actual yields as reported, and omitting possible influences such as sufficiently high temperature for crop drydown, which can influence harvesting, could introduce biases in the parameters inferred for the other phases.

Developmental values are reported as percentages of total acreage having attained a particular stage on a weekly basis. We linearly interpolate these data to daily values and, if the data do not cover 0 or 100%, linearly extrapolate to these end values in the adjacent weeks. Cumulative distributions of development stage are converted into instantaneous daily fractions by subtracting the total percentile of acreage in the following stage of development and dividing by a factor of 100, $P_{p,d} = (C_{s,d} - C_{s+1,d})/100$. $P_{p,d}$ represents the fraction of the planted area in each state within each phase, p, on day, d (Fig. 2.1). Note that crops across a state can be in several phases on any given day, and in many states this is indeed the case during the middle of the growing season.

Incorporating this detailed temporal information on growing phases is important because of the variability in both the seasonal cycle of temperature and cropping calendars. Planting has shifted about two weeks earlier across the US corn belt over the last three decades[75], and Southern maize is typically planted about a month earlier than in the North. There is also substantial interannual variability in the timing and amplitude of the seasonal cycle in temperature, as well as evidence for a general shift toward earlier

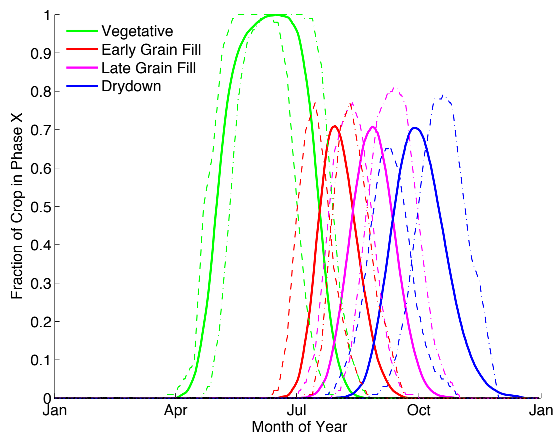


Figure 2.1: The fraction of planted area in Iowa in each of four development phases. Solid lines show the mean developmental phase distributions across all reported years, dashed lines are for the earliest planting date (March 26th, 2012), and dot-dashed lines are for the latest planting date (April 21st, 2008), nearly a full month later. Iowa is the largest producer of maize in the US, with over a third of the state's area dedicated to maize cultivation.

seasons by a few days over the last century[151]. The combined effects of variations in the seasonal cycle and planting date permit for substantial changes in the temperatures that a crop may experience during a given growth phase.

To incorporate development data into predictor variables, daily GDD is weighted by the fraction of crop in a given phase, $\mathrm{GDD}_p = \sum_d P_{p,d}\mathrm{GDD}_d$, where the sum is over the days comprising a given growth period as a function of state and year. KDD_p is calculated analogously. GDD_p and KDD_p are then used as predictors for county yield in a multiple linear regression,

$$Y_{y,c} = \beta_{0,c} + \beta_{1,i}y + \sum_{p=1}^{4}\left(\beta_{2,i,p}\mathrm{GDD}'_{y,c,p} + \beta_{3,i,p}\mathrm{KDD}'_{y,c,p}\right) + \epsilon_{y,c}. \tag{2.5}$$

Here, as in Eqn. 2.4, the β terms are defined for each state, i, as dictated by the scale at which the development data are reported, and values are estimated using ordinary least squares. As with Eqn. 2.4, primes on GDD and KDD indicate that the mean has been removed to prevent interaction with the $\beta_{0,c}$ term. These model results have a mean coefficient of determination of 0.69, with generally better fits in the North than the South and, of course, superior fits than the single season sensitivity (Fig. 2.2). We note that it is also possible to select a different T_{high} for each growing phase[138] within each state, but that such an approach would introduce a large number of adjustable parameters that would be partially redundant with the sensitivity parameters.

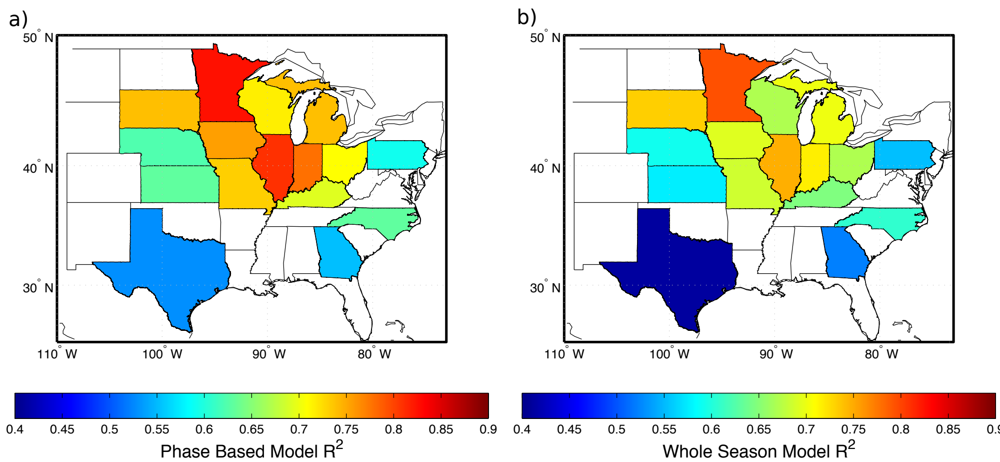


Figure 2.2: Correlation between observed and predicted yields. (a) Squared cross-correlation between developmentally-resolved model predictions and observations of yield, and (b) between whole-season model prediction and yield. In all cases, the more resolved model gives a slightly higher correlation, as follows from the greater degrees of freedom.

The use of specific crop phase dates for defining GDD and KDD is critical to the performance of our model. The supplemental material contains a counterfactual example where phase dates are fixed to their average times across years, whereupon the inferred sensitivities are unphysical, and the explained variance is reduced. Also see[115,116,10] for further discussion regarding the importance of correctly resolving growth stages in considering yield sensitivity.

Generally, the sensitivity to GDDs are found to have a positive coefficient across each phase and state, whereas KDDs have a negative coefficient across states (Fig. 2.3). As each state contains various cultivars having different GDD maturity ratings, the generally positive coefficient of GDD is interpreted as reflecting greater yields for longer maturing varieties[48]. That an increase in GDD may further benefit yield is also likely related to the degree to which carbon uptake, chlorophyll production, and growth may be inhibited at lower temperatures[95,137,138] as well as the fact that GDDs and mean temperature are strongly correlated. Specifically, the correlation between daily GDDs and the daily average temperature calculated for each county included in our analysis gives an average Pearson's coefficient of $r = 0.94$. Also in keeping with the inferred sign of the response, KDDs are expected to damage yield through desiccation, accelerated development, and, at especially high temperatures, tissue and protein damage[127,31,156].

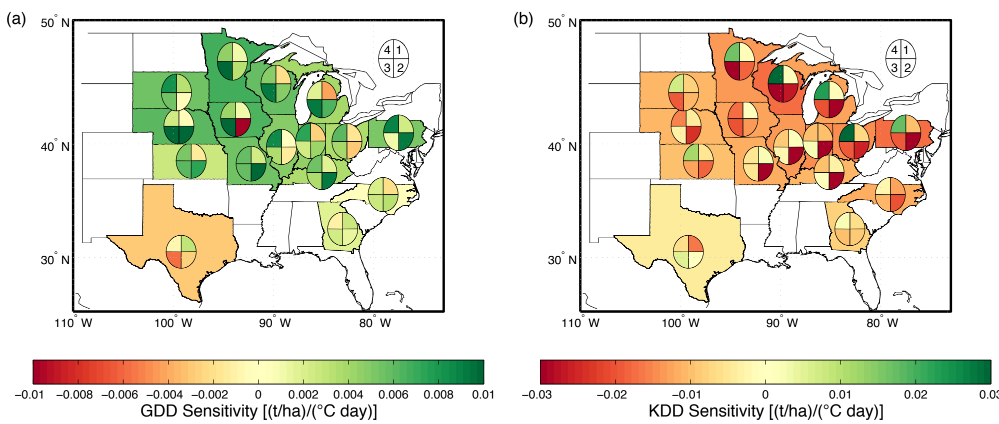


Figure 2.3: Yield sensitivity to growing and killing degree days. Phase sensitivity is indicated by shading within the wheels corresponding to: (1) vegetative, (2) early grain filling, (3) late grain filling, and (4) drydown. The whole season sensitivity is indicated by the background shading of each state. (a) Growing degree day (GDD) sensitivity is largest in the northern states during early and late grain filling. (b) Killing degree day (KDD) sensitivity is generally largest during early grain filling, but late grain filling is of a comparable magnitude in the North.

Uncertainties associated with $\beta_{i,p}$ sensitivities are calculated using bootstrap resampling. Each county is resampled 1000 times using individual years as independent replicates. In addition, we perform a more conservative block resampling in which all counties within a given state and year are resampled together as a unit. This reduces the effective degrees of freedom by a factor of nearly 100 and provides an upper estimate for the uncertainty (Fig. 2.4), but in this case GDD and KDD sensitivity in many state and stage combinations are difficult to distinguish, which runs counter to the the overall consistency observed between states and physiological expectation. County based bootstrap estimates are, therefore, used for cited uncertainties.

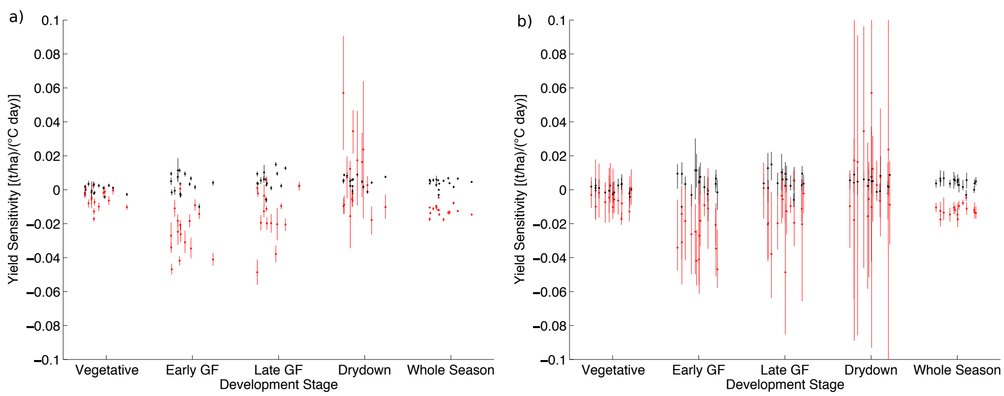


Figure 2.4: Confidence intervals calculated using state-level and county-level aggregation. (a) Yield sensitivity for GDDs (black) and KDDs (red) for each stage and whole-season values, where spacing along the x-axis is purely for visual purposes. Vertical bars indicate the 95% confidence level, and are obtained through a bootstrapping procedure where data is resampled at the county level according to year. This approach assumes that county-level data is independent. (b) In order to account for spatial dependence, uncertainties are also estimated using a block-bootstrap procedure where yields are resampled according to year at the state level. In this case, there are fewer degrees of freedom permitted for estimation, leading to larger variance in the result. Actual uncertainties are expected to reside between these two end-member cases. Note that in either case the early and late grain filling phases — which we focus on — have the most clearly distinct KDD and GDD sensitivity estimates. GF indicates the grain filling stages.

2.4 Results

Each phase of development represents a unique period of the maize plant's phenological cycle and entails a different response to environmental conditions. The overall life cycle is divided between vegetative and reproductive phases, with roughly half of each growing season spent in each. During the vegetative phase a seedling expands its surface area and the leaf area index of the plant is set, influencing the amount of radiation that can be intercepted over the remainder of its lifecycle[1,16]. Sensitivity to both KDDs and GDDs are low relative to other stages (see Fig. 2.3 and Table 2.1), though Texas shows pronounced sensitivity to KDDs at -0.017 [(t/ha)/(°C day)] (95% c.i. -0.019 to -0.016), possibly because overall hotter temperatures make seedlings particularly vulnerable[63].

The early grain filling phase, as defined here, begins with the emergence of silks from the ends of the ears and begins the reproductive portion of the plants' life cycle. As has long been recognized[149,35], yields are highly susceptible to elevated temperatures during silking and early grain filling[66,116,138,85,61,83]. Indeed, we find that average sensitivity to KDDs across states during this phase is a factor of four greater than during the vegetative phase at -0.025 [(t/ha)/(°C day)] (95% c.i. -0.024 to -0.026). Sensitivity to high temperatures results from damage to silks and fewer kernels being fertilized or other factors influencing kernel viability[4,22,32,29]. This phase also accounts for about 20% of final kernel dry mass[1] and, therefore, entails responses similar to those found during late grain filling, discussed below.

Late grain filling is the combination of the doughing and dented stages, and is when the majority of photosynthate and carbon reserves are transferred into the growing kernels. At this point, yield damages are generally a result of lower final kernel mass rather than lower total kernel number. High temperatures are known to directly reduce kernel

State	Veg.[G]	EGF[G]	LGF[G]	Dry.[G]	Veg.[K]	EGF.[K]	LGF[K]	Dry.[K]	WS[G]	WS[K]
Georgia	2.5	1.6	2.3	-1.3	-6.4	-9.1	-9.6	2.7	1.6	-7.8
Illinois	0.0	-1.5	3.6	8.7	1.0	-47	-2.2	-8.8	4.9	-14
Indiana	-2.8	4.1	2.3	7.6	-10	-41	2.1	-10	4.6	-15
Iowa	1.0	-10	13	4.2	-0.5	-14	-20	-18	6.5	-13
Kansas	-1.6	7.5	6.1	5.1	-5.7	-18	-13	12	2.8	-9.6
Kentucky	1.8	9.5	3.8	5.6	-3.1	-34	1.0	-9.7	3.7	-10
Michigan	-4.2	6.7	9.5	1.6	-1.2	-35	-20	24	3.9	-13
Minnesota	1.0	3.4	15	4.7	-1.8	-18	-38	16	6.8	-13
Missouri	2.4	11	6.0	5.7	2.6	-42	-5.7	-5.5	5.5	-12
Nebraska	-0.6	11	10	2.2	-4.6	-25	-3.5	-16	6.1	-11
North Carolina	-2.2	3.5	2.7	2.1	-13	-21	-11	-2.2	0	-12
Ohio	-1.6	-3.0	3.8	6.1	-7.3	-26	-20	34	3.6	-15
Pennsylvania	2.4	9.4	1.0	8.9	-9.9	-31	-20	17	5.3	-18
South Dakota	3.4	-0.6	5.5	8.3	-8.1	-11	-19	7.3	5.7	-11
Texas	3.2	-2.6	-6.0	-0.9	-17	0.5	5.7	-6.6	-3.1	-4.6
Wisconsin	-2.0	5.0	9.4	5.0	-1.7	-27	-49	57	5.8	-17

Table 2.1: Yield sensitivity to growing degree days [G] and killing degree days [K] broken down by growth phase: Veg. for Vegetative, EGF for Early Grain Filling, LGF for Late Grain Filling, Dry. for Drydown, and over the whole growing season [WS]. Units are (kg/ha)/(°C day).

mass[71,147], consistent with the high sensitivity we find. In addition, high temperatures can lead to acceleration through the growth phase, reducing the total number of days of grain filling and lowering kernel mass[27,14,46,6,159,106,167]. On average, yield sensitivity during late grain filling is smaller than during early grain filling, with mean losses from KDDs of -0.014 [(t/ha)/(°C day)] (95% c.i. -0.013 to -0.015). Wisconsin has the greatest sensitivity with -0.05 [(t/ha)/(°C day)] (95% c.i. -0.04 to -0.06) losses and Texas is the least vulnerable to KDDs at 0.006 [(t/ha)/(°C day)] (95% c.i. 0.004 to 0.008).

With regard to GDDs during late grain filling, the greatest increase in yield occurs in Minnesota during this phase with values of 0.015 [(t/ha)/(°C day)] (95% c.i. 0.014 to 0.016). The mean increase is 0.0055 [(t/ha)/(°C day)] (95% c.i. 0.005 to 0.006), consistent with cultivars that are able to take advantage of greater accumulation of moderate temperatures and longer period of radiation interception having a higher yield[71,27,90]. The fact that Texas has a positive late grain filling KDD sensitivity estimate and a negative GDD sensitivity may be because collinearity of the predictors confounds some of the results, similar to Iowa's negative GDD sensitivity during early grain filling. Note that while high KDDs shorten the duration of grain filling, the total accumulated GDDs are generally higher in years with higher KDDs, consistent with previous work on development under hotter conditions[167].

The end of the plant's life cycle is the drydown phase, when the plant ceases to photosynthesize and kernels lose water, generally drying from just over 30% moisture to about 20% moisture when ready for harvest. Sensitivity parameters indicate a positive effect from KDDs in many northern states, possibly because insufficient drydown is most probable there, with consequences for vulnerability to pests, mold, or other pre-harvest losses. Statistical studies including but not independently resolving the drydown phase presumably conflate the positive effects of KDDs during drydown with negative effects during grain development. Some states in the eastern corn belt still indicate strong GDD sensitivity during the drydown phase possibly because the late grain filling interval in the USDA data extends into the drydown phase, or that the higher GDDs play a similar role to KDDs in promoting drying. Altogether, these results highlight the variability of the temperature response according to developmental phase.

It is useful to make a direct comparison between whole-season sensitivity and the phase-based sensitivity estimates. Whole season sensitivity implicitly sums over the product of the distribution of KDDs (or GDDs) and sensitivity throughout the growing season. A development phase that was highly sensitive but experienced no KDDs, for example, would not contribute to whole-season KDD sensitivity. Thus, in order to provide a direct comparison of whole-season sensitivity to phase-based sensitivity, we weight each phase according to the fraction of KDDs that it accounts for and estimate the slope between the two measures. Slope is estimated using a York fit[170], which has the advantage of accounting for uncertainties in both the ordinate and abscissa.

The best-estimate slope between weighted drydown-phase KDD sensitivity and whole-season KDD sensitivity is weak and negative at -0.1 (95% c.i., -0.2 to 0.1), consistent with the foregoing discussion that KDDs can be beneficial for drydown in the most Northern states, whereas they are typically detrimental during other growth phases. The slope for the vegetative phase is also negative and weak at -0.2, as well as uncertain (95% c.i., -0.5 to 1.1), consistent with generally low KDD sensitivity during this phase. Of greater pertinence is that the slope between KDD sensitivity for whole season and early grain fill is 1.1 (95% c.i., 0.5 to 2.8), indicating that the spatial variation observed over the whole season are substantially determined by variations in early grain filling (Fig. 2.5). Similarly, the slope with late grain fill is 0.6 (95% c.i., -1.2 to 1.7) indicating a further correspondence (Fig. 2.5). Together, the grain filling phases of development account for the observed pattern of sensitivity to KDD, and are the focus of attention hereafter.

The estimated spatial variations in grain filling sensitivity are consistent with field trials where the responses of temperate and tropical maize to heat exposure were examined prior to and through early reproductive development[127]. In these trials, well-watered temperate and tropical varieties gave similar yields under normal temperature

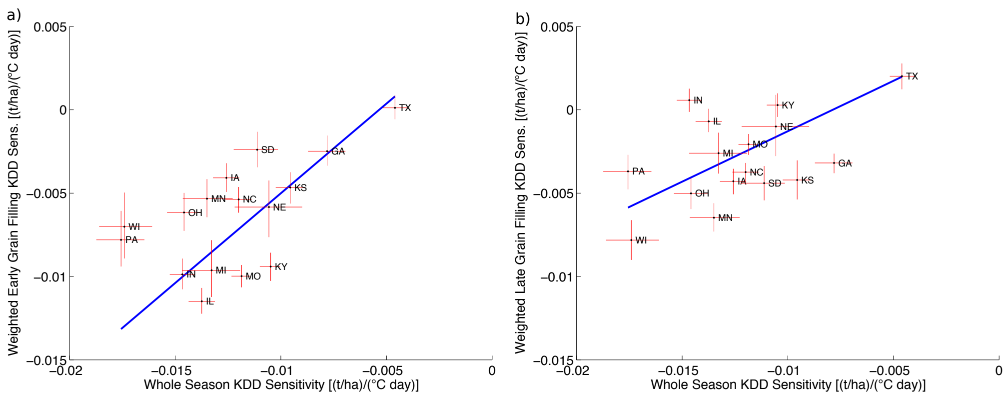


Figure 2.5: Relationship between grain filling sensitivity and whole season sensitivity to KDDs. The red crosses associated with each state are the respective 95% confidence intervals for the sensitivity estimates. a) The R^2 between weighted early grain filling and whole season KDD sensitivity is 0.37 and the York fit slope is nearly 1.1. b) The R^2 between weighted late grain filling and whole season KDD sensitivity is 0.27 and the York fit slope is 0.61. This indicates that variations in both grain filling sensitivities are, on the whole, an important driver of the entire variation in whole season sensitivity.

conditions, but when exposed to higher temperatures during what was likely the late blister, milking, and doughing stages, the temperate varieties responded by accelerating through grain filling and having larger yield reductions. Specifically, temperate varieties showed a 21 day decrease in the duration of the reproductive period as a consequence of heating, compared to a five day decrease in tropical hybrids and no decrease in temperate-tropical hybrids. Furthermore, temperate varieties had a greater decline in conversion of radiation to biomass when exposed to higher temperatures during early grain filling.

The USDA development data permits for an examination of changes in the duration of grain filling in response to high temperatures across the Eastern US. We find that the durational response to KDDs closely follows the number of KDDs experienced in a given state. States whose climatological average KDDs during early grain filling are

State	Veg.[G]	EGF[G]	LGF[G]	Dry.[G]	Veg.[K]	EGF[K]	LGF[K]	Dry.[K]	WS[G]	WS[K]
Georgia	890	400	550	280	110	100	130	40	2120	380
Illinois	780	310	480	230	60	40	50	10	1800	160
Indiana	790	300	460	240	60	30	40	10	1780	140
Iowa	800	330	330	220	50	30	20	10	1670	110
Kansas	860	350	490	250	90	80	110	30	1940	310
Kentucky	840	370	440	270	80	70	70	20	1920	240
Michigan	730	320	310	150	30	20	10	0	1500	60
Minnesota	730	330	310	140	40	20	10	0	1520	80
Missouri	800	300	480	250	60	50	80	20	1840	210
Nebraska	850	310	490	210	90	50	60	10	1870	220
North Carolina	870	360	520	340	80	70	90	30	2090	260
Ohio	780	270	460	190	50	20	20	0	1700	100
Pennsylvania	800	290	410	160	60	30	20	0	1650	110
South Dakota	790	240	340	170	70	30	30	10	1540	150
Texas	1080	410	600	270	170	130	210	80	2350	590
Wisconsin	740	280	310	140	30	10	10	0	1470	60

Table 2.2: The planting area weighted mean growing [G] and killing [K] degree days in each state and growing phase: Veg. for Vegetative, EGF for Early Grain Filling, LGF for Late Grain Filling, Dry. for Drydown. As well as summed over the whole season [WS]. All values are in units of (°C day) and rounded to the nearest ten.

below the median (<37 KDDs for MI, WI, MN, PA, IA, OH, SD, and IN) show an average decrease in the duration of early grain filling by 0.04 days per KDD. States clustered in the third quartile of exposure to KDDs (37 < KDD < 66; IL, NE, KY, and MO) show a shortening of the early grain filling phase by 0.01 days per KDD. And three out of four states in the upper quartile (>66 KDDs; NC, GA, TX, but not KS) show the opposite sign of response, on average across the four states, increasing the duration of early grain filling by 0.09 days per KDD (Fig. 2.6a). Similar to early grain filling, late grain filling at the low end of the KDD climatology shows an average decrease in duration of 0.12 days per KDD(<50 KDDs); those at the mid-range (50 < KDD < 85) show a weaker decrease at 0.06 days per KDD, and those at the highest range (>85 KDDs) show an increase in duration of 0.04 days per KDD (Fig. 2.6b). Although the climatological values of KDDs differ between early and late grain filling, the same states are kept in each climatological category.

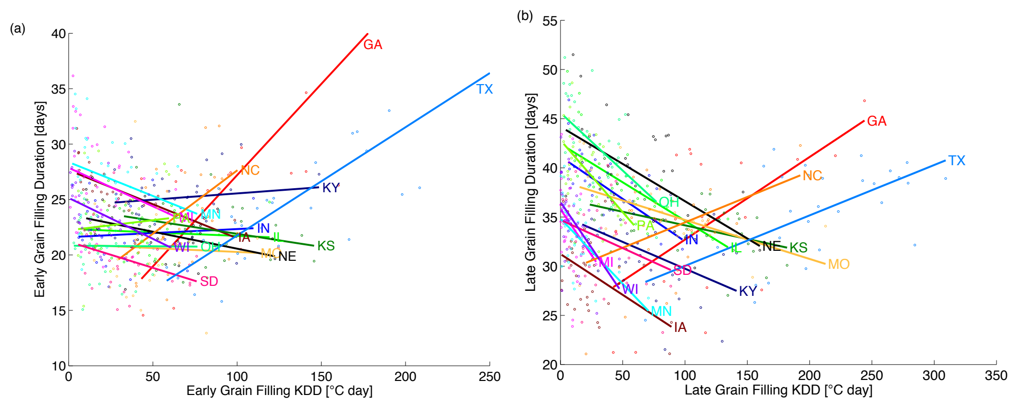


Figure 2.6: Relationship between killing degree days and duration of grain filling. Northern states show a decrease in the duration of both (a) early grain filling and (b) late grain filling in seasons with greater KDDs, whereas Southern states show an increase in duration. These regional variations in duration may represent a physiological trait important in determining differential sensitivities to KDDs. For readability, the axes for early grain filling truncate the most extreme values for Georgia, Texas, and North Carolina

Changes in the duration of grain filling are primarily associated with interannual variability, as opposed to long term trends. The detrended length of early grain filling has an average standard deviation across states of 3 days, whereas the average trend is toward lengthening at 0.16 days/year. Similarly, late grain filling varies by nearly 4 days and has a lengthening trend of only 0.05 days/year. Standard deviations are similarly larger than trends in just the three Southern states with elongated grain filling phases during hotter seasons. These results strongly suggest that steady technological changes are not the source of the KDD-duration relationship, and are consistent with variations in the duration of grain filling as features of given cultivars.

The variations of grain filling duration as a response to high temperatures found here generally accord with the aforementioned field trial results[127], presuming that hybrids in the South are most similar to those of tropical or temperate-tropical origin. That both early and late grain filling phases indicate similar patterns with respect to climatological KDDs also suggests that these results are robust. Combining early and late grain filling into a single phase gives a similar result but with smaller fractional changes in duration because high KDDs do not generally persist equally across the early and late phases.

2.5 Discussion and Conclusion

Longer grain filling with hotter temperatures can be associated with lower sensitivity to high temperatures on account of pattern correspondence between acceleration and sensitivity across the US, similar responses seen in field trials, and on the physiological basis of longer duration leading to greater kernel mass, so long as crops remain adequately watered[41,127]. The physiological pathway by which temperature variation influences the timing of the transition out of grain filling is unclear, though evidence for the role of reaching a critical moisture content[55] suggests that increased drying associated with higher temperatures and higher vapor pressure deficits would lead to an earlier transition, as observed in the North. Refining our understanding of how temperature influences grain filling duration, especially in the South and in tropical varieties, may lead to a better understanding of how to reduce damages from a hotter climate.

Correspondence between KDD sensitivity and climatology over the whole season was identified in an earlier study and offered as a basis for inferring the adaptability of cultivars to higher temperatures[18]. The association of yield sensitivity to KDDs and variations in grain filling duration documented here (also see Fig. 2.7) provides a more physiologically based perspective on patterns of KDD sensitivity. An important question, however, is why has a modification such as increasing the duration of grain filling in response to higher temperature not yet been introduced into Northern states if it reduces yield losses? More general versions of this question have been raised elsewhere[142], and one possibility is that such a modification only becomes physiologically feasible under warmer conditions, possibly because of a longer growing season[19,116]. In this speculative case, lengthening of grain fill duration in response to higher temperatures would constitute a climate change adaptation in the sense articulated by[79]. The question remains, of course, as to whether elongated duration of Southern grain filling would be transferrable to Northern cultivars under conditions of a warming climate and whether it would prove effective in mitigating yield losses that would otherwise accrue.

Building from previous controlled field-scale studies of yield loss in the presence of altered temperature[127,126] appears useful for furthering our understanding of potential adaptation to climate change. Field trials could be conducted to determine whether Southern varieties could be advantageously grown at Northern latitudes under higher temperatures, or, more elaborately, Northern cultivars could be similarly tested after breeding for longer duration of grain fill in response to higher temperatures.

The risks posed by climate change for agricultural production remain uncertain, as highlighted by the fact that the Fourth Intergovernmental Panel on Climate Change Assessment Report[43] suggested an overall increases in temperate maize production under conditions of moderate warming with adaptation, whereas the most recent Fifth Assessment Report[121] suggested losses. This variability appears to result from the en-

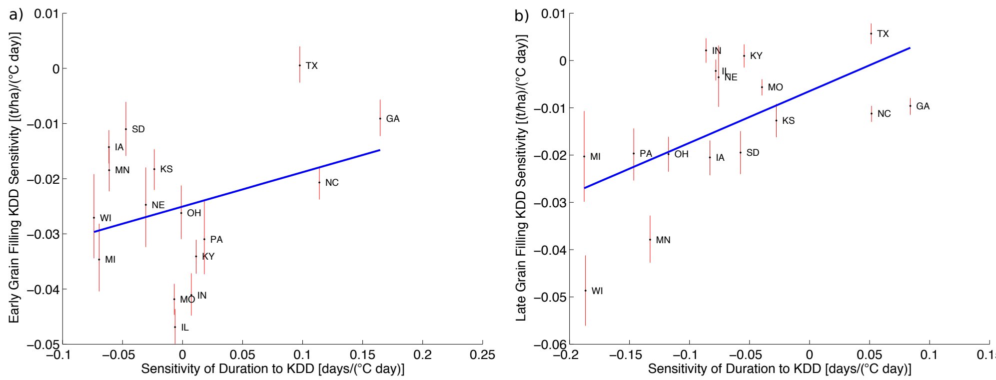


Figure 2.7: Relationship between KDD sensitivity and duration of grain filling Vertical red lines are the 95% confidence interval associated with each sensitivity. a) The relationship between early grain filling rate per KDD and sensitivity provides some indication of adaptation, but the fit is not particularly strong, with an R^2 of 0.1. b) The relationship between late grain filling rate per KDD and sensitivity provides further evidence of a physiological basis for latitudinal adaptation. The linear fit, in blue, fits the data with an R^2 of 0.36.

semble of available studies having substantial spread, and that subtle shifts in modeling frameworks can have significant influences on individual results. It is suggested that increasing the physiological interpretability of simple statistical models used to explore large-scale changes in production may help to reduce some of this ambiguity through better bridging their results with more complete agricultural models[132] and facilitating testing of results against field-scale trials.

2.6 Supplemental Models

To compare with prior work that used a fixed fraction of the growing season prior to harvest to assess temperature sensitivity[61], we fix the development period across years by taking the mean of the weights for each state, $P_{p,d}$, and applying those to all years (Fig. 2.1). Whereas early grain filling clearly remains the most sensitive phase, late grain filling estimates are almost entirely different - indicating a negative sensitivity across

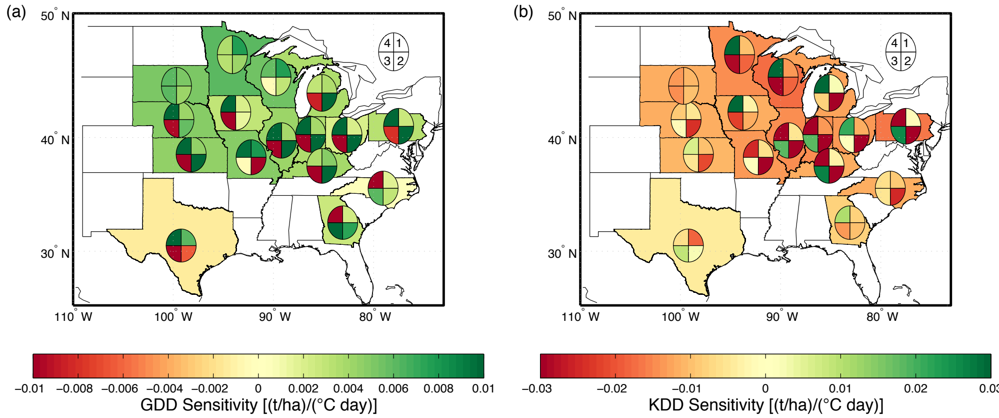


Figure 2.8: GDD and KDD Sensitivity with fixed growing season. (a) When growing stage dates are fixed to average state-wide values, many states exhibit a negative relationship between GDD and yield during late grain filling, and a strong positive relationship betweeen GDD and yield during the drydown phase of development. (b) KDD sensitivity is also counter-intuitive, with high temperatures during late grain filling generally indicated as beneficial. These results indicate the importance of correctly specifying phase dates when attempting a more resolved analysis of sensitivity.

much of the corn belt and sometimes a positive response to KDDs (Fig. 2.8). This result is unsupported by any biological explanation and, apparently, arises from incorrectly sampling the weather actually associated with late grain filling. Given that there is also a trend toward earlier planting[75] which has the effect, when the seasons are fixed, of shifting actual late grain filling dates into what is defined as the drydown phase this has likely contributed to confused sensitivity estimates under fixed development dates.

As the drydown phase represents a period where the crop is no longer biologially active we construct an alternative model which omits this phase and focuses only on the vegetative, early grain filling, and late grain filling phases (Fig. 2.9). The parameter estimates are largely unchanged, and given that grains are still vulnerable until harvest we prefer the model which includes the drydown phase. Note that incorporating the

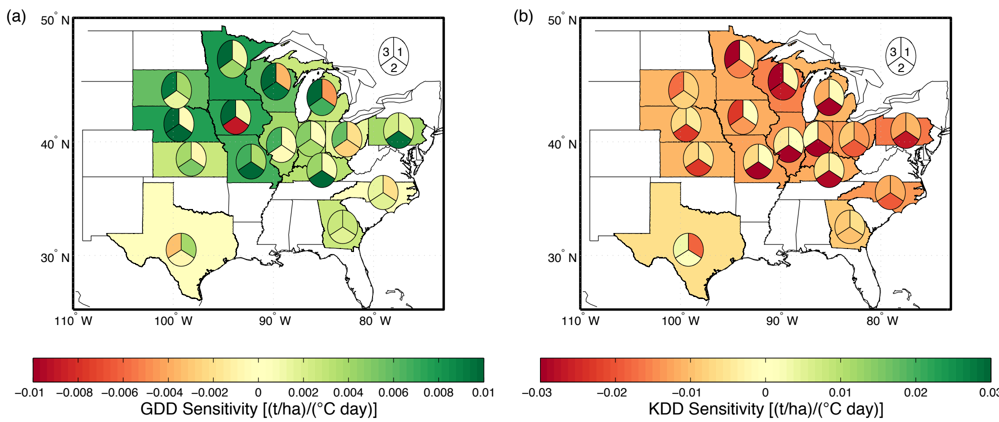


Figure 2.9: GDD and KDD Sensitivity without a drydown phase. (a) GDD sensitivity estimates and (b) KDD sensitivity estimates are largely unchanged when the drydown phase is omitted from the analysis.

drydown phase as part of the late grain filling phase may bias the parameter estimates on account of the substantial differences between the two.

3

Adaptation and Temporal Trends

3.1 Abstract

The weather that US maize has been exposed to during its growth has changed over the 20$^{\text{th}}$ century as a result of changes in climate as well as changes in planting dates and development time. Planting dates have moved an average of 9 days earlier, spend an average of 9 days less time in the field awaiting harvest, and have a 9 day longer grain

filling period between 1981 and 2014. Applying a linear model that incorporates phenology and yield data from 16 states enables the separation of yield trends attributable to trends in climate and shifting of development timing. The estimates indicate that, on average, climate trends and timing trends have contributed 8% and 10% of the yield increase, presuming that yield sensitivity to interannual variability may be scaled to estimate that associated with decadal trends. Temperature trends have generally been beneficial through cooling of the hottest temperatures in the North. However, Texas is an outlier which has experienced yield losses from both hotter temperatures and a warmer baseline climate. These results indicate that ongoing adaptation of crops to take advantage of the climatological seasonal cycle along with trends in temperature account for non-trivial portions of the overall improvements in yield. The ongoing adaptation to the climatological seasonal cycle is indicative of the capacity to adapt to a changing climate, at least for this intensively managed crop and in the context of the small changes experienced to date.

3.2 Introduction

Maize yields have increased substantially over the 20th century, with average US yield increasing by over 0.1 t ha^{-1} yr^{-1} from 1981 to 2014. This improvement is typically ascribed to technology, the sum of cultivar and agronomic improvements. Thus, this definition omits the effect that concurrent climate trends have also had on yield. Generally, analyses of the climatic effect on yield trends have been estimated with a single temperature trend over the growing season[85,84]. However, it has been shown that temperature sensitivity varies substantially over the course of crop development[127,138,20]. Similarly, fixed planting and harvest dates are often necessary at large scales and in the absence of more accurate data, but regional analyses indicate that these dates have moved earlier across important growing regions[102,75,76,136,89]. While simplifying assumptions are often necessary at the global scale, a more detailed analyses may highlight mechanisms that are indistinguishable under broad scale assumptions. Through a detailed analysis of trends within the growing season we are able to determine the relative contributions of climate and developmental timing to yield trends. This distinction refines how climatic change has impacted maize yields and indicates how farmers have temporally adapted to their historical growing environment.

Earlier work has highlighted the substantial role that spatial adaptation may play in reducing damages from a warmer climate[18,20]. Similarly, it has been suggested that simple temporal adaptations, such as longer maturing cultivars, may benefit yields in a warmer climate[37,116]. By examining the details of historical adaptation to the seasonal cycle we may gain some insight into the processes and limitations of temporally adapting to a warmer future. Farmers have conducted a long term experiment in optimizing their yield by exercising their limited control over two key features which set the course of the growing season. First, when crops are planted, which is restricted by the hardiness of the cultivar and the readiness of the fields[75]. Second, the maturity rating of their cultivar, which determines the temperature modulated time needed by the crop to fully develop[1]. After selecting these two elements the plants will grow according to the weather of the season. These steady adjustments of planting date and maturity ratings over time has lead to substantial changes in the temperature environment the crop experiences over the growing season. These changes in the temperature environment may be translated into a yield trend by assuming that the interannual temperature sensitivity of crop yield may be scaled to estimate a decadal trend.

The phenology trends observed in the heavily-managed agroecosystem of US maize has been attributed primarily to changes in management[75]. This is, perhaps, surprising, given that there is every indication that unmanaged ecosystems have responded significantly to local warming[118]. Long term records indicate that a range of phenological indicators for both plant and animal species now occur substantially earlier in both Europe[103] and the United States[17,104,47]. Earlier dates for leaf out and flowering are particularly common. Indeed, the planting date trend in the US is even greater than the trend towards earlier phenological spring in unmanaged ecosystems[143]. In contrast, European farmers appear to lag the phenological shifts of unmanaged ecosystems[102]. The contrasting phenological patterns of managed and unmanaged ecosystems further illustrates the dual roles of management and climate in setting the developmental timing of agroecosystems.

Here, we address the degree to which changes in historical planting and development timing associated with US maize have led to improvements in yield. The total climatic trend within four development phases is decomposed into two components, a climate component with fixed developmental phases and a timing component with variable developmental phases and a fixed background climate. Across most states both timing and climate have generally benefitted yields contributing, in different states, as much as 47% and 34% respectively to the each state's total temporal yield trend.

3.3 Methods

State level crop development data and county level yields from the United States Department of Agriculture/National Agriculture Statistic Service (USDA/NASS)[123] from 1981-2014 are available for 17 states in the Eastern US, except for Texas (1985-2014) and Georgia (1981-1999). These development data are combined with weather data from

467 United States Historical Climatology Network weather stations from the Global Historical Climatology Network[101] and interpolated with a Delaunay Triangulation[12] to the center of each county to approximate the daily weather experienced by the crop. Counties with greater than 10% of their harvested area irrigated according to the four 1997-2012 censuses of agriculture are removed from the analysis as they are known to be significantly less sensitive to temperature[18], which eliminates Colorado and reduces the states analyzed to 16 and the total counties to 1187.

Maize yield is modeled with two metrics of accumulated thermal time. Moderate conditions are modeled with growing degree days (GDD), the average of truncated maximum and minimum temperatures between 9-29°C, a common metric for accumulated thermal time that is also widely used in simple statistical models of crop yield[85,38,18,155]. Similarly, damaging conditions are summarized with killing degree days (KDD), maximum temperatures over a damaging threshold, here taken as 29°C. See chapter 2 for a more complete description of the calculation of GDD and KDD. Other terms including precipitation, freezing days, and potential sunshine hours were experimented with but did little to improve the skill of the model.

Development data are available for six distinct growing stages: planting, silking, doughing, dented, mature, and harvested. These are combined into four growing phases (1) from planting to silking is the vegetative phase, (2) from silking to doughing is the early grain filling phase, (3) from doughing to mature is the late grain filling phase and (4) from mature to harvested is the drydown phase, just as in chapter 2. In the USDA/NASS database the stages are presented as weekly percentages of crop development, which are linearly interpolated to daily values and extrapolated to 0 and 100% in surrounding weeks if the data do not naturally extend that far. When the stages are combined into the four phases of development they are converted into daily fractions for each state in each phase, see chapter 2 for details. The days within each phase are calculated by summing these fractional weights, this ensures that portions of the growing season in multiple phases are not double counted when determining the length of each phase.

The daily GDD and KDD within each county are weighted by the fraction of the state in each development stage as $\mathrm{GDD}_p = \sum_d P_{p,d}\mathrm{GDD}_d$. Here, GDD_p is the total GDD experienced within a given phase, p, and $P_{p,d}$ is the fraction of the state's crop that is in that phase on each day, while GDD_d is the daily GDD. The sum is taken over the variable days that the crop was in each phase within each year. The weighted GDD and KDD variables are combined into a panel model of yield as follows,

$$Y_{y,c} = \beta_{0,c} + \beta_{1,i}y + \sum_{p=1}^{4}\left(\beta_{2,i,p}\mathrm{GDD}'_{y,c,p} + \beta_{3,i,p}\mathrm{KDD}'_{y,c,p}\right) + \epsilon_{y,c}. \tag{3.1}$$

Here, $Y_{y,c}$ is the yield, Y, in metric tons/hectare during year, y, in county c. The β terms are the estimated coefficients for each state, i, except for $\beta_{0,c}$, which is a county level mean yield. The $\beta_{1,i,p}$, $\beta_{2,i,p}$, and $\beta_{3,i,p}$ terms are all at the state level and calculated for each phase, p. The $\beta_{1,i,p}$ represent the total temporal yield trend, of which a component is due to the trends in GDD_p and KDD_p, which will be explored in detail below. The $\beta_{2,i,p}$ and $\beta_{3,i,p}$ represent interannual GDD and KDD sensitivity, respectively. It is assumed that this sensitivity is fixed over the duration of this study, equivalent to assuming no ongoing adaptation over decadal timescales[18]. The primes on $\mathrm{GDD}'_{\mathrm{y,c}}$ and $\mathrm{KDD}'_{\mathrm{y,c}}$ indicate that the mean has been removed to prevent interaction with $\beta_{0,c}$.

To calculate statewide trends in GDD and KDD a single value is approximated for each year in each state with weights according to the total planted area within each county:

$$\mathrm{GDD}_{y,i,p} = \sum_c \mathrm{GDD}_{y,c,p} A_c / A_i. \tag{3.2}$$

The state wide value $\mathrm{GDD}_{y,i,p}$ is calculated in each year, y, state, i, and phase, p, by summing across county, c, values, GDD_c. These are weighted by the area, A_c, of maize planted in that county and normalized by the total planted area of the state, A_i. A weighted statewide KDD is calculated analogously. The time trend, Δ, in GDD and KDD is calculated with an ordinary least squares fit, and is shown in Fig. 3.1a,b. The uncertainty in the thermal time trend of each state is calculated by taking 1000 random draws from the bootstrapped uncertainty distributions of the GDD and KDD trends, see Fig. 3.2a,b. The distribution of trends in GDD and KDD were calculated by using the same sample of years to preserve temporal correlation.

Figure 3.1, Trends in GDD and KDD, on the following page: The trend within each phase of each state is indicated by the colors within wheel. Phases begin in the upper right with vegetative and proceeding clockwise to drydown in the upper left, as indicated by the numbered circle in the NE of the map. **Total Climate Trends**: a) The GDD trend tends to be concentrated in the middle of the growing season, and in the Western Corn Belt during late grain filling when yields benefit the most. The cooling during the vegetative phase is from both a shift towards earlier planting and climatic cooling while the decrease during the drydown phase is largely from earlier harvesting. b) Killing degree days have declined in the vegetative phase when yields are largely insensitive to hotter conditions with weak trends in other phases. **Climatic Change Trends** c) The climate GDD trends are all close to zero, with some warming indicated towards the end of the growing season in the East. d) The pattern of the climate KDD trends are quite similar to the total climate trends, particularly in the North suggesting that climatic change has a substantial influence on the total pattern. **Timing Trends** e) The GDD trends from timing changes are quite close to the total GDD trend. f) The KDD trends from timing shifts are negligible in the North but increase further South. In Georgia the concentration of KDDs during early grain filling has a particularly detrimental effect on yields.

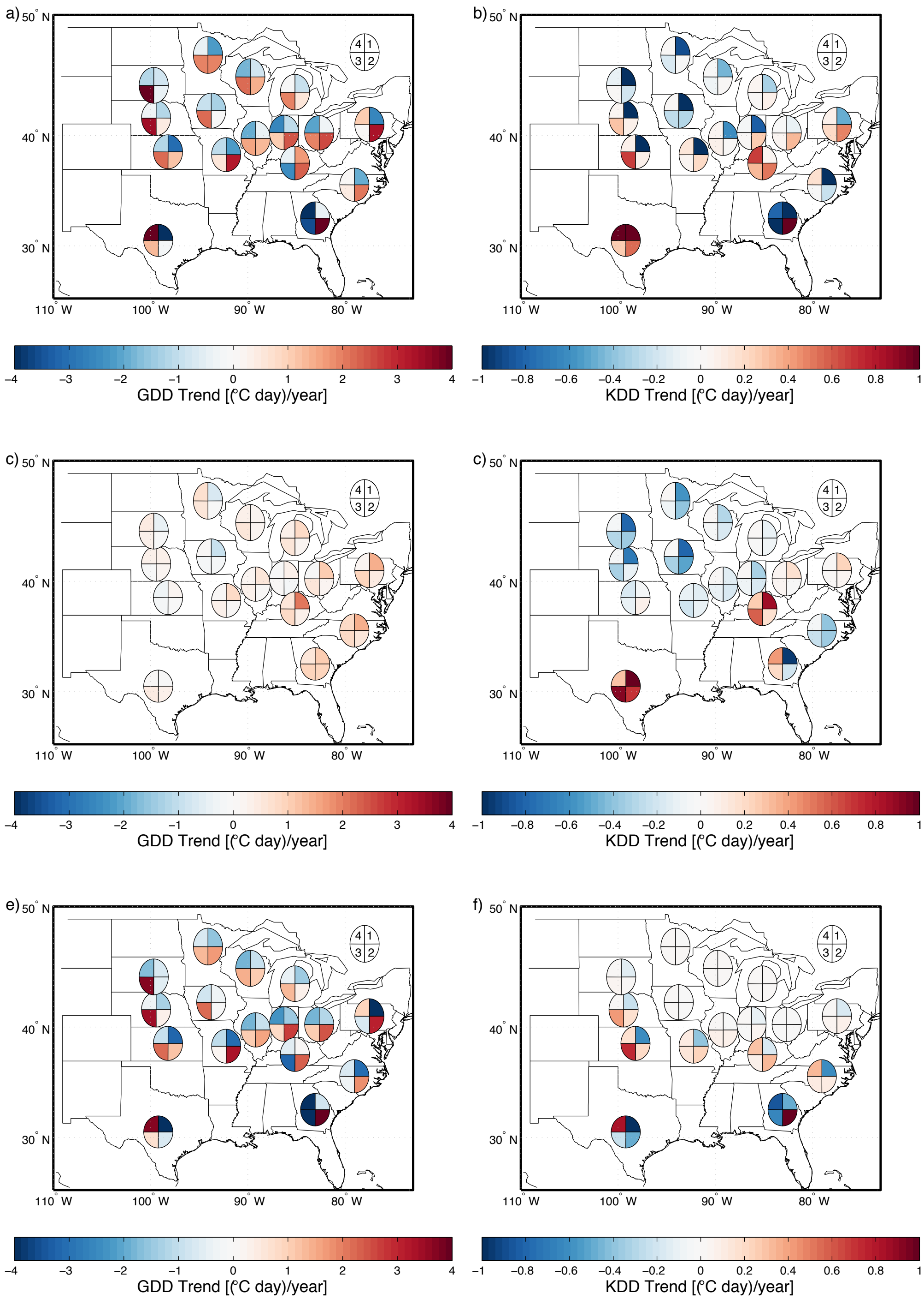


Figure 3.1: (Continued) Trends in GDD and KDD

The time trends for both GDD and KDD are then decomposed into two components, one due to timing and the other to climatic change. The climatic component of the trend is estimated by using fixed planting and development dates for every year, Fig. 3.1c,d. By fixing the development phases but using the historically variable weather the yearly management adjustments are removed and the climatic component of the yield trend is isolated. The fixed phases may be expressed as P_{p,d_0}, where the d_0 index indicates that counting begins and progresses according to the same days every year. The weather experienced still varies according to its historical values, only the developmental progress of the crop is fixed across years.

The timing trend is calculated with the historically variable development phases, $P_{p,d}$, identical to the original calculation, but with a fixed seasonal climate to calculate daily GDD and KDD, Fig. 3.1e,f. The fixed seasonal climate is estimated for each county by fitting the observed time-series of minimum and maximum temperatures separately with a two-term fourier model. This climatology is then used to estimate GDD_p and KDD_p for each development phase. By fixing the background climate but allowing the developmental phases to vary as they have historically this trend is soley a result of the management decisions to shift planting times and cultivar types.

By combining the time trends of GDD and KDD within each phase and their respective sensitivities we can estimate their compound effect on the yield trend according to the following:

$$\Delta Y_i^{GK} = \sum_{p=1}^{4} \Delta \mathrm{GDD}_{i,p}\beta_{2,i,p} + \Delta \mathrm{KDD}_{i,p}\beta_{3,i,p}. \tag{3.3}$$

Where ΔY_i^{GK} indicates the yield trend in state, i, resulting from the interannual yield sensitivity to GDD and KDD, $\beta_{2,i,p}$ and $\beta_{3,i,p}$, from eqn. 3.1, during each phase, p, and the corresponding trends of growing degree days, $\Delta\mathrm{GDD}_{i,p}$, and killing degree days,

$\Delta\text{KDD}_{i,p}$. The ΔY_i^{GK} trends are calculated for the three distinct estimates of GDD and KDD. First, a total climate trend that does not distinguish between the contributions of climatic change and timing. Then the GDD and KDD trends are decomposed into these two components, as described above. In both the management and the climatic trend assessments the GDD and KDD sensitivity parameters are maintained from eqn. 3.1, as calculating sensitivities with fixed development has been shown to produce unphysical estimates[20]. Bootstrap confidence intervals were constructed to assess the uncertainty on each of the yield trend models from 1000 samples incorporating the uncertainty in both the trend estimates and the sensitivity parameters. In all cases the same years were sampled for both GDD and KDD trends to preserve temporal correlation between these quantities. When assessing the uncertainty of other quantities bootstrap samples are always taken across years, such that all 16 states are always present in an estimate.

3.4 Results

The GDD trends across growing phases indicate substantial variation across the season, Fig. 3.1a. The middle of the season generally has more GDDs, but 15 states see a trend towards fewer GDDs during the vegetative and 13 during the drydown phases. These are typically the least sensitive phases to GDDs influence on yields. The more sensitive grain filling phases see a substantial increase in GDDs, only five states see any decrease between these phases and no state has a decrease in both. Median estimates indicate decreases of -1.1 and -1.0 °C day yr^{-1} (95% c.i. -1.9 to -0.8 and -1.5 to -0.4) in both the vegetative and drydown phases, while early and late grain filling have both increased by 1.7 °C day yr^{-1} (95% c.i. 1.1 to 2.2 and 1.0 to 2.2). This is a substantial change in the structure of heat units experienced over the growing season, and it is striking that

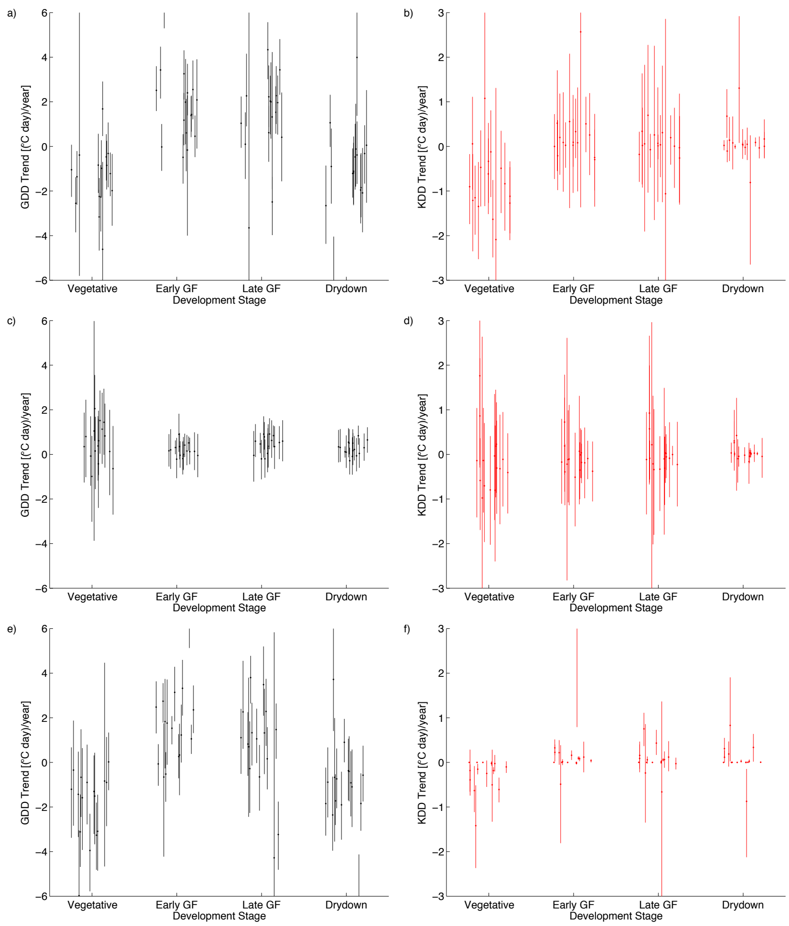


Figure 3.2: Uncertainty in GDD and KDD trends The best estimate of each state's trend is indicated by a solid point and the vertical lines are 95% bootstrapped confidence intervals. For clarity each point has been horizontally jittered and the boundaries of the figure have been truncated, omitting Georgia's early grain filling and drydown trends. **Total Climate Trends** a) The pattern of increasing GDDs during the grain filling phases and declining GDDs during the vegetative and drydown phase is clear for most states even with the considerable uncertainty of many trends. b) The KDD trends are more uncertain, but there is a clear cooling signal during the vegetative phase. **Climatic Change Trends** c) The uncertainty on the climatic GDD trends indicate that nearly all are indistinguishable from zero. d) The KDD trends are similarly uncertain and structureless. **Timing Trends** e) The structure of the timing GDD trends mirrors that of the total GDD trend, though the pattern of increase in the middle of the season and decrease during the vegetative and drydown phases is even more distinct. f) The uncertainty on many of the timing KDD trends is negligible because northern states experience so few in their climatologies.

GDDs have been concentrated where they are most beneficial to yield and decreased where they are the least.

In general KDD trends are much weaker than GDD trends, Fig. 3.1b, and quite uncertain, Fig. 3.2b. The KDD trends are dominated by the tendency towards a cooler vegetative phase, when median KDDs have decreased by -0.9 °C day yr^{-1} (95% c.i. -1.2 to -0.5), when the plants are less sensitive to KDDs. Many states do see a modest increase in KDDs during the highly sensitive early grain filling stage, with a median increase of 0.1 °C day yr^{-1} (95% c.i. -0.1 to 0.4). This suggests that uniformly shifting planting dates earlier may have limited utility if this sensitive phase is pulled into a warmer portion of the seasonal cycle, which is tested below when the timing trend is analyzed. Texas and Kentucky are the only states to see a uniform increase in KDDs across all of their growing phases, though Kentucky's vegetative trend is nearly zero. Perhaps most striking are those fortunate states in the Western Corn Belt which have increased their GDDs, particularly during the critical late grain filling stage while also experiencing a decline in KDDs.

That management had a substantial influence on the trends of GDD and KDD can be seen by examining trends in planting dates, Fig. 3.3a. The first day of planting has moved earlier by a median estimate of -0.26 days yr^{-1} (95% c.i. -0.35 to -0.18), amounting to over 9 days earlier over the 34 year course of the record. At the other end of the season, the decrease in GDDs during the drydown phase is likely a result of the increasingly early final day of harvest, Fig. 3.3b. The median final day of the drydown phase - corresponding with the last harvest - has moved earlier, changing by -0.25 days yr^{-1} (95% c.i. -0.47 to -0.15). In contrast, the increase in GDDs in the middle of the season is likely a result of selecting longer maturing cultivars, as evidenced by the increased duration of the grain filling phases, Fig. 3.3c. The median length of the grain

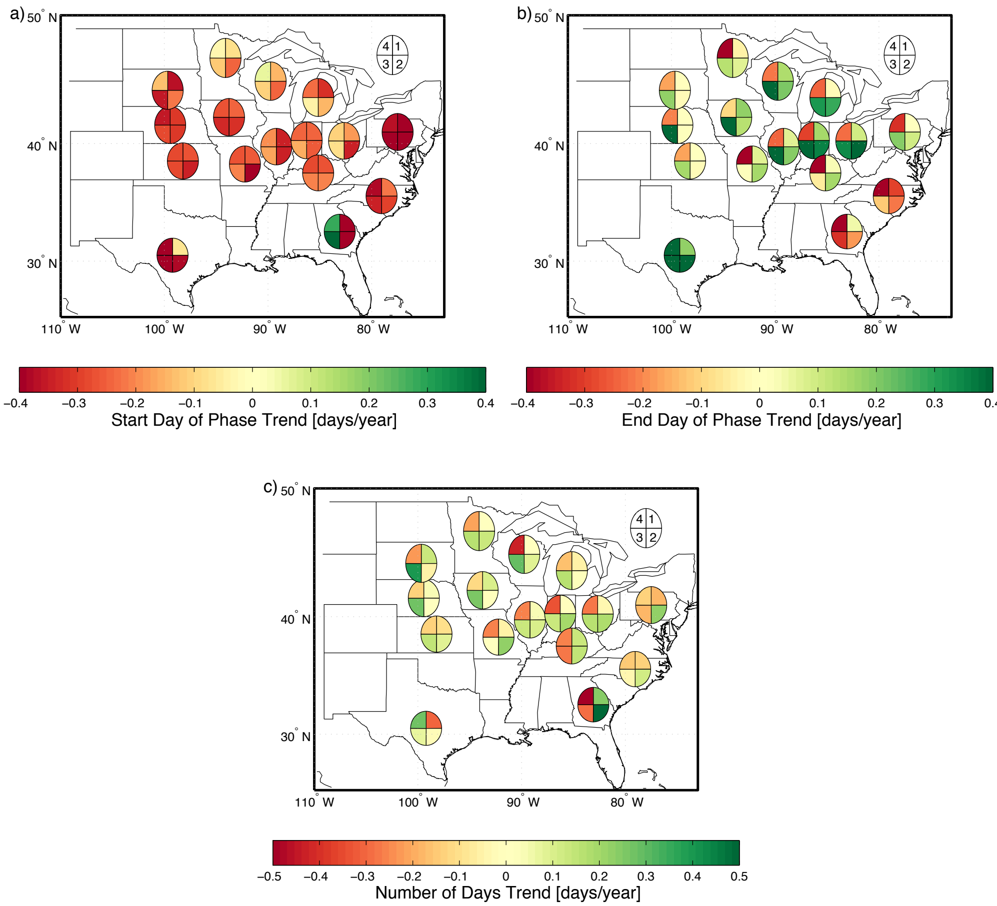


Figure 3.3: Trends in start and end dates and length of development phases a) The start date of each phase has moved earlier in every state other than Georgia and Wisconsin. This is most likely a result of earlier planting shifting the dates of the other development phases. b) The end date trends show more variability, though generally indicate that harvesting comes earlier in all states other than Texas. The middle of the growing season has tended towards later grain filling dates, which when combined with the trend towards earlier start dates indicate more total time spent in grain fill. c) In every state other than Texas the drydown phase has shortened, while the middle of the growing season has lengthened. The shortened drydown phase is a result of earlier harvests while the lengthened middle is likely from longer maturing cultivars and accounts for much of the trend towards more GDDs in this period.

filling phases have increased by 0.11 and 0.14 days yr^{-1} (95% c.i. 0.08 to 0.15 and 0.07 to 0.19) for early and late grain filling respectively. Taken together this lengthening equates to another 9 days spent in these sensitive phases.

The climatic change component of GDD and KDD trends, calculated with fixed development phases are quite different from the total climate trend, Fig. 3.1c,d. Without the trend towards earlier planting and other changes in phase length there are only weak trends towards increased GDDs, particularly in the easternmost states of Pennsylvania, North Carolina and Kentucky, Fig. 3.1c, but most states have negligible trends across all phases, the greatest increase is still during late grain filling with a median increase of 0.5 °C day yr^{-1} (95% c.i. 0.2 to 0.7). The patterns of KDD reduction are similar between the total climate KDD trends and the climatic change KDD trends, but generally weaker. The strongest signal is again the cooling trend during the vegative phase, but this is reduced to -0.2 °C day yr^{-1} (95% c.i. -0.6 to 0.2).

There are several possible mechanisms behind this cooling KDD trend. One possibility, which would still place some control with the farm is the suppression of high temperatures though elevated evapotranspiration rates[7] from expanding and intensifying row crop agriculture. Indeed, this mechanism has been proposed to be responsible for a centennial decline in extreme late summer temperatures[107]. However, there are other possibilities such as increasing precipitation during the late spring and early summer over the eastern US, particularly in the Southeast[122] as well as suggestions that biogenic and anthropogenic aerosols may contribute to cooling in this area[60]. Other hypotheses include land cover change[13] or local changes in circulation[117]. While the climatic KDD trend is fortunate for yields, the myriad potential explanations complicates extrapolating these results into future climates.

The timing contribution of GDD and KDD trends is estimated using a fixed climatology with historically variable development dates, Fig. 3.1e,f. Given the weak contribution to the total GDD trend from the climate change GDD trend it is unsurprising that the timing GDD trends are nearly identical to the total climate trends, the most appreciable difference, expectably, is during late grain filling, with an increase of 1.1 °C day yr^{-1} (95% c.i. 0.5 to 1.7). All other phases are within 0.25 °C day yr^{-1} of the total season trend, with overlapping 95% confidence intervals. In contrast, the northern states have almost entirely negligible KDD trends across all phases. This is unsurprising, in that KDDs overwhelmingly occur in the North through weather events, whereas southern crops experience them climatologically, and correspondingly these crops have been adapted to such circumstances[18,20].

The yield benefits of the trend towards earlier planting have been noted[76], but here we are able to distinguish the relative benefits of the whole suite of management adjustments. According to the total climate yield trend the greatest yield benefit has been from the elongation of late grain filling, amounting to a mean increase of 10 kg ha^{-1} yr^{-1} (95% c.i. 7.2 to 13), and the greatest drag has been from increasing KDDs during early grain filling with mean losses of -5.3 kg ha^{-1} yr^{-1} (95% c.i. -12 to 1.4). These are followed by increases in GDDs during early grain filling with a mean increase of 8.7 kg ha^{-1} yr^{-1} (95% c.i. 6.0 to 12), but surprisingly the penultimate source of loss is cooling during drydown, indicating mean losses of -4.9 kg ha^{-1} yr^{-1} (95% c.i. -7.4 to -2.3).

Breaking down the total climate yield trend in terms of its constituent components of timing and climate change suggests even more precise sources of these yield trends. That this decomposition accounts for nearly all of the total climatic effect is indicated by the close correspondence of the yield trends calculated for each state through the total climatic trend and that obtained by summing the two components. The values are nearly identical with a Pearson's correlation coefficient of 0.96, and a relationship just

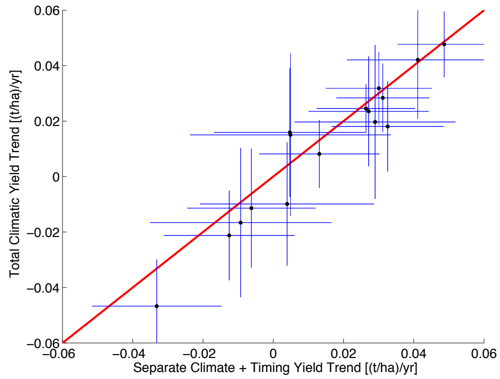


Figure 3.4: The total climate yield trend and its components of climatic change and timing. The best estimate of the total climate yield trend and the sum of the climatic change and timing components is indicated by the black dot. Blue crosses represent 1 standard deviation uncertainties on these estimates and the red line is a one-to-one line for reference. The close correspondence between these estimates suggests that nearly all of the total climate trend is contained in these two components.

shy of one to one, Fig. 3.4, with a york fit slope of 1.1 (95% c.i. 0.9 to 1.4). The model suggests that several states have experienced a substantial increase in yields as a result of both favorable climatic change and adjustments of the cropping calendar and cultivar type, Fig. 3.5. Five states have combined increases from timing and climatic change that account for over 40% their total temporal yield trend, Minnesota, Missouri, Nebraska, North Carolina, and Pennsylvania, and the majority of this increase is from the timing trend. Surprisingly, several states, including some substantial maize producers in the Corn Belt: Illinois, Indiana and Ohio, indicate a negative yield effect from their timing adjustments, as do Georgia, Kentucky, and Texas.

The primary source of this negative yield impact from timing changes, particularly in the Corn Belt states is a shorter drydown phase with a consequent decline in GDDs, Fig. 3.5b. These states have a much greater GDD sensitivity during this phase, with a mean sensitivity of 7.6 (kg/ha)/(°C day) (95% c.i. 7.1 to 8.0) compared to the remaining

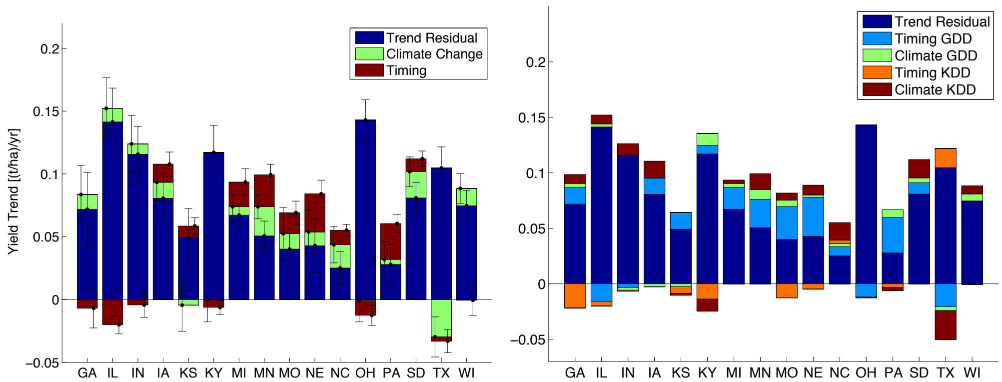


Figure 3.5: The components of the total temporal yield trend The sum of all components of the bar graph is the observed yield trend from 1981-2014. a) The whiskers indicate 1 standard deviation uncertainties on each component of the estimate. While the technological residual is substantial for many states, several, such as Minnesota, Nebraska and Pennsylvania have significantly benefited from timing trends. b) The yield trends due to timing and climate may be further broken down into GDD and KDD components. The greatest distinguishable component of the yield trend is the increased GDDs from changes in developmental timing and the greatest drag is an increase in KDDs, much of which is also due to timing trends. Note that several states have a negative effect from timing GDDs, which results from a shorter drydown phase in every state other than Texas.

states with a mean of 4.4 (kg/ha)/(°C day) (95% c.i. 3.9 to 4.9). The source of these anomalous coefficient estimates is unclear and as such the negative impact of the variable development estimate should be interpreted conservatively. In fact, if the drydown phase is omitted, and the sensitivities and trends are recalculated, the Corn Belt states no longer indicate a negative impact from timing trends, Fig. 3.6. Indeed in the three phase model, every state other than Georgia, which has anomalously large trends towards a longer and hotter early grain filling, indicate a benefit from the timing trends. Texas is the only state which suffers from significant climatic change trends, while Kansas, Kentucky and Ohio indicate a marginal negative effect. Under the three phase model Minnesota, Missouri, Nebraska, South Dakota and Wisconsin all indicate that greater than 50% of their total temporal yield trend is a result of timing and climatic trends.

In Wisconsin, greater than 50% of the total temporal yield trend results exclusively from the timing trend. In aggregate, the three phase model indicates that 20% of the mean total temporal trend is a result of management adjustments while only 8% is from climatic change. Together, these results suggest that farmers' adaptations to their historical climate have had a far greater influence on yields than the modest and surprisingly beneficial climatic change experienced to date.

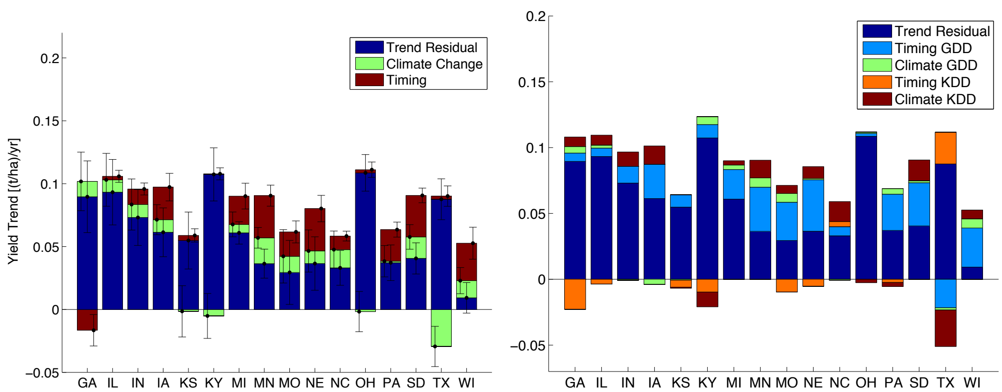


Figure 3.6: Three phase model: components of the total temporal yield trend Similar to figure 3.5 but using a three phase model which omits the drydown phase. a) Without the drydown phase only Georgia indicates a decline in yield as a result of timing trends and Texas is the only state with a significant decline in yields due to climate change. Note that Kentucky, Ohio and Kansas do indicate modest declines. b) The yield decline in Georgia is due almost entirely to the increase in KDDs during early grain filling. Illinois, Kansas, Kentucky, Missouri, Nebraska and Pennsylvania show modest declines from timing KDDs but these are offset by timing trend increases in GDD.

The two primary management shifts that appear to have influenced thermal time yield trends are the trend towards earlier planting and longer grain filling. By shifting cultivation earlier in the calendar year farmers have altered the portion of the seasonal cycle sampled by the crop at each subsequent phase of development, and on the whole this sampling has benefited yields. The timing trends have generally benefitted yields through increasing exposure to GDDs, but simulataneously KDD exposure has increased. This trade-off is one of the limits on the yield benefits from a continued shift towards earlier planting, which will also be hampered by shortening daylength earlier in the year[5]. However, the historial evidence appears to indicate that we have not yet reached the point that earlier planting generally negatively affects yields. Similarly, the longer maturing varieties will only continue to improve yields so long as the warmer conditions necessary for their maturation don't also bring substantial increases in damaging temperatures.

3.5 Discussion and Conclusions

Agricultural regions of the Eastern US have steadily adjusted their development schedules since record keeping began with dominant trends towards earlier planting and longer grain filling. For the most part this appears to be driven by improvements in agricultural management and technology and not a result of climate change. These agronomic adjustments are a substantial fraction of the total temporal yield trend across a number of highly productive states. This highlights how substantially farmers have adjusted their development schedules to the historical seasonal cycle, and provides some insight into potential and limitations on adaptations to a hotter climate. Perhaps surprisingly, the climatic change trends across the corn belt have also been a boon to yields, though substantially less than might have been estimated if the agronomic component had not been separated.

Perhaps most importantly these results highlight that predicting how climate change will affect crop yields is likely to be considerably more nuanced than had previously been estimated. In particular, the limits to adjustments by management[75,76] as well as the interaction between seasonal climate variability and change[151,42] will need to be taken into account when developing more accurate forecasts of crop yields. Trend analyses which do not account for such phenomena risk underestimating the effect of a changing climate on crop yields[85,84]. The historical adjustments illustrated here indicate how both crop development and management substantially moderate the effect that weather has on yield. In particular, the timing of the silking and early grain filling window in relation to the seasonal cycle is likely to be at least as important as global warming until the anthropogenic signal is substantially stronger over the Eastern US. This work suggests that continuing to evaluate changes in the seasonal cycle along with crop development will be an important component of adjusting maize agriculture to a hotter world.

Taken together these results further emphasize that details matter when considering the long term interaction of crops and climate. Much of the agriculturally relevant temperature trend is the result of actions that farm managers have collectively undertaken and the resulting adjustments of the growing season. The timing of these shifts has not occurred by accident, though there may still be room for improvement. Furthermore, the structure of the temperature trends within the phenological cycle of the crop supports the substantial role that human agency has played in improving yields through adapting to the historical climatology. Given that the climatic trend has been largely benevolent over the region considered here it would be highly instructive to conduct a similar analysis over a region which has experienced a greater magnitude of anthropogenic global warming.

Reducing yield losses from a warmer environment is a critical component of adapting humankind to life on a hotter planet and this work shows how farmers have already adapted their planting schedules to improve yields in accord with the physiological sensitivity of their crops. The statistical model applied here may prove useful in facilitating future adaptations by bridging the understanding of the simpler models which operate at broader scales and the complexity of field scale studies.

3.6 Iowa Case Study

To indicate how substantially development dates may shift exposure to the seasonal cycle, the phases of Iowa and the climatology from Story County are displayed in Fig. 3.7. These figures indicate the careful balance between early planting leading to a long warm late grain filling period and an early grain filling period falling during a particularly hot portion of the season. This is evident in Fig. 3.7b which shows the development cycles for the earliest and latest planting dates in Iowa. The earliest recorded planting came in 2012 and this aligned the most sensitive portion of the development cycle with the warmest period in the climatology. After the crop was damaged by this exposure the long warm grain filling period was of little benefit.

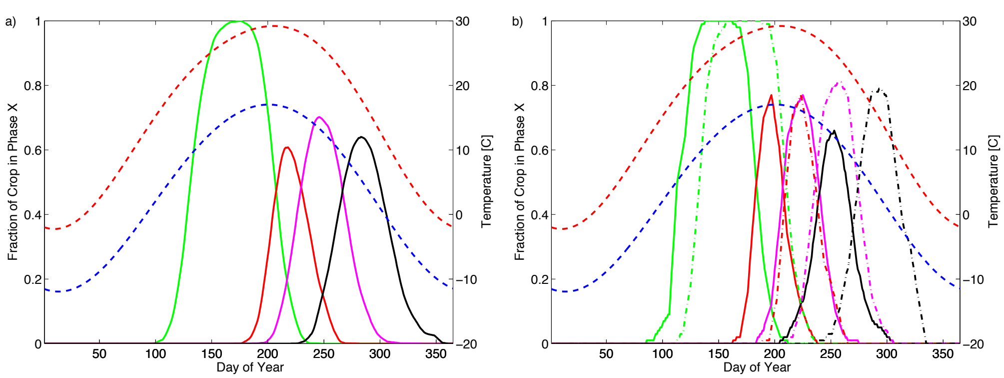


Figure 3.7: Iowa development and climatology The development data are presented as the fraction of the state in each phase of development, according to the y-axis on the left side. The color of each development phase is as follows: vegetative, green; early grain filling, red; late grain filling, magenta; drydown, black. Similarly the dashed lines correspond to the climatology in Story County, IA with red the maximum temperature and blue the minimum temperature, and represented by the right side y-axis. a) The average development and climatology in IA and Story County. b) The earliest planting dates (solid: March 26th, 2012) and the latest planting dates (dot-dashed: April 21, 2008). Note how the 2012 planting lined up the sensitive early grain filling phase with the peak of the climatology, contributing to substantially lower yields.

4

Modeling yield loss during historic heat waves

4.1 Abstract

Hot temperatures are known to negatively affect maize yield, an effect that has been described using simple linear statistical models depending on the sum of cumulative

temperatures above specified thresholds. Here we compare the performance of a suite of such statistical models in the context of US maize yield from 1981-2014 with a focus on describing the response during the heatwaves of 1983, 1988, and 2012. Models employing a uniform temperature sensitivity across the growing season or across large spatial domains generally underestimate yield loss from these heatwaves, particularly 2012. Using cumulative vapor pressure deficit as an alternative environmental metric does not reduce these model-data differences. Differences are reconciled, however, when higher spatial and temporal data are applied used in a model with variable temperature sensitivity across growth phases. These results suggest that temporally and spatially resolved statistical models are important for accurate representation of the consequences of heat waves.

4.2 Introduction

It is well established that maize yield is highly correlated with temperature variability, particularly hot temperatures[110,24,140]. This relationship is often represented in simple statistical models with a fixed yield sensitivity to cumulative temperatures above a certain threshold[140,85,18]. Other studies, however, have highlighted how sensitivity varies over the course of the growing season[115,116,10,138,20], with the transition from the vegetative developmental phase into the reproductive phase generally indicated as the most sensitive interval. Variations in sensitivity across space have also been identified[130,127,18,20], where cultivar selection and management practices in climatologically hotter regions evidently confer lower sensitivity to high temperatues.

Simple statistical models have also employed a range of explanatory variables to indicate yield losses. Many studies have measured damaging environmental condtions with the cumulative sum of temperatues above a threshold[110,24,140,85,116,18], whereas others have used vapor pressure deficit as a predictor of the negative effects of temperature and drought on crops[88,83]. Vapor pressure deficit accounts for both changes in absolute humidity and temperature, and, therefore, is potentially a more complete indicator of stress. Other changing environmental factors implicated in yield losses include ozone exposure[81,155], which may also interact with elevated temperatures. Here we focus on cumulative temperature sums and vapor pressure deficit as predictors of yield loss.

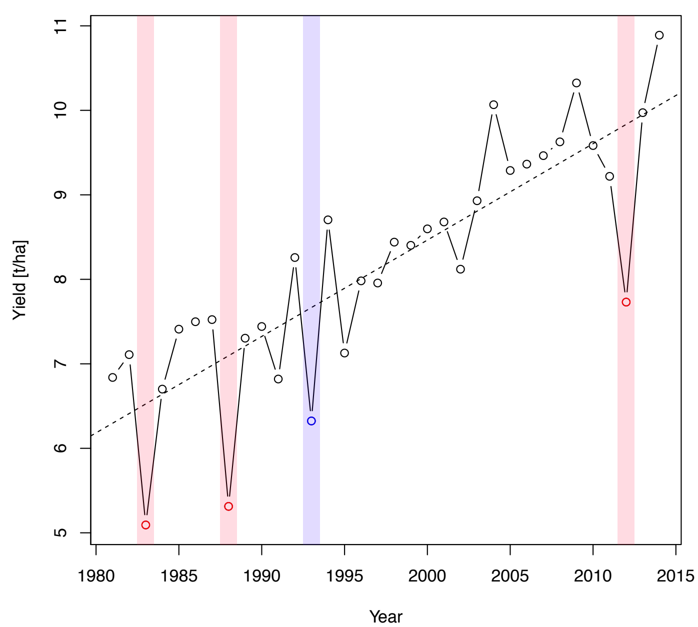


Figure 4.1: Mean US Maize Yield. Each black circle indicates mean US yields for a given year. The red highlighted points are the three years highlighted in the text with substantial losses from heat while the blue highlighted point suffered substantial yield losses from flooding. The dashed line indicates the linear fit between yield and time, which is a result of agronomic and cultivar improvements and adjustments in planting and development timing which have modulated the temperature experienced by the crop.

The recent record of average US maize yield (fig. 4.1) indicates four years of exceptional loss. Yield losses in 1983, 1988, 1993, and 2012 were respectively 22%, 25%, 18%, and 21% below the expected trend between 1981-2014. Note that these percentages are effectively lower bounds because counties not reporting any harvest do not figure into the averages. Of these four years, all but 1993 coincide with exceptionally high temperatures across the US corn belt, extending from Nebraska in the West to Ohio in the East. The yield losses in 1993 were a result of extreme flooding[64] and are not further considered, except to note that changes in precipitation may also be expected[68,114,113].

Here we study the yield response during 1983, 1988, and 2012 using a range of statistical models variously representing spatial and temporal variations in yield sensitivty, as well as various representations of environmental stress, in order to determine which representations are most adequate for describing yield outcomes during these extreme years.

4.3 Data and Methods

The most basic distinction incorporated into all representations that we consider is between mild beneficial temperatures and high damaging temperatures. Temperature data are from United States Historical Climatology Network (USHCN) weather stations in the Global Historical Climatology Network[101] from 1981–2014. Interpolation is to the county level through a Delaunay Triangulation[12]. Counties with greater than 10% of their harvested area irrigated according to the four 1997-2012 censuses of agriculture are removed from the analysis as they are known to be significantly less sensitive to temperature[18], which eliminates Colorado and reduces the states analyzed to 16 and the total counties to 1187.

Heat unit metrics are used to predict yield, with a procedure identical to chapter

2. Mild, beneficial temperatures are quantified using growing degree days (GDDs), a common metric for tracking crop development. GDDs are calculated as the sum over a selected interval of days of daily heat units, $\mathrm{GDD_d}$, which are defined in accordance with[1],

$$\mathrm{GDD}_d = \frac{T^*_{\mathrm{min,d}} + T^*_{\mathrm{max,d}}}{2} - T_{\mathrm{low}}, \tag{4.1}$$

where

$$T^*_{\mathrm{max,d}} = \begin{cases} T_{\mathrm{max,d}} & \text{if} \quad T_{\mathrm{low}} < T_{\mathrm{max,d}} < T_{\mathrm{high}}, \\ T_{\mathrm{low}} & \text{if} \quad T_{\mathrm{max,d}} \leq T_{\mathrm{low}}, \\ T_{\mathrm{high}} & \text{if} \quad T_{\mathrm{max,d}} \geq T_{\mathrm{high}}. \end{cases} \tag{4.2}$$

$T^*_{\mathrm{min,d}}$ is defined with equivalent thresholds to $T^*_{\mathrm{max,d}}$. T_{low} is set to 9°C and T_{high} to 29°C, close to traditional values for GDDs[1]. GDDs are interpreted as increasing yield through benefiting the successful development of longer maturing cultivars.

Damaging heat units are quantified as killing degree days (KDD) in a manner similar to that of GDDs,

$$\mathrm{KDD}_d = \begin{cases} T_{\mathrm{max}} - T_{\mathrm{high}}, & \text{if} \;\; T_{\mathrm{max}} > T_{\mathrm{high}}, \\ 0, & \text{if} \;\; T_{\mathrm{max}} \leq T_{\mathrm{high}}. \end{cases} \tag{4.3}$$

The use of a T_{high} value of 29°C accounts for temperatures above an optimal threshold, as well as for the possibility of damage through desiccation or accelerated development. This value is also close to a number of previous statistical studies describing the effect of elevated temperatures on yield which used values ranging between 29–32°C.[24,140,85,18,65].

the USDA/NASS has development data that allows for constraining differential sensitivity across the growing season. There are data available to distinguish six stages of crop development which are aggregated into the following four phases: vegetative, early grain filling, late grain filling, and drydown. The procedure is identical to that in chapters 2 and 3. The developmental data are available from 1981-2014 for all 16 states in the study except for Texas (1985-2014) and Georgia (1981-1999). The data are reported as percentages of total acreage having attained a particular stage of development and the reports are issued on a weekly basis. The weekly data are converted to fractions and interpolated to daily values, $C_{s,d}$, which indicate the cumulative fraction of crop in a given stage, s, on day, d. If the data do not extend to 0 or 1, they are linearly extrapolated to these end values in adjacent weeks. The cumulative distributions of each development stage are converted into instantaneous daily fractions of the intervening phase by subtracting the total fraction of acreage in the following stage of development, $P_{p,d} = (C_{s,d} - C_{s+1,d})$. $P_{p,d}$ is the fraction of the planted area in each state within each phase, p.

The state level data are complemented by high resolution development and yield data in Iowa, which are available between 1994-2012. The state is divided into nine agricultural districts for which eight stages of crop development are distinguished: planting, emerged, tasseling, silking, milking, doughing, dented, mature. State level harvested data indicate the end of the growing season. The nine stages are used to determine eight phases of crop development, in a manner analogous with that of the state level data. However, the stages of tasseling and silking require special attention as they occur over similar periods of time. As a result both are cut-off with the milking stage. This results in temperature values being counted twice across this period of time, but this is necessary to distinguish these two periods in the crop's development. Iowa data thus have nine times the spatial resolution and twice the temporal resolution of the more widely available state level data, though their shorter time interval necessarily omits the hot years of 1983 and 1988, restricting the models to the hot year of 2012. The eight phases of crop development are then steadily reduced and combined to produce a range of models.

An alternate or complimentary measure of environmental stress is vapor pressure defecit (VPD). VPD is calculated according to the standard algorithm employed by the Food and Agricultural Organization[51], where saturation vapor pressure is defined,

$$e_s = 0.6108 \left(\exp\left(\frac{17.27 \times T}{T + 237.3} \right) \right). \tag{4.4}$$

with T in Celsius, and e_s in kPa. Daily average vapor pressure, e_a, is then estimated as the simple average of the saturation vapor pressure at the highest and lowest temperatures scaled by the, respective, lowest and highest relative humidities,

$$e_a(T_{avg}) = \left(e_s(T_{max}) \frac{RH_{min}}{100} + e_s(T_{min}) \frac{RH_{max}}{100} \right) /2 \tag{4.5}$$

Although clearly only approximate, this representation has the advantage of only requiring daily minima and maxima. Vapor pressure deficit is then calculated as,

$$\mathrm{VPD}(T, RH) = e_s(T_{avg}) - e_a(T_{avg}), \tag{4.6}$$

where $e_s(T_{avg})$ is approximated as $(e_s(T_{max}) + e_s(T_{min}))/2$. A cumulative VPD metric, defined as $\mathrm{cVPD} = \sum_d \mathrm{VPD}_d$, is employed to gauge environmental stress, where the sum is taken over all days of the growing season or relevant development phase.

Alternatively, a metric for VPD whereby the relative humidity data are omitted has been used[88] and then VPD is calculated soley as a function of temperature,

$$\mathrm{VPD}(T) = e_s(T_{max}) - e_s(T_{min}). \tag{4.7}$$

This formulation has the advantage of more than doubling the available years and quadrupling the available weather stations.

Weather stations which record humidity from the Weather Bureau Army-Navy (WBAN)[109] network are used to compare the two VPD metrics, with data available between 1984–1997, except in Texas where records begin in 1985. Similar to the USHCN weather stations, WBAN stations are nearest neighbor interpolated in time and to each county in order to calculate VPD. The temperature-only VPD estimate has a cross-correlation with the standard FAO approach of 0.93 when averaged across the 113 WBAN stations within the states of this study. Omitting relative humidity, however, leads to VPD estimates with standard deviations that are over 1.5 times greater than the FAO values, which when applied in a linear model would tend to bias the sensitivity parameters low.

All of the spatial and temporal scales described are combined with the yield metrics into a complete linear model with the following form,

$$Y_{y,c} = \beta_{0,c} + \beta_{1,i} y + \sum_{p=1}^{N} \left(\beta_{2,i,p} \mathrm{GDD}'_{y,c,p} + \beta_{3,i,p} \mathrm{KDD}'_{y,c,p} + \beta_{4,i,p} \mathrm{cVPD}'_{\mathrm{y,c,p}} \right) + \epsilon_{y,c}. \quad (4.8)$$

$Y_{y,c}$ represents the yield in county c and year y expressed in metric tons per hectare (t/ha). The $\beta_{0,c}$ term is a county dependent intercept, whereas other β terms are uniform across each state or agricultural district, i. If the i subscript is omitted, then spatial variation in sensitivity is ignored and the model represents an entire field, usually the Eastern US. The $\beta_{1,i}$ term is a temporal trend to incorporate the range of modifications that have improved yield over this time period. The primes on the $\mathrm{GDD}'_{y,c,p}$, $\mathrm{KDD}'_{y,c,p}$, and $\mathrm{cVPD}'_{y,c,p}$ terms indicate that the mean has been removed. The sensitivity parameters are allowed to vary over each phase, p, from 1 to N. The values for phases may indicate a single whole season, $N = 1$, the four phases available at the state level

$N = 4$, or various subsets of phase for the Iowa data. Similarly, the damage metric is determined by setting $\beta_{3,i,p}$ or $\beta_{4,i,p}$ equal to 0.

The scale over which the model is applied are summarized in fig. 4.2.

4.4 Results

4.4.1 Yield and KDD Distributions and Maps

To determine the level of model complexity needed to produce unbiased estimates during these extreme events we will consider a collection of models which vary the spatial and temporal resolution of their temperature sensitivity. However, before pursuing the details of these models it is useful to examine the adequacy of KDD as a simple linear predictor of yield. That such a simple representation may be sufficient is supported by a close correspondence between the positively skewed distribution of KDD anomalies and negatively skewed distribution of detrended yields, fig. 4.3. The yield generated by the linear models that we confine ourselves to considering will neccessarily produce a distribution that is a linear combination of the predictor variable distributions, making the correspondence in KDD and yield distributions an important indication that the model has the potential to capture extreme losses in yield.

The correspondence between KDDs and yield losses in the three hottest years is reinforced by the spatial pattern of yield loss and elevated temperatures indicated by fig. 4.4. These heat events are generally centered on Iowa and Illinois, and extend further west than east, with 1988 also reaching further north. Spatially, the correlations are quite high between the detrended yield and KDD anomalies with Pearson's correlation coefficients of -0.71, -0.59, and -0.77 for 1983, 1988, and 2012 respectively. The similarity of the spatial patterns coupled with the correspondence of the distributions suggests that

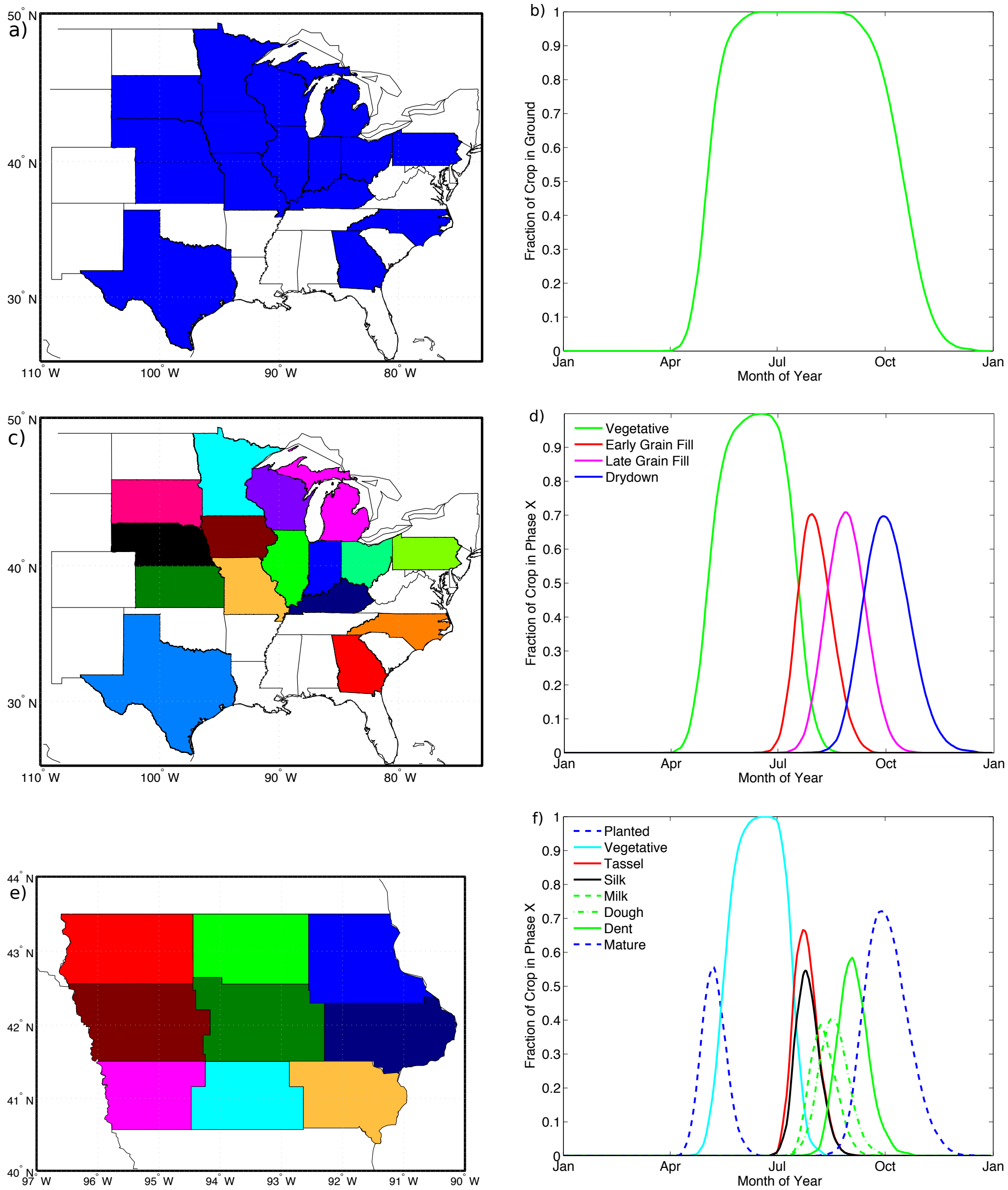


Figure 4.2: Spatial and temporal scales of analysis Identical colors indicate where temperature sensitivity values would be the same a) Fixed temperature sensitivity across space. b) Fixed temperature sensitivity across time. c) State scale spatially variable temperature sensitivity. d) State scale temporally variable sensitivity. e) Agricultural district scale spatially variable sensitivity. f) Agricultural district scale temporally variable sensitivity. Here the blue dashed lines would have differing sensitivity, but both the Planted and Mature phases are not necessary for an adequate model. Similarly the three green phases are the components of the grain filling phase, which provide the least biased estimates when combined into a single phase.

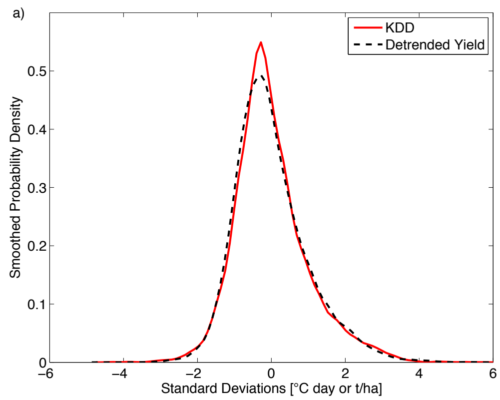


Figure 4.3: Killing degree days and detrended yield. a) The kernel smoothed distributions of detrended yield and KDD indicate the close correspondence between these quantities. Note that in order to highlight this relationship the abcissa has been reversed for the yield distribution, such that low yield years have a positive standard deviation.

KDD over the whole growing season should be an adequate predictor of yield loss.

4.4.2 Varying Temporal Sensitivity

To begin testing the adequacy of models in capturing yield declines during heat waves spatially invariant models are tested first, the i subscripts are omitted in Eq 4.8. The majority of studies[139,140,85] employing regression models with sensitivity to extreme temperature do not allow sensitivity to vary over space and this model is most comparable to those. The simplest such model with KDD as the metric of extreme temperatures also has a fixed temperature sensitivity across time. More formally, $\beta_{4,i,p}$ is set to zero in Eq 4.8 and $N = 1$. A more complicated model allows the temperature sensitivity to vary over time, N= 4, similar to[116,10]. The time varying and invariant models are first compared by grouping all county years together. Then each development phase is divided into subgroups based on the anomaly of KDD experienced. These anomalies are always taken relative to the local mean such that an anomalously hot year in Texas

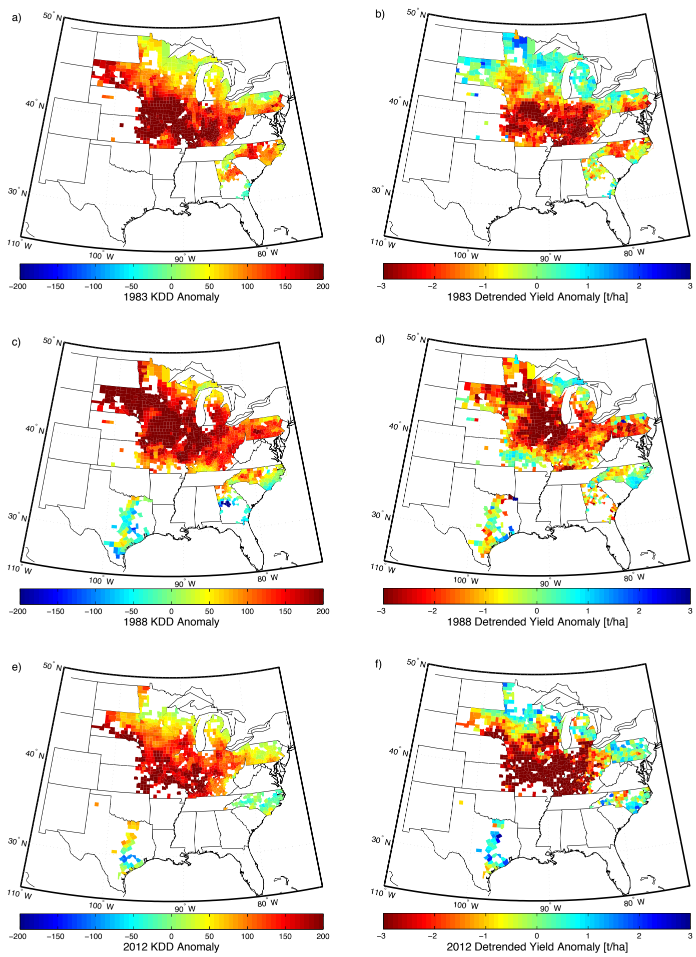


Figure 4.4: Low yielding hot years. a,c,e) Killing degree day (KDD) anomalies, a metric to estimate temperature damaage, corresponding to the years 1983, 1988, and 2012, respectively. b,d,f) Detrended yield anomalies for the same three years. Note how well the spatial pattern of KDD anomalies correlates with the pattern of yield anomalies.

is relatively comparable to a hot year in Minnesota even though the climatologies differ substantially between these regions. The KDD anomalies are divided into percentiles according to the following seven categories, from 0-2.5, 2.5-5, 5-10, 10-90, 90-95, 95-97.5, and 97.5-100, this allows us to focus on those most extreme events in the tails of the KDD distribution, and these categories are dominated by the hot years of 1983, 1988, and 2012.

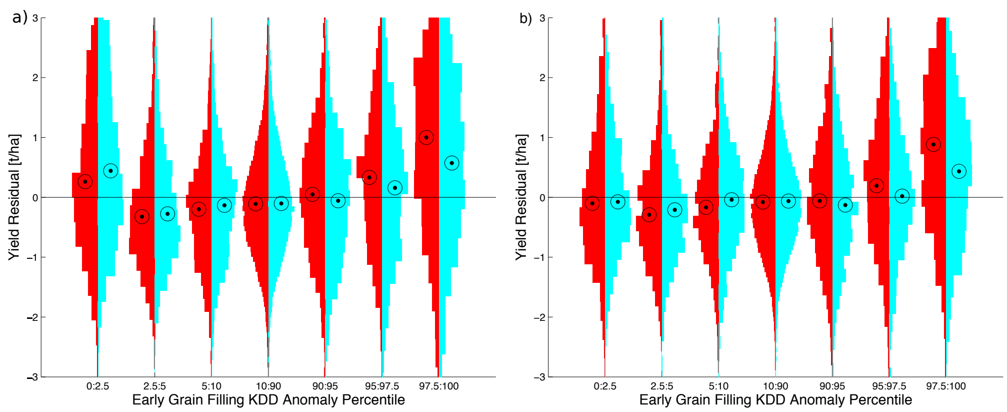


Figure 4.5: Yield residuals for KDD models summarized by Early Grain Filling quantiles. The individual elements of each violin plot are an estimate of yields within a given county and a given year. The histograms in red indicate the fixed sensitivity and in cyan the developmental sensitivity. The bin widths are adaptive and give an approximation of the number of points within each of the percentiles. The total number of points is over 34,000. During the early grain filling phase the hottest 5% of county years indicate substantial bias with the fixed sensitivity model while the stage based model does somewhat better. Positive residuals indicate that the model results have yields that are biased high. a) Whole US model with no spatial variation in sensitivity. b) State model with spatial variation in sensitivity.

The three hottest years account for over 70% of the entire county year group. Of those, 2012 is by far the largest, accounting for 46% of the top category by itself. It should be noted that the fourth largest heat wave in this dataset was in 1996 and while it extended across over $\frac{3}{4}$ as many counties as 1988, it was concentrated in the South and the marginal contribution of Southern states to US yield prevented this heat wave from significantly reducing mean US yield (fig. 4.1). The time varying residuals are directly compared with the whole season residuals in fig. 4.5a, with each model represented by half of the violin plot in each category. Note that both models appear adequate during years of cool and normal early grain filling phases, but that the median estimates diverge substantially in the hottest categories. In the hottest 2.5% of KDD anomalies the fixed whole season sensitivity indicates a median bias across all county years of 1.0 t/ha. The bias is reduced, but not eliminated by the inclusion of time varying sensitivity with the bias of the hottest 2.5% of county years just under 0.6 t/ha.

4.4.3 Varying Spatial Sensitivity

It has been shown that temperature sensitivity varies substantially across large spatial domains[18,20], and given the extent of these heat waves the biased estimates may result from omitting this variation. Formally, the i subscripts are allowed to vary in eqn. 4.8. As with the fixed spatial model, there is a further comparison between a model with temperature sensitivity that varies over time and one that does not. The spatially varying coefficients do not appreciably improve the model fit during the hottest years (fig. 4.5b), with a median bias of 0.9 t/ha. However, the time varying sensitivity reduces the bias to just over 0.4 t/ha. The incorporation of spatial sensitivity did reduce the bias, but not as much as incorporating temporal variation in temperature sensitivity. In relative terms the median observed yields during the hottest 2.5% of KDD anomalies was just under 57% of aggregated median yield during the 1981-2014 period, but the fixed whole season sensitivity would have estimated median yields equal to 72% of the median yield, as opposed to the stage based sensitivity with 65%. This bias is consistent across almost all states though appears particularly pronounced in Illinois, Indiana, and Kentucky which were severely affected by the summer of 2012.

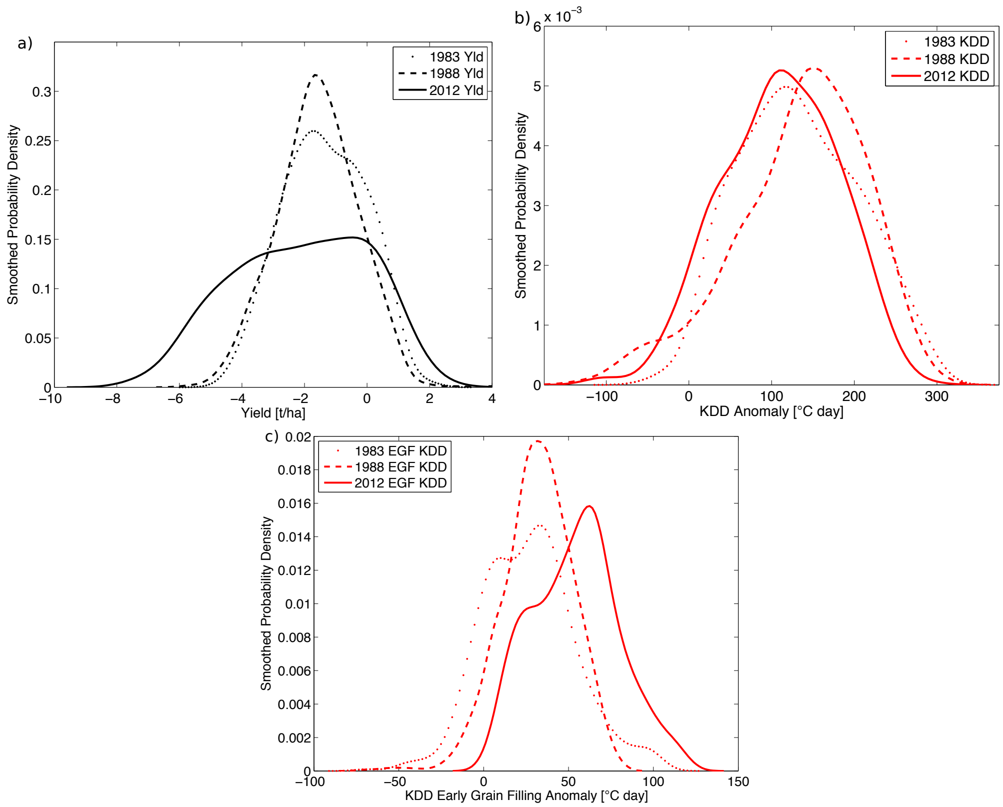


Figure 4.6: Distributions of detrended yields and KDDs during lowest yielding years. a) The detrended yield distributions in 1983, 1988, and 2012. b) The anomaly of KDDs over the entire growing season in the three lowest yield years. Note that 2012 is not substantially different from 1983 b) The distribution of KDDs during early grain filling (EGF). During this sensitive period of development 2012 was substantially hotter than either 1983 or 1988.

To further illustrate the importance of resolving temperature sensitivity over time the KDD anomalies over the entire season are compared with those during the early grain filling phase. The 1983, 1988, and 2012 heatwave years all contain substantial positive anomalies in KDDs, though the year with the largest decline in yields, 2012, is not obviously the hottest, fig. 4.6. Indeed, 1983 and 2012 are almost indistinguishable when comparing KDDs over the entire season. The real impact of the weather in 2012 is evident when comparing the distributions of KDDs during the most sensitive period of development, early grain filling, fig. 4.6b. While 2012's growing season was not substantially warmer than previous hot years, the elevated temperatures occurred inordinately around early grain filling. Indeed, almost the entire distribution indicates positive anomalies, and the mean of the distribution is just over 2-standard deviations warmer than a typical year. Properly resolving the timing as well as the magnitude of 2012's temperature anomaly is critical to properly estimating it's effect on yields.

4.4.4 Out of Sample Predictions for Hot Years

The previous yield estimates suggest that incorporating temporal variation in temperature sensitivity reduces the bias during the years with exceptionally hot early grain filling. However, these models naturally include more free parameters and a further test is called for. A more stringent test is applied to the four variations of the KDD model to determine the relative importance of spatial and temporal variation in sensitivity by predicting out of sample yields. To do this all available years other than 1983, 1988, and 2012 are used to estimate the coefficients in eqn. 4.8. Then the yields of each county in all three years are predicted as a group and individually, fig. 4.7. For the grouped years the least biased predictions allow sensitivity to vary over space and time with a median bias of 0.23 (95% c.i. 0.19-0.29), though excluding temporal variability is statistically

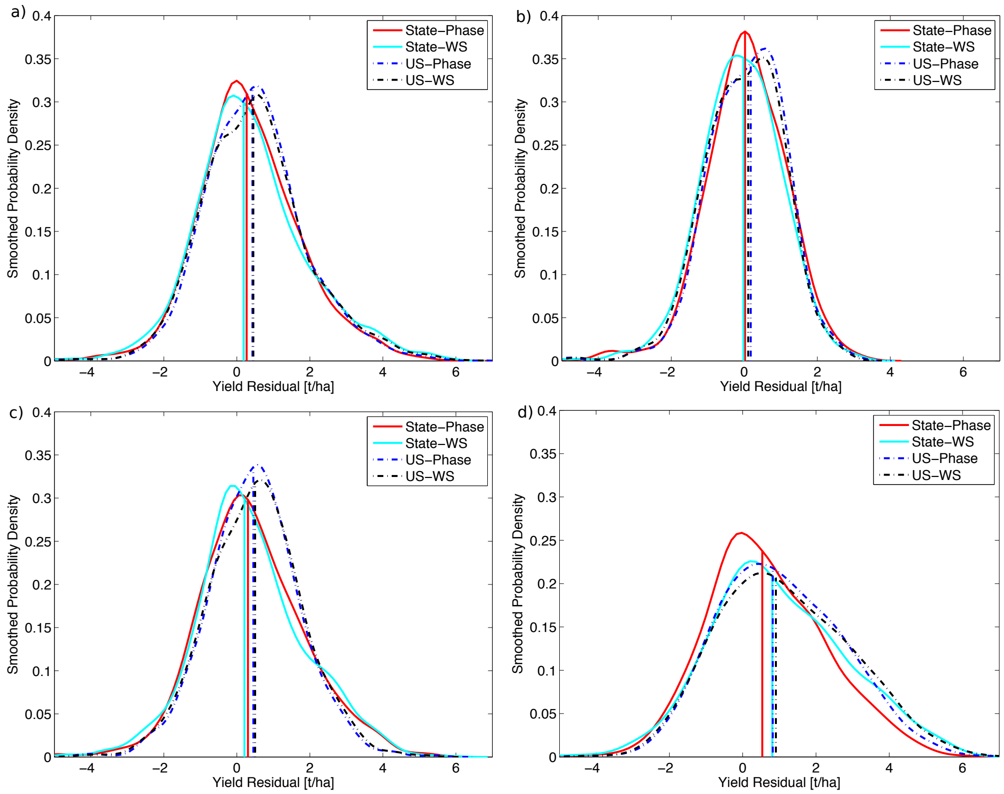


Figure 4.7: Yield distributions from out of sample predictions. Each distribution represents one of the four KDD models with sensitivity parameters inferred from every year other than 1983, 1988, and 2012. a) The distribution of residuals for all three years aggregated together. Vertical lines indicate the median of the distribution b) The distribution of residuals for 1983, note that this year the state level models were relatively unbiased. c) The distribution of residuals for 1988, when the least biased model was the whole season model with spatially varying coefficients. d) The distribution of residuals for 2012, when the model with both spatially and temporally varying coefficients produces the best estimates.

indistinguishable, see table 4.1. The importance of representing varying sensitivity over both space and time is reinforced by the predictions in 2012, which is also the year which generally has the most biased estimates. The least biased prediction is the time and space varying model with a median bias of 0.5 t/ha (95% c.i. 0.4 to 0.6), followed by the model which varies over space but not time. However, for both 1983 and 1988 it is the models which include spatial but no temporal variation in sensitivity that provide the least biased estimates at -0.06 t/ha (95% c.i. -0.15 to 0.02) and 0.26 t/ha (95% c.i. 0.15 to 0.36). In all years the KDD anomalies are spread over a large enough region that the spatial variation in sensitivity plays a significant role in minimizing biased yield predictions, but in 2012 the particular concentration of KDDs during early grain filling indicates the additional importance of capturing the temporally varying sensitivity. These details challenge selecting a single optimal model. Despite this, the spatially and temporally varying model produced the best predictions in 2012 and the aggregated years and was only marginally worse than the purely spatially varying models in 1983 and 1988. This suggests that the incorporation of physiological details is generally worth the additional parameters required to estimate the more complicated model.

4.4.5 High Resolution Iowa Analysis

The failure of the spatially and temporally varying model to eliminate the biased yields in 2012 suggests that more information is needed to adequately capture this heat wave. The higher resolution data available for Iowa permit for a more detailed examination of the role that spatial and temporal scale play in reducing the bias of predicted yield during 2012. For brevity this analysis is restricted to out of sample predictions, and all models are formulated with sensitivities that omit 2012 from the training data. The spatial sensitivity is allowed to vary at the agricultural district level or held fixed

Year	fSfT	vSfT	fSvT	vSvT
1983	0.06 (-0.07-0.14)	-0.06 (-0.14-0.01)	0.14 (0.05-0.22)	0.07 (0.02-0.13)
1988	0.50 (0.43-0.61)	0.26 (0.15-0.36)	0.48 (0.37-0.56)	0.30 (0.21-0.38)
2012	0.95 (0.78-1.1)	0.78 (0.64-0.94)	0.86 (0.74-1.1)	0.49 (0.36-0.62)
All	0.42 (0.36-0.47)	0.24 (0.18-0.30)	0.42 (0.36-0.47)	0.23 (0.19-0.29)

Table 4.1: The median model bias for hot years. The four models are summarized by whether the temperature sensitivity is allowed to vary or is fixed over both space and time. Each four letter model column heading corresponds to one model, fSfT has fixed spatial and fixed temporal sensitivity, vSfT has variable spatial and fixed temporal sensitivity, fSvT has fixed spatial and variable temporal sensitivity, while vSvT has variable spatial and temporal sensitivity. Values are presented in t/ha and the parentheses indicate the 95% boostrapped confidence interval.

across the entire state, equivalent to including or omitting the i subscripts in eqn. 4.8. Similarly, the importance of temporal sensitivity is explored by including up to eight phases of development, i.e. $N \leq 8$. From a full suite of 100 models, 36 were selected for comparative and explanatory purposes and more fully described in table 4.2 and the median biases of each are summarized in fig. 4.8.

Two elements are immediately apparent from this analyis. First, spatial variation in sensitivity fails to improve predictions at the agricultural district level. However, in order to signifcantly reduce the bias the model must contain a highly detailed representation of the tasseling and silking period. Both of these phases, despite occuring over nearly the same time period must be included in the model to reduce the bias to statistical insignificance. Neither the combination of silking and tasseling together, nor either phase included separately eliminates the biased estimate. For example, a model with all eight phases has a bias of 0.31 t/ha (95% c.i. -0.05 to 0.70) while merging the silking and tasseling phases raises this to 0.90 t/ha (95% c.i. 0.69 to 1.23). The least biased model is a four phase model including the vegetative, tasseling, silking, and a

Model	fSfT	R^2	vSfT	R^2	vSvT	R^2	fSvT	R^2
PVTSMODA	1.1 (0.9-1.4)	0.60	1.5 (1.1-1.8)	0.62	1.6 (1.1-2.2)	0.76	0.3 (0.0-0.6)	0.73
PVSMODA	1.0 (0.7-1.2)	0.62	1.2 (0.9-1.5)	0.64	1.7 (1.4-2.0)	0.75	0.8 (0.4-1.1)	0.72
PVTMODA	1.0 (0.7-1.2)	0.62	1.2 (0.9-1.5)	0.64	1.5 (1.1-1.8)	0.79	0.9 (0.5-1.2)	0.71
PVT-SMODA	1.0 (0.7-1.2)	0.62	1.2 (0.9-1.5)	0.64	1.5 (1.0-1.7)	0.73	0.9 (0.5-1.2)	0.71
VTSgf	1.4 (1.2-1.7)	0.58	1.6 (1.2-2.0)	0.60	0.6 (0.1-1.4)	0.72	0.0 (-0.2-0.5)	0.70
VSgf	1.3 (0.9-1.5)	0.59	1.4 (1.1-1.9)	0.61	0.8 (0.5-1.2)	0.73	0.6 (0.4-0.9)	0.68
VTgf	1.3 (0.9-1.5)	0.59	1.4 (1.1-1.9)	0.61	0.6 (0.1-1.1)	0.73	0.6 (0.4-0.9)	0.69
VT-Sgf	1.3 (0.9-1.5)	0.59	1.4 (1.1-1.9)	0.61	0.6 (0.1-0.9)	0.74	0.6 (0.4-0.9)	0.68
VT-Sgf*	1.3 (0.9-1.5)	0.59	1.4 (1.1-1.9)	0.61	0.6 (0.1-0.9)	0.74	-0.0 (-0.4-0.2)	0.67

Table 4.2: The phases included in the model are as follows: Planted (P), Vegetative (V), Tasseling (T), Silking (S), Milking (M), Doughing (O), Dented (D), and Mature (A), where each is defined by the stage that begins it, except for the vegetative phase which is considerably longer than the others and begins with the emerged stage. A dash between phases indicates they have been merged into a single phase and the merged milking, doughing and dented phases are summarized as grain filling (gf). The four models that correspond with each of the included phases are fixed over space and fixed over time (fSfT), variable over space and fixed over time (vSfT), variable over space and variable over time (vSvT), and fixed over space and time (fSvT). The first column indicates the median bias in 2012 with the 95% confidence interval in parentheses, and the R^2 column immediately following is the squared cross correlation of that model against the entire yield record. The final row, marked with a star indicates the model which uses a linear combination of the sensitivity estimates from the TS phases of the VTSgf model for its merged tasseling and silking sensitivity phase based sensitivity. All median estimates are rounded to tenths and R^2 values to hundredths.

single merged grain filling period consisting of the milking, doughing and dented phases, the bias of this model is 0.05 t/ha (95% c.i. -0.20 to 0.52). A subset of phases coupled with an additional degree of freedom around the most sensitive period produces the best predictive coefficient estimates.

Particular attention was paid to the period around tasseling and silking in this analysis as that was around the time that KDDs peaked in 2012. As is clear from table 4.2 and fig. 4.8 the particular representation of this time period is critical to producing

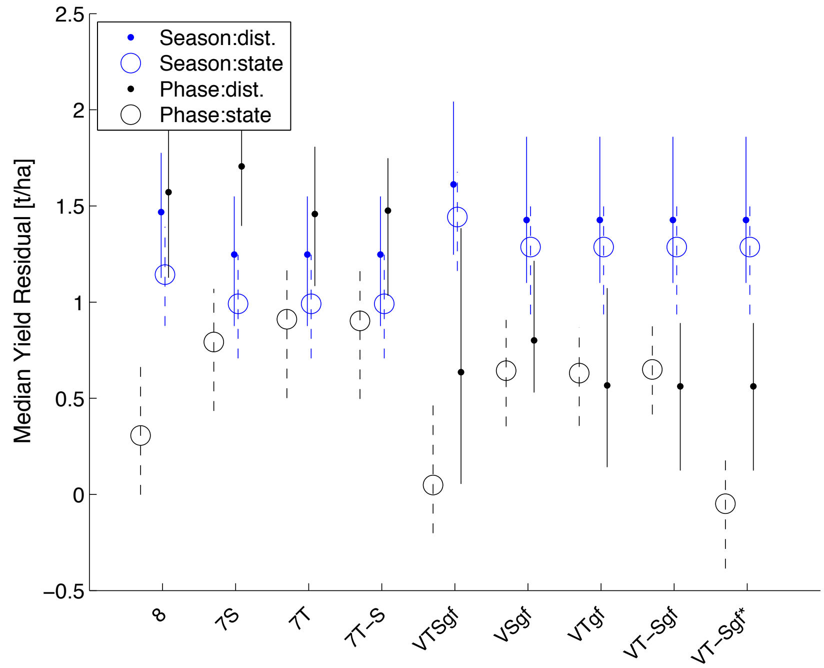


Figure 4.8: Median yield residuals for 2012 in Iowa from 36 different models. The abcissa indicates the number of developmental phases included in each of the models as well as a lettered abreviation to indicate which phases are included in the model. The open circles correspond to the models with a fixed spatial sensitivity over the entire state, and dots indicate spatial variation in sensitivity at the agricultural district level. Similarly, black symbols indicate temporal variation in sensitivity over the growing season while blue symbols indicate a fixed temporal sensitivity over the whole season. Vertical lines indicate the 95% confidence interval on the median estimate from a bootstrap sampling of counties included in the median estimate. The sensitivity parameters to compute the yields in 2012 were calculated from a training data set from 1994-2011.

unbiased estimates of 2012. To further test the appropriateness of the separate tasseling and silking estimates their separate sensitivies were added together and applied to the estimated KDDs during the combined tasseling and silking phase. This combined estimate is nearly as good as the one with distinct phases, with a median bias of -0.05 t/ha (95% c.i. -0.41 to 0.20). Using the KDD sensitivity estimated from the out of sample combined tasseling and silking phase produced a median bias of 0.65 t/ha (95% c.i. 0.43 to 0.87). When the tasseling and silking phases are aggregated or considered alone they miss the increasing disparity between KDDs experienced during tasseling and silking in hotter years which did not occur in 2012, fig. 4.9, despite the fact that tasseling and silking are highly correlated, with a Pearson's correlation coefficient of 0.98. This disconnect is indicated in the KDD sensitivities from the silking, tasseling, and combined tasseling-silking models of -16, -10, and -11 kg/ha (°C day)$^{-1}$ in comparison with the linearly combined KDD sensitivity from the individual tasseling and phases of -28 kg/ha (°C day)$^{-1}$, a factor of two to three greater. Properly resolving the sensitivity during this extremely vulnerable period is critical to making accurate forecasts of future yield losses.

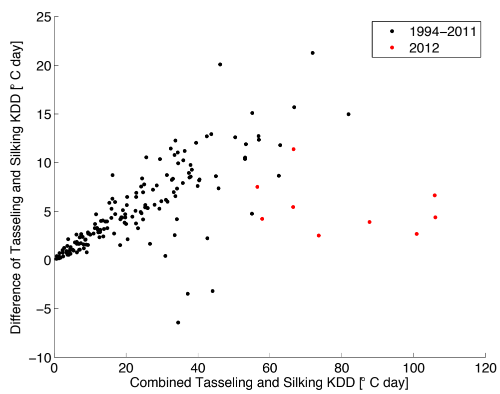


Figure 4.9: Tasseling and silking KDD exposure convergence in Iowa in 2012 Each point indicates an agricultural district for a given year in Iowa. Generally as KDDs increase tasseling and silking diverged, with tasseling experiencing more KDDs. However, in 2012 with record breaking temperatures, both sensitive phases were nearly equally exposed. This convergence illustrates why both phases must be modeled to adequately capture the yield loss in 2012.

4.4.6 Vapor Pressure Deficit as Extreme Temperature Metric

The final model uses cVPD in place of KDD as the predictor of extreme damage by setting $\beta_{3,i,p}$ to zero in eqn. 4.8. However, it should be noted that KDD and cVPD are

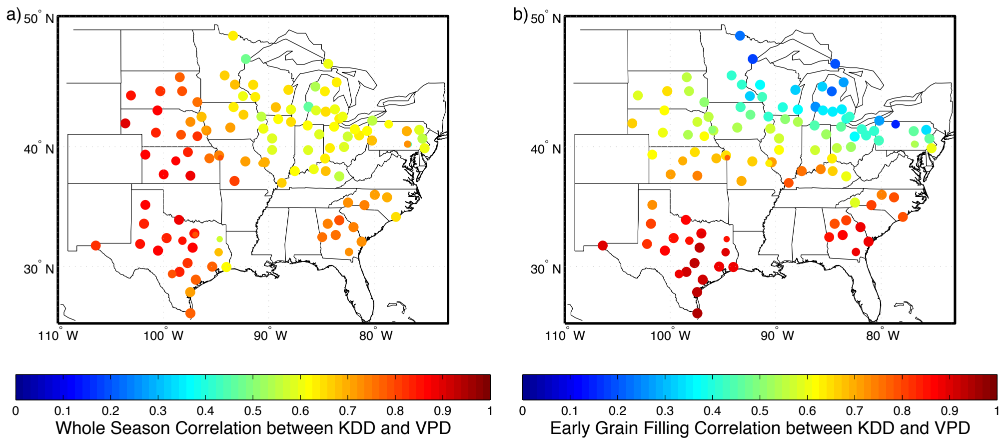


Figure 4.10: Correlation between cVPD and KDD a) The correlations between cVPD and KDD are generally quite high across the entire year. Though they trend from highest in the Southwest to lowest in the far North. b) Generally the correlations are lower during each of the growing phases, but for the critical early grain filling phase they remain relatively high.

highly correlated. Indeed, across the entire year in the western portion of the study region Pearson's correlation coefficients are typically high (r> 0.8), and similarly across the South (r> 0.7), fig. 4.10a. Even across the North the correlations rarely drop below 0.6, indicating that much of the information contained in cVPD is shared with KDD. However, a more nuanced picture appears when the correlations are taken within individual growing phases. While the correlation is even higher in these shorter windows across the South (r> 0.9), the North is generally more poorly correlated (r< 0.5), fig. 4.10b. Despite this, the pattern of sensitivity estimates across the growing season (not shown) is quite similar between KDD and cVPD, and between the high correlations and the similar temporal patterns it is likely that most of the information contained in one is also in the other.

A similar suite of four models are compared for the cVPD estimates as the KDD esimates, identically modifying eqn. 4.8 to vary the sensitivity parameters over both

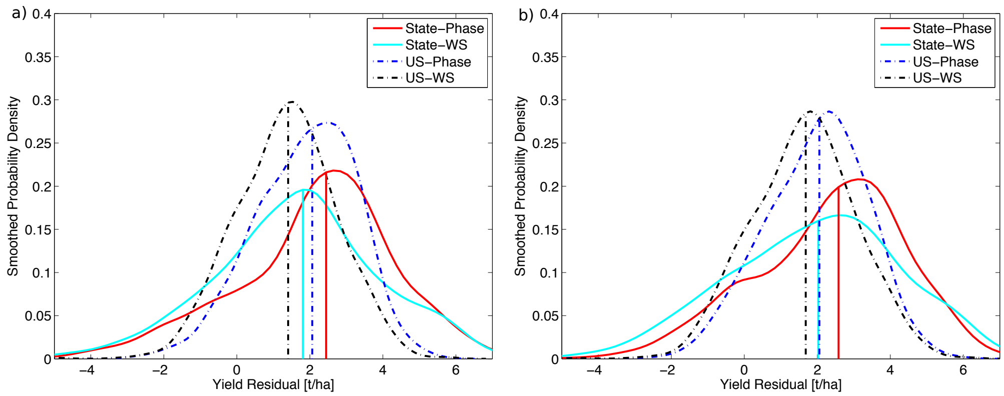


Figure 4.11: Out of sample predictions for 1988 with varied VPD estimates. Both models are significantly biased, and the improvements in resolution do not appear to help. The WBAN stations are significantly sparser than the USHCN stations which may, in part, be responsible for this. a) The full FAO VPD estimate, including relative humidity b) The alternative VPD estimate, which only depends on minimum and maximum temperature.

space and time. First, the two representations of cVPD including and ignoring relative humidity are compared, restricing the analysis to the years with the WBAN data and thus tested only on the year 1988. While the cVPD(T,RH) is marginally less biased than cVPD(T), both still indicate substantial biases for the full suite of models. The least biased models are the models with the fewest parameters, aggregating sensitivity over both space and time, though these still have median biases of 1.4 t/ha (95% c.i. 1.3 to 1.5) and 1.7 t/ha (95% c.i. 1.6 to 1.8), fig. 4.11. Despite a significantly smaller bias, the values are close enough that the full USHCN data are analyzed using the VPD(T) approximation, though it should be noted that a superior fit may be possible with better relative humidity data.

The cVPD developmental model does not improve the fit of the model, and produces inferior out of sample predictions during the hottest years. The same set of four models is compared here, where both spatial and temporal sensitivity is allowed to vary from the whole US and season scale to individual state and developmental phase. All of

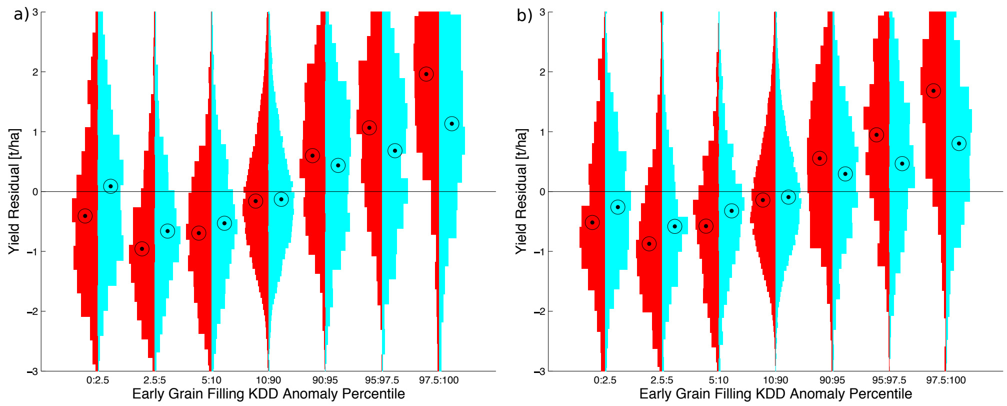


Figure 4.12: Yield residuals for cVPD models summarized by Early Grain Filling quantiles The bias is larger when cVPD is used as the predictor of extreme condtions in place of KDD. The categories are identical to those in fig. 4.5 for a straightforward comparison. a) Whole US model with no spatial variation in sensitivity. b) State model with spatial variation in sensitivity.

the hottest years are substantially biased (Fig. 4.12), and more so than for the KDD model. In fact, the penultimate category of the 95-97.5 percentile is nearly as biased in the cVPD model as the KDD model was in the hottest 97.5-100 percentiles, with a minimum bias of 0.5 t/ha from the phase based model. The hottest county years are as biased as 2.0 t/ha for the fixed spatial and temporal model.

The out of sample estimates for the colllected years of 1983, 1988 and 2012, fig. 4.13, again indicates that the least biased model has both spatially and temporally varying coefficients. However, the least biased model is still significantly worse than the KDD model with a median bias of 1.1 t/ha (95% c.i. 1.0 to 1.2). This holds true in 1983, with a median bias of 0.9 t/ha (95% c.i. of 0.8 to 1.0) as well as 2012 with a bias of 1.2 t/ha (95% c.i. 1.0 to 1.4). In 1988, just as with the KDD model, the least biased model, at 1.2 t/ha (95% c.i. 1.1 to 1.3), has spatially but not temporally varying coefficients - though none of the models stand out from each other as significantly different. It is striking that these results are quite different, and less biased, than the WBAN stations and underlines the importance of the higher resolution USHCN weather stations as well.

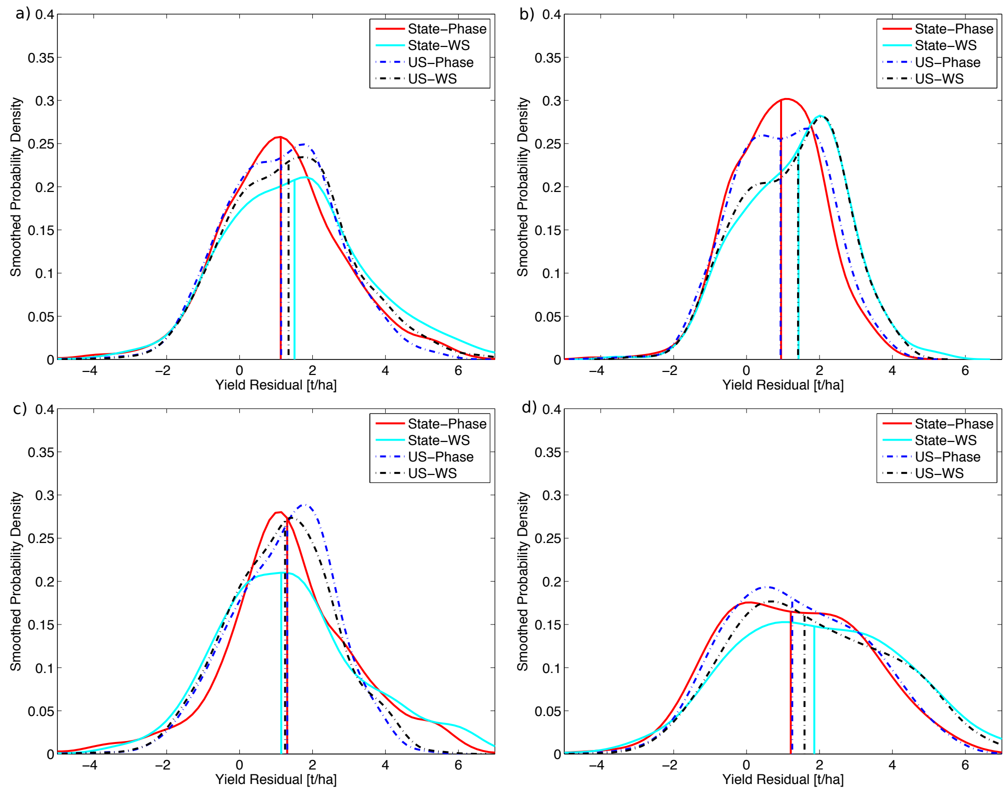


Figure 4.13: Yield distributions from out of sample predictions with VPD model. Each distribution represents one of the four VPD models with sensitivity parameters inferred from every year other than 1983, 1988, and 2012. a) The distribution of residuals for all three years aggregated together. Vertical lines indicate the median of the distribution b) The distribution of residuals for 1983, in the VPD model the lease biased estimates are from the time varying sensitivity models. c) The distribution of residuals for 1988, when the least biased model was again the whole season model with spatially varying coefficients. d) The distribution of residuals for 2012, when the models with temporally varying coefficients were the least biased.

4.5 Discussion and Conclusion

It should be noted that this study is explicity concerned with weather losses to yield. While such extreme weather events may be some indication of expected yield losses in a broadly warmer climate, they are not necessarily an extrapolation to a warmer climate given the range of options available to adapt to slowly varying conditions[2,37,18] that are not available for a single extreme event. However, as such extreme events are also more likely in a warmer future, improving our understanding of limitations in predicting such extreme yield losses is critical to preparing for them. Some modeling work has dismissed the utility of using statistical models to study yield responses to extreme events[144], but this work suggests that with an appropriate physiological representation such scenarios may be reasonably well predicted. This work indicates that improving forecasts of agricultural damage will require the use of higher resolution data as well as a deeper understanding of the mechanisms behind yield loss during sensitive phases of development and complements other recent work which highlights the importance of phenology[161,128], scale[28] and higherto neglected processes of yield loss[154].

The bias exhibited by the least variable models to extreme conditions during the most sensitive phases of maize development highlights the importance of capturing more realistic details of crop physiology in a statistical modeling framework. While this bias may not be directly transferable to average years that are much warmer as we move into an increasingly hot 21st century, the likelihood of getting such extreme years is also expected to increase as indicated by both statistical studies[96,42,97,40] and dynamical models[39,56,77,30]. The attention on extreme events has also highlighted the substantial role that land surface – atmosphere interactions play in generating heat waves and drought[171,53] which will be affected by the health and development state of field crops.

This work has further highlighted the need for a more accurate understanding of how extremes will change under a warming climate given the particular importance of the tail of the temperature distribution during early grain filling to yield impacts. In fact, it has been shown that extremes can change quite differently than the mean[69] and so a simple perturbation of the current climatology for estimating effects from long temporal averages[18,84] may lack important details. It is an improved understanding of these more precise changes in the physical climate system in conjunction with the more detailed response of crops as indicated by the developmental sensitivity that will ultimately serve to improve our forecasts of how global warming will affect maize and other crops.

This work has highlighted the importance of improving the resolution of agricultural analysis. The coarsest models were usually substantially more biased and unable to match the yield distributions over a wider range of conditions than the models which were more tuned to their local environment. While this necessarily involves estimating more free parameters, the general structure of the models is still simple and the required data for these estimates is not necessarily substantial. An important additional element of this study is the point at which further detail becomes unnecessary and may, in fact, impede prediction - as was indicated for spatial sensitivity variation at the agricultural district scale. The relevant scale for spatial variation in coefficients would appear to be the state level, while finer spatial scales, at least over states as homogeneous as Iowa did not substantively improve yield predictions. However the Iowa data demonstrate that both high resolution data and a model formulation capable of capturing the full sensitivity during the most sensitive phases is required to reduce the yield bias during 2012. This is a problem because the critical stages of tasseling and silking are separately aggregated into the end of the vegetative phase and the milking stage in the state level USDA data. More detail on this highly sensitive period of development would be extremely valuable for isolating the effects of damaging heat waves and, perhaps, forecasting their effect. While the availability of high quality development data outside of the United States may be a challenge, there is some promise in forecasting phenological development with satellite data[105,62]. Without incorporating these details into forecasts of a warmer future we risk underestimating the effects which are likely to be most damaging to agricultural productivity.

Beyond the additional information needed in the physical climate forecast this work highlights the need to further predict the interaction between the physical climate system, the decisions of the farm manager, and the development phase of the crop. When the crop is planted is a critical determinant of final yield and a warmer climate should allow for more flexibility in planting[37,116] which will then affect the timing of all the later stages of development within the seasonal cycle. Furthermore, the interaction of temperature with crop development further compounds the uncertainty of which phase a crop will be in when damaging weather conditions occur. Further work should look to combine these elements of physical climate forecasting, farm management decisions, and crop development and the compound uncertainty of all these models into an increasingly complete analysis of how food production will change in a warmer world.

5

Conclusion

Adaptation to climate change is a sensitive, perhaps too easily politicized topic. It is all too easy for a discussion regarding the reduction of damages brought about by a warmer climate to lead towards downplaying the risks of global warming. It is the last intention of this work to pull the dialogue regarding anthropogenic climate change in such a direction. Mitigation of greenhouse gas emissions must remain a priority even as work like that presented here will aid in developing adaptation strategies to already inevitable warming. However, the spatial variation in temperature sensitivity and temporal control over temperature exposure indicated here must play a more substantial role in modeling an environment that is increasingly shaped by humans. The large body of work regarding damage to agriculture from a warmer world in the absence of human adaptation runs the opposite risk of overstating the damages from a warmer environment and similarly endangering efforts to mitigate warming if such dire predictions prove untrue. In this work I have striven to indicate the real risks a warmer climate poses to maize agriculture at the same time that I have shown how the incorporation of some principal elements of maize physiology and farmer control into models of how climate and weather affect crop yields suggest options for managing that risk.

If there is a set of principals that have guided this research it is the search for pattern, process, and scale. The pattern of spatial sensitivity unveiled at the county level in chapter 1, and paired with the local climatology was what set this whole study in motion. However, this result raised a question of process. What might serve as a physiological basis for the coupling of temperature sensitivity and climatology? This question ultimately lead towards the relationship between cultivar growth duration and climatology described in chapter 2. The pattern coupled to the process provides a foundation for a testable hypothesis regarding how maize crops have been adapted to their local environments and a potential pathway towards future adaptation in a hotter climate. The coupling of spatial sensitivity with temporal development in turn lead to further questions about how crops had been adapted to their local environment over time, not just at the cultivar level, but in terms of management and planting schedules as well. This temporal adaptation lead to the work in chapter 3 and the observed patterns of cooling and warming over the growing season were in turn described by alterations in the managerial processes of earlier planting and longer maturing cultivars, respectively.

Questions of scale persisted throughout these analyses, but take center stage in the analysis of extreme events in chapter 4. Here, we were able to explore the spatial and temporal scales at which meaninful variation occurred in temperature sensitivity. From this analysis, the most relevant scale of spatial variation appears to be approximately the state level, at least for states as homogeneous as Iowa. Temporally the highest resolution available was critical to resolving the greatly increased sensitivity of the tasseling and silking phases, but the grain filling phase sensitivity appeared more reliably estimated when it was more coarsely resolved rather than estimated separately for each constituent sub-phase. By identifying the relevant scales of variation this work points towards the data needed to apply a similar analysis in other regions or to other crops.

Incorporating insight from finer spatial scales has also been part of an effort to incorporate a broader component of the agricultural research community into the discussion of how crops will be affected by climate change. Anecdotal conversations with members of the agronomy community have suggested that the coarser analyses produced by the climate and economics community have been written off by the agronomists for a lack of meaningful detail. As indicated in the introduction, the middle path of this research has worked towards bridging that divide in a consistent and transparent manner. The processes of adaptation revealed here may provide the larger scale global modeling community with new ideas to incorporate or the field researcher to explore in even greater detail.

There are several directions this research may go from here. The most straightforward is the application of a similar program to crops other than maize. Soy beans and wheat are nearly as widely grown in the United States as maize and therefore may indicate some similar local climatological adaptations. For example, is it possible to identify similar relationship between duration of growth phases and climatology in these crops or is such a relationship unique to maize? If it is unique, what about the maize crop has enabled such an adaptation and could it be incorporated into others? Similarly, has the development of these crops been affected by changes in managment and climate? Expanding to other crops also raises the possibility of substituting crops which become more suitable for a warmer future than those which have been grown historically. For example, maize has been expanding in Northern Minnesota and North Dakota and one wonders if the current Canadian Wheat Belt will become the Corn Belt of the future. The details presented in this research may help to answer when such a transition would be fruitful.

Of broader interest, the importance of temporal variation in sensitivity and its role in the devastating losses in 2012 highlights the importance of capturing this time period more reliably outside regions with development data like that available from the USDA. Coupling the USDA development data with remote sensing products like the Normalized Difference Vegetative Index (NDVI) or sun-induced fluoresence (SIF) provide a path towards modeling phenological development in the absence of agricultural survey data. Calibrating these estimates with the USDA data would allow for an assessment of the uncertainty that would accompany such an estimate. The USDA data, particularly at the agricultural district scale could also be used to more precisely quantify how exact the estimate of critical phenological stages must be for a useful estimate of crop sensitivity and yield loss. The analysis in chapter 4 begins to probe this question, but there is more room to explore how finely resolved the window of tasseling and silking must be when estimating yield losses.

An even more applied, but potentially very beneficial direction for this research to move in is to build a coupled model of seasonal forecasting and crop development. This would involve optimizing planting dates and cultivar selection around expected weather over the course of the growing season. The refinements needed in seasonal forecasting are a substantial hurdle to this line of inquiry. However, the coupling of the early planting in 2012 with the peak of the heat wave around tasseling and silking suggests that improvements in this area could be of tremendous practical benefit to agricultural extension offices. This would also require a more detailed large scale description of crop development under varied temperature conditions, but the USDA development data shoud allow for such a model to be constrained. There are, of course, some substantial economic incentives to develop such a system which would extend beyond adapting to a warmer climate.

Humans began a global experiment ten-thousand years ago when they began selecting particular plants to optimize the landscape for their own ends. The process of industrialization has lead to another global experiment in altering the surface temperature of the planet. It remains to be seen whether the ultimate results of industrialization will prove disastrous for agriculture, but it is certain that there is an opportunity to adapt to the changing climate humans are creating. The degree to which agriculture can be adapted to a changing climate will depend on realizing the types of adaptation suggested by the research described here as well as keeping the absolute magnitude of warming to a level that such adaptations will still be relevant.

A

Archeobotanical Applications

An alternative use of growing degree days (GDD) is to apply them as a spatial indicator to infer thermal niche constraints on the spatial distribution of a crop. In many respects this application is closer to the original agronomic function of GDDs as a predictor of crop growth and development[94,93]. Here, I provide a brief overview of work more fully described in D'Alpoim Guedes and Butler (2014), where we use GDDs to aid in interpreting archeobotanical data at a collection of archeological sites in Southwest China, of which seven are presented here. In particular, GDDs allow us to address how thermal time constraints likely delayed the spread of rice to the highly productive region of the Sichuan Basin and help explain the prevalence of both millet and western domesticates in highly mountainous regions of Southwest China. We find that the orographically isolated Sichuan Basin had limited pathways for tropical rice to migrate into it, and thus the development of temperate varieties was likely critical to agricultural settlement in this region. Furthermore, the thermal niche estimates in the most mountainous areas of Southwest China never indicate long term stability for rice agriculture and these cool conditions likely pushed agriculturalists towards more cold tolderant millets and then wheat and barley once these became available.

The seven sites discussed here may be divided into three categories, fig. A.1. In modern day Hunan province, two sites, Bashidang and Pengtoushan both indicate the presence of rice agriculture from as early as 7500 calibrated BC[33]. Less than a thousand kilometers to the west of these sites, on the other side of the Daba mountain range in modern day Sichuan province rice does not appear in the Chengdu Plain and Guiyuanqiao sites until after 3000 cal BC. The Sichuan Basin, as the broad relatively flat expanse at the eastern end of the province is called, is an exceptionally productive region of rice agriculture in modern China[54] and a delay of 4000 years to spread such a short distance suggest there was a substantial barrier to the transmission of rice agriculture into this region. In contrast, the other three sites never indicate a substantial presence of rice agriculture. The intervening site in the Daba mountains, Zhongba, is dominated by millets as is the Sichuan highland site of Yingpanshan. Yingpanshan is less than 100 kilometers northwest of the Chengdu Plain sites but there is no evidence of rice. Finally, the site furthest to the Southwest, in modern day Yunnan province, Haimenkou, steadily drops rice out of it's crop mix in favor of millets and eventually

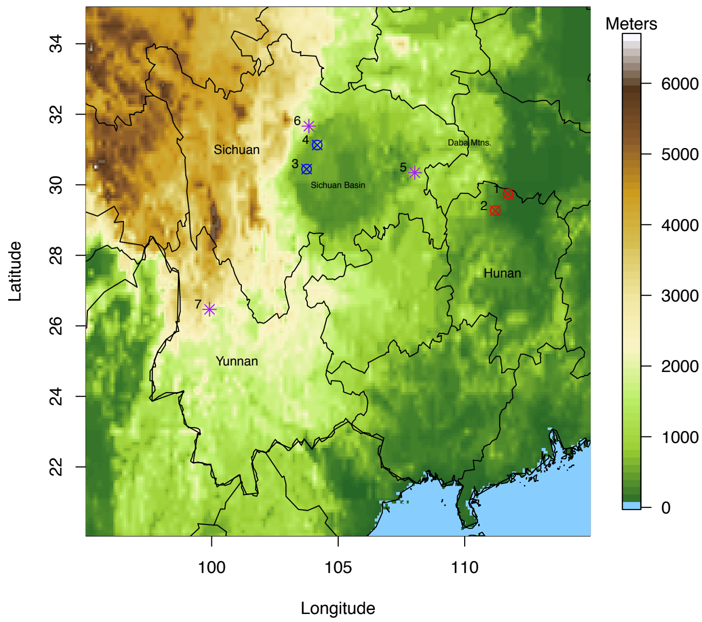


Figure A.1: Archeological Sites The three categories of site are represented by different colors and symbols. Red exes with circles indicate the earliest rice sites 1) Pengtoushan and 2) Bashidang. The blue exes with circles are the later rice sites of the Sichuan Basin 3) Chengdu Plain Sites and 4) Guiyuanqiao. Finally, the millet dominated sites are indicated by the purple burst patterns 5) Zhongba, 6) Yingpanshan, and 7) Haimenkou.

wheat. See D'Alpoim Guedes and Butler (2014) for details of these sites records.

Previously, archeologists examining the spread of agricultural crops have predominantly argued over the importance of growing season length[70] or a modified function of monthly maximum and minimum temperature, called effective temperature[11], to determine whether a region would be viable for a particular crop. However, these measures, respectively, do not account for the more detailed temperature requirements of many crops or make use of more detailed agronomic data available for many cultivars. Growing degree days address both of these issues. Here, the daily heat unit for growing degree days, GDD_d is defined for each day, d, as,

$$\mathrm{GDD}_d = \begin{cases} T_{\mathrm{mean},d} - T_{\mathrm{base}} & \text{if} \quad T_{\mathrm{mean},d} > T_{\mathrm{base}}, \\ 0 & \text{if} \quad T_{\mathrm{mean},d} \leq T_{\mathrm{base}}. \end{cases} \tag{A.1}$$

Here, $T_{\mathrm{mean},d} = (T_{\mathrm{max},d} + T_{\mathrm{min},d})/2$ each day. These daily units are then summed over every day in the calendar year $\sum_d \mathrm{GDD}_d$, as there is no information on the seasonal cycle of ancient cropping. Crop specific limitations on growth are incorporated through the base temperature and yearly GDD requirements which vary substantially across these crops. Rice has a base temperature of 10°C, and temperate rice requires at least 2500 GDD to mature while tropical rice requires at least 2900 GDD. Wheat and Barley, much more cold tolerant crops, calculate GDDs with a base temperature of 0°C, and require at least 1800 and 2000 GDD respectively. Millets are estimated with a base temperature of 5.5°C, and require minimum GDDs of 2000 for foxtail millet and 2100 GDD for broomcorn, though the lack of research on modern millets makes these somewhat more uncertain estimates[23,94,93].

Daily temperatures are taken from the Global Historical Climatology Network (GHCN)[100]. Southwest China has a sparse but even network of weather stations that report to the GHCN, fig. A.2. In total there are 95 stations in the years 1951-2012 spread between China and Northern Thailand. The sample region is larger than the sites described to accomodate regions that other researchers may be interested in, but which did not have data which we examined in detail. To develop a smooth temperature field and estimate GDDs over the entire region a krigging technique was applied[52] to interpolate the daily station temperatures onto a 5 arc-minute digital elevation model of the region, ETOPO5[112]. The krigging was done over great-circle distances, and elevation was in-

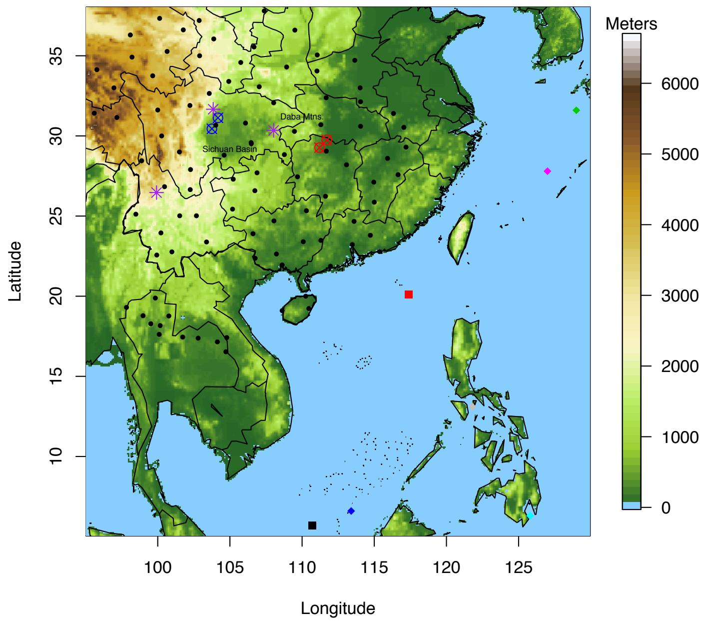


Figure A.2: Weather Stations and Sea Cores. Each black dot represents a weather station in this expanded view of the study region, and the archeology sites are as in fig. A.1. The sea cores used to indicate regional temperatures in this area are indicated by colored squares ($U_{37}^{K'}$) and diamonds (Mg/Ca) based on the proxy type used to infer temperature.

corporated as a co-variate. Because GDDs have a non-linear threshold relationship with mean temperature, the daily temperatures were krigged and then yearly GDD totals calculated and saved from these daily estimates. The krigging estimates were able to pick up a seasonal cycle in the lapse rate, which was in reasonable agreement with other modern estimates[78].

To estimate the spatial structure of the temperature field a fixed exponential variogram was applied to mean lapse rate corrected temperatures. An exponential variogram, γ, was fit using non-linear least squares, implementing the Levenberg-Marquardt algorithm and had the form,

$$\gamma(x) = \sigma^2 + \rho(1 - \exp(-x/\theta)). \tag{A.2}$$

In typical krigging terminology, σ^2 corresponds to the nugget, ρ is the sill, and θ is the range, and x is the mean distance-binned variogram estimate. The fit was reasonable with a squared cross correlation, $R^2 = 0.70$, but there was substantial variability around the mean values to which the estimate was fit. For simplicity this single best fit to mean temperatures was applied to each day rather than recalculating the variogram for each new krigging estimate.

These krigging estimates allow a reasonable estimate of the smooth modern GDD field across Southwest China. Estimates of paleoclimatic conditions were taken from seven publically available sea core records compiled in[92] and originally studied by[120,72,150,74,153,152,168] with temperature reconstructions shown in fig. A.3. These cores do not indicate a consistent signal over the time period of 6500-400 BCE during which there were considerable changes in crop production across this region. Local pollen records provide another potential constraint on temperature variability[67], but the signal is likely to be confounded by alterations in habitat brought about by the introduction of agriculture to a site, and this challenges a clean interpretation of the physical climate signal. So rather than conducting a formal regional temperature reconstruction, we perturb modern temperatures by $\pm 1°$C and examine the sensitivity of the rice growing region to these moderate anomalies, which are within the scope of temperature swings indicated by the sea cores. The analysis serves to indicate how sensitive crop ranges are to temperature variability rather than produce a formal reconstruction of the archeological growing niches.

The first question suggested by the archeobotanical evidence regarded the slow trans-

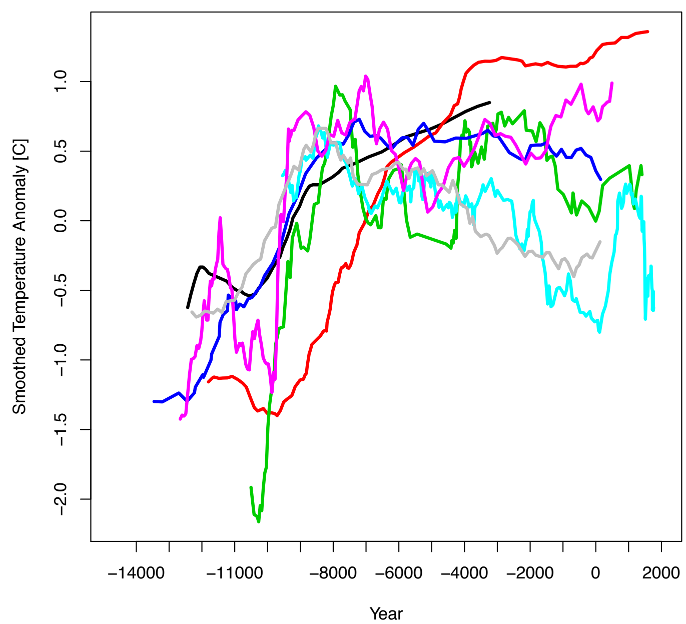


Figure A.3: Smoothed and centered sea core temperatures. The proxy temperatures indicated the expected latitudinal gradient and are de-meaned and smoothed with an eleven point two-sided moving average to indicate the broad features of temperature in the region. There is a clear signal coming out of the last ice age, but after that there is significant regional variability, which challenges a simple local reconstruction. The colors of each line correspond to the color of each point in figure A.2.

mission of rice agriculture from the Hunan province sites into the Sichuan Basin. The GDD estimates, fig, A.4 indicate that under modern conditions only the cool adapted temperate rice, with GDD requirements as low as 2500°C days per year have a continuous corridor in the Southwestern corner of the Sichuan Basin by which farmers could have diffused their rice cropping techniques into the area. Perhaps more interesting, under a 1°C cooling, fig. A.4b, this corridor is closed and the Sichuan Basin is an isolated island of potential rice production separated by formidable mountainous barriers. The corridor of continuously cultivable land widens considerably under the warming perturbation, fig. A.4c, though tropical rice is still barred from continuous cultivation through the mountain range. Perhaps most striking is that even under the warming perturbation all three sites dominated by non-rice agriculture are outside the estimated cultivable range of temperate rice, though they hover on its margin.

The quantitive measure of crop suitability provided by GDDs indicates that the long delay for rice to move into the Sichuan Basin was likely a result of the orographic barrier of the Daba mountains. The development of temperate rice varieties was likely a critical component of this movement, which is supported by the grains found in the Sichuan Basin having the short and thick morphology of temperate rice[33]. Of course, the mountains would not have prevented a rapid advance of agriculturists[134] over the landscape, and the lack of continuously cultivable land would not have been a barrier to leap-frog expansion. Another possibility is the adoption of agriculture by local communities through cultural diffusion, but there is little evidence that suggests local hunter gatherers adopted an agrarian lifestyle[34]. The GDD analysis suggests that the development of temperate rice varieties, perhaps aided by an extended warm period, would have allowed the settled communities outside of the Sichuan Basin to diffuse in and set up their agrarian rice based lifestyle without the need for a rapid advance, though such a scenario cannot be ruled out.

When the thermal time constraints are applied to the more cold tolerant millets and western domesticates the cultivable region widens considerably, fig. A5. All of the sites dominated by millet remains are well within the range of both of these crop types, and the considerably more mountainous regions to the West begin to open up as well. Given that these sites are out of the regularly cultivable area of temperate rice the importance of millets to these sites is immediately clear. If these communities had planted rice, there would have been a good chance that it did not reach maturity. This is highlighted by

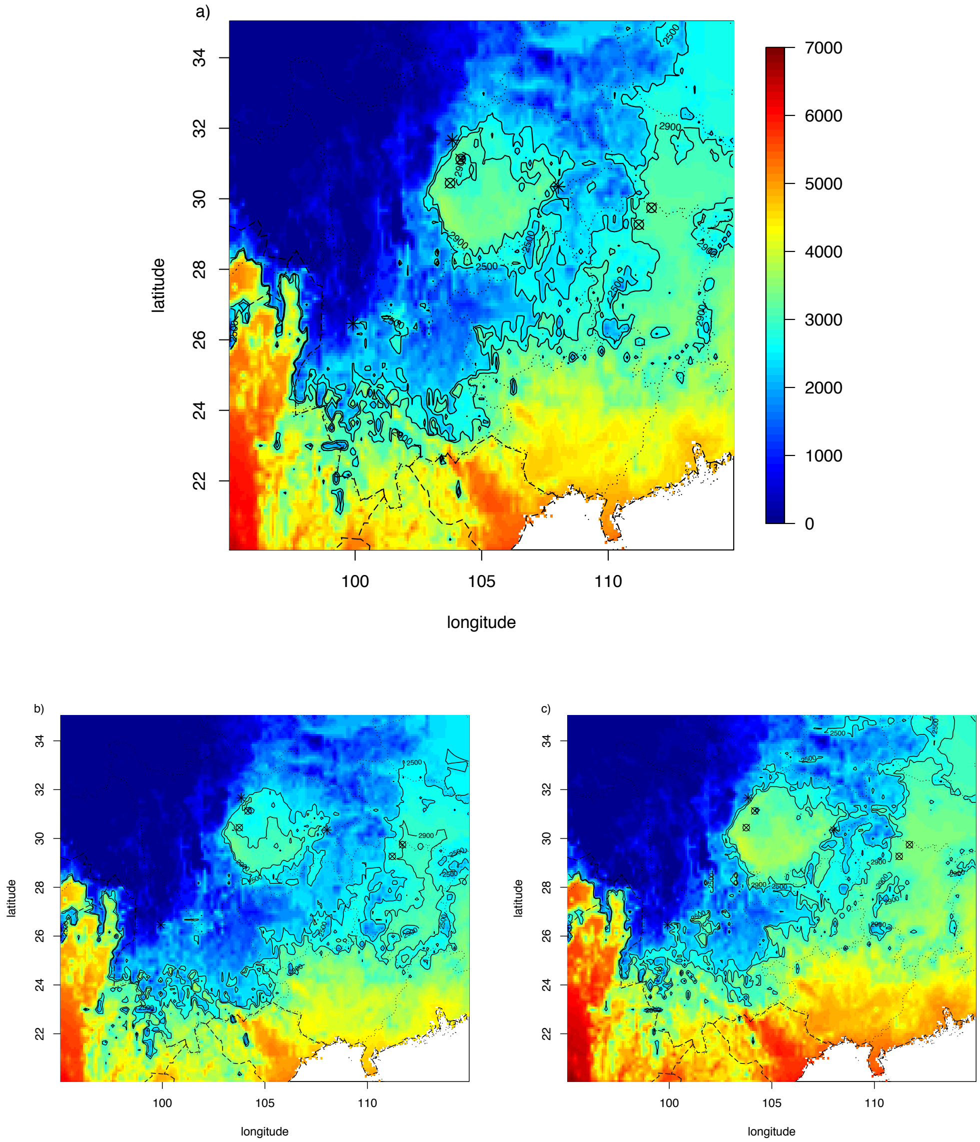


Figure A.4: Rice Growing Degree Day Limits The color scale indicates the range of GDD from a base temperature of 10°C. The contours indicate growing regions for temperature rice (2500 GDD) and tropical rice (2900 GDD). Dotted lines are province boundaries and dashed lines are national boundaries. a) GDDs calculated from modern temperatures averaged over 1951-2012 b) Mean daily temperatures decreased by 1°C prior to calculating GDDs c) Mean daily temperatures increased by 1°C prior to calculating GDDs.

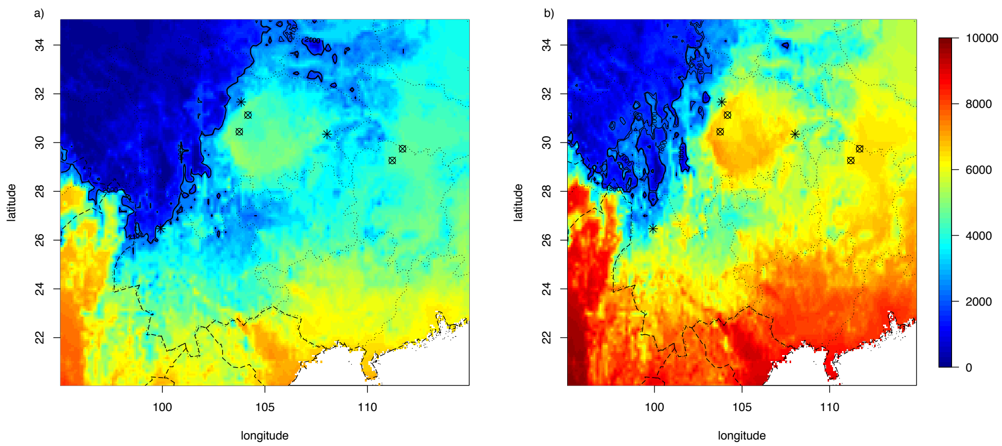


Figure A.5: Millet, Wheat and Barley GDD Limits The color scale displays GDDs calculated for base temperatures of 5.5°C for the millets and 0°C for wheat and barley. The contours indicate the cultivable regions for each crop, dotted lines are province boundaries and dashed lines are national boundaries. a) Foxtail millet requires at least 2000 GDD while broomcorn needs 2100 giving them nearly overlapping cultivation ranges. b) Wheat requires at least 1800 GDD for maturation and barley at least 2000 GDD, they are widely cultivable including into many of the mountain valleys. These limits expand and contract only marginally under the modest temperature perturbations and are omitted for brevity.

the sites close to the rice growing communities, Zhongba and Yingpanshan. Despite the close proximity these sites maintained a millet based agriculture even as rice growing communities developed around them. Haimenkou, the Southwesternmost site of the millet group, is perhaps more striking for the change in crop composition excavated at this site. The earliest evidence indicates that rice may have made up a third of its crop mix, but over time this was steadily replaced by millet and then wheat. There are areas that rice could potentially have been grown in near Haimenkou, the closest of which is 30km away, according to the coarse digital elevation model applied here. Under modern conditions temperate rice would have thrived in about a third of years. However, the GDD estimates clearly indicate that millets and wheat would have been much safer crops to cultivate. Growing degree days show that all of these sites were better suited to crops which mature in cooler condtions, in agreement with the archeological record.

The use of growing degree days to analyze crop suitability helps to bring modern agronomic insight to bear on classic archeological questions regarding the spread of agriculture. This analysis has highlighted the importance of temperate rice varieties for settling the Sichuan Basin and the widespread importance of millets for agrarian communities in mountainous sites. Further work could produce more refined estimates of paleoclimate to more closely couple the timing of agrarian settlement or crop transition with climatic events. Similarly, more refined models of crop suitability, perhaps incorporating precipitation as well, would help to refine why particular crops were selected at their respective sites. The archeobotanical data could also be used as an additional paleoclimate proxy to add into other temperature reconstructions. While the situation of early agricultural communities settling territory is considerably different than contemporary humans adapting to a changing climate, the archeological record provides an opportunity to investigate the many ways in which humans have adapted themselves to novel conditions and illuminate the utility of crops, such as millets, which are not as widely grown under contemporary conditions. By investigating historical human adaptations we may be able to gain some insight into hitherto unconsidered options for our own uncertain future.

References

[1] Abendroth, L., Elmore, R., Boyer, M., & Marlay, S. (2011). *Corn growth and development. PMR 1009.* Iowa State University Extension, Ames, Iowa.

[2] Ainsworth, E. A. & Ort, D. R. (2010). How do we improve crop production in a warming world. *Plant Physiology*, 154, 526–530.

[3] Allen, M. R., Frame, D. J., Huntingford, C., Jones, C. D., Lowe, J. A., Meinshausen, M., & Meinshausen, N. (2009). Warming caused by cumulative carbon emissions towards the trillionth tonne. *Nature*, 458(7242), 1163–1166.

[4] Andrade, F., Otegui, M., & Vega, C. (2000). Intercepted radiation at flowering and kernel number in maize. *Agron. J.*, 92, 92–97.

[5] Auffhammer, M. & Schlenker, W. (2014). Empirical studies on agricultural impacts and adaptation. *Energy Economics*, 46, 555–561.

[6] Badu-Apraku, B., Hunter, R., & Tollenaar, M. (1983). Effect of Temperature during Grain Filling on Whole Plant and Grain Yield in Maize (*Zea Mays* L.). *Can. J. Plant Sci.*, 63, 357–363.

[7] Barker, T., Campos, H., Cooper, M., Dolan, D., Edmeades, G., Habben, J., Schussler, J., Wright, D., & Zinselmeier, C. (2005). *Plant Breeding Reviews*, volume 25, chapter Improving Drought Tolerance in Maize. John Wiley and Sons.

[8] Battisti, D. & Naylor, R. (2009). Historical warnings of future food insecurity with unprecedented seasonal heat. *Science*, 323, 240–244.

[9] Beadle, G. W. (1939). Teosinte and the origin of maize. *Journal of Heredity*, 30(6), 245–247.

[10] Berry, S. T., Roberts, M. J., & Schlenker, W. (2013). *Corn Production Shocks in 2012 and Beyond: Implications for Harvest Volatility.* University of Chicago Press.

[11] Binford, L. (2011). *Constructing Frames of Reference: An Analytical Method for Archeological Theory Building Using Hunter-gatherer and Environmental Data Sets*. Berkeley: University of California Press.

[12] Boissonnat, J.-D., Devillers, O., Pion, S., Teillaud, M., & Yvinec, M. (2002). Triangulations in CGAL. *Computational Geometry*, (pp. 5–19, as implemented in Matlab 2010b).

[13] Bonan, Gordon, B. (2001). Observational Evidence for Reduction of Daily Maximum Temperature by Croplands in the Midwest United States. *Journal of Climate*, 14, 2430–2442.

[14] Borrás, L., Slafer, G., & Otegui, M. (2004). Seed dry weight response to source-sink manipulations in wheat, maize and soybean: a quantitative reappraisal. *Field Crops Research*, 86, 131–146.

[15] Boserup, E. (1965). *The Conditions of Agricultural Growth*. London: George Allen and Unwin Ltd.

[16] Boyer, J. (1970). Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. *Plant Physiol.*, 46, 233–235.

[17] Bradley, N. L., Leopold, A. C., Ross, J., & Huffaker, W. (1999). Phenological changes reflect climate change in Wisconsin. *Proc. Natl. Acad. Sci. USA*, 96, 9701–9704.

[18] Butler, E. E. & Huybers, P. (2013a). Adaptation of US Maize to Temperature Variations. *Nature Clim. Change*, 3, 68–72.

[19] Butler, E. E. & Huybers, P. (2013b). US maize adaptability: reply. *Nature Clim. Change*, 3, 691–692.

[20] Butler, E. E. & Huybers, P. (2015). Variations in the sensitivity of US maize yield to extreme temperatures by region and growth phase. *Environ. Res. Lett.*, 10, 034009, doi:10.1088/1748–9326/10/3/034009.

[21] Canfield, D. E., Glazer, A. N., & Falkowski, P. G. (2010). The evolution and future of earth's nitrogen cycle. *Science*, 330(6001), 192–196.

[22] Cárcova, J. & Otegui, M. (2001). Ear temperature and pollination timing effects on maize kernel set. *Crop Sci.*, 41, 1809–1815.

[23] Cardenas, A. C. (1983). A pheno-climatological assessment of millets and other cereal grains in tropical cropping patterns. Master's thesis, University of Nebraska, Horticulture.

[24] Carlson, R. (1990). Heat Stress, Plant-Available Soil Moisture, and Corn Yields in Iowa: A Short- and Long-Term View. *J. of Prod. Agric.*, 3, 293–297.

[25] Cassman, K. G. (1999). Ecological intensification of cereal production systems: Yield potential, soil quality, and precision agriculture. *Proceedings of the National Academy of Sciences*, 96(11), 5952–5959.

[26] Cassman, K. G., Grassini, P., & van Wart, J. (2011). *Handbook of Climate Change and Agroecosystems*, chapter Crop Yield Potential, Yield Trends and Global Food Security in a Changing Climate. Imperial College Press: London.

[27] Cavalieri, A. & Smith, O. (1984). Grain filling and field drying of a set of maize hybrids released from 1930 to 1982. *Crop Science*, 25, 856–860.

[28] Challinor, A. J., Parkes, B., & Ramirez-Villegas, J. (2015). Crop yield response to climate change varies with cropping intensity. *Global Change Biology*, (pp. doi: 10.1111/gcb.12808).

[29] Cicchino, M., Rattalino Edreira, J., & Otegui, M. (2010). Heat stress during late vegetative growth of maize: Effects on phenology and assessment of optimum temperature. *Crop Sci.*, 50, 1431–1437.

[30] Coumou, D. & Robinson, A. (2013). Historic and future increase in the global land areas affected by monthly heat extremes. *Environ. Res. Lett.*, 8, doi:10.1088/1748–9326/8/3/034018.

[31] Crafts-Brandner, S. J. & Salvucci, M. (2002). Sensitivity of Photosynthesis in a C4 Plant, Maize, to Heat Stress. *Plant Physiol*, 129, 1773–1780.

[32] Craufurd, P. & Wheeler, T. (2009). Climate change and the flowering time of annual crops. *J. Exp. Bot.*, 60(9), 2529–2539.

[33] D'Alpoim Guedes, J. & Butler, E. E. (2014). Modeling constraints on the spread of agriculture to Southwest China with thermal niche models. *Quaternary International*, 349, 29–41, http://dx.doi.org/10.1016/j.quaint.2014.08.003.

[34] D'Alpoim Guedes, J., Jiang, M., He, K., Wu, X., & Jiang, Z. (2013). Site of Baodun yields earliest evidence for the spread of rice and foxtail millet agriculture to south-west China. *Antiquity*, 87(337), 758–771.

[35] de Bruyn, L. & de Jager, J. (1978). A meteorological approach to the identification of drought sensitive periods in field crops. *Agric. Meteorol.*, 19, 35–40.

[36] De Laulanié, H. (2011). Intensive Rice Farming in Madagascar. *Tropicultura*, 29(3), 183–187.

[37] Deryng, D., Sacks, W., Barford, C., & Ramankutty, N. (2011). Simulating the effects of climate and agricultural management practices on global crop yield. *Global Biogeochem. Cycles*, 25, GB2006, doi:10.1029/2009GB003765.

[38] Diffenbaugh, N., Hertel, T., Scherer, M., & Verma, M. (2012). Response of corn markets to climate volatility under alternative energy futures. *Nature Clim. Change*, 2, 514–518.

[39] Diffenbaugh, N. S. & Ashfaq, M. (2010). Intensification of hot extremes in the united states. *Geophysical Research Letters*, 37, L15701, doi:10.1029/2010GL043888.

[40] Duffy, P. & Tebaldi, C. (2012). Increasing prevalence of extreme summer temperatures in the U.S. *Climatic Change*, 111, 487–495.

[41] Duvick, D. (2005). Genetic Progress in Yield of United States Maize (*Zea Mays* L.). *Maydica*, 50, 193–202.

[42] Easterling, D., Evans, J., Groisman, P. Y., Karl, T., Kunkel, K., & Ambenje, P. (1999). Observed variability and trends in extreme climate events: A brief review*. *Bulletin of the American Meteorological Society*, (pp. 417–425).

[43] Easterling, e. a. (2007). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, chapter Food, Fibre and Forest Products. Cambridge University Press.

[44] Easterling, W. (2011). *Handbook of Climate Change and Agroecosystems*, chapter Guidelines for Adapting Agriculture to Climate Change. Imperial College Press: London.

[45] Edgerton, M. (2009). Increasing crop productivity to meet global needs for feed, food, and fuel. *Plant Physiol.*, 149, 7–13.

[46] Egli, D. (2004). *Advances in Agronomy*, volume 83, chapter Seed-Fill Duration and Yield of Grain Crops. Elsevier.

[47] Ellwood, E. R., Temple, S. A., Primack, R. B., Bradley, N. L., & Davis, C. C. (2013). Record-breaking early flowering in the eastern united states. *Plos One*, 8(1).

[48] Elmore, R. (2009). *The Corn and Climate Report*. Iowa State University.

[49] Evans, L. (1993). *Crop Evolution, Adaptation, and Yield*. Cambridge, UK: Cambridge University Press.

[50] Evans, L. (1998). *Feeding the Ten Billion.* Cambridge, United Kingdom: Cambridge University Press.

[51] FAO (2014). Chapter 3 - meteorological data.

[52] Fields Development Team (2006). Tools for Spatial Data. National Center for Atmospheric Research, Boulder, CO.

[53] Fischer, E. M., Seneviratne, S., Vidale, P., Lüthi, D., & Schär, C. (2007). Soil Moisture-Atmosphere Interactions during the 2003 European Summer Heat Wave. *Journal of Climate*, (pp. 5081–5099).

[54] Frolking, S., Qiu, J., Boles, S., Xiao, X., Liu, J., Zhuang, Y., Li, C., & Qin, X. (2002). Combining remote sensing and ground census data to develop new maps of the distribution of rice agriculture in China. *Global Biogeochem. Cycles*, 16(4), 1091, doi:10.1029/2001GB001425.

[55] Gambín, B., Borraás, L., & Otegui, M. (2007). Kernel water relations and duration of grain filling in maize temperature hybrids. *Field Crops Research*, 101, 1–9.

[56] Gao, Y., Fu, J., Drake, J., Liu, Y., & Lamarque, J.-F. (2012). Projected changes of extreme weather events in the eastern United States based on a high resolution climate modeling system. *Environ. Res. Lett.*, 7, doi:10.1088/1748–9326/7/4/044025.

[57] Gardner, B., Blad, B., & Watts, D. (1981). Plant and air temperatures in differentially-irrigated corn*. *Agric. Meteorol.*, 25, 207–217.

[58] Gerland, P., Raftery, A. E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B. K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G. K., & Wilmoth, J. (2014). World population stabilization unlikely this century. *Science*, 346(6206), 234–237.

[59] Gifford, R., Thorne, J., Hitz, W., & Giaquinta, R. (1984). Crop productivity and photoassimilate partitioning. *Science*, 225, 801–808.

[60] Goldstein, A. H., Koven, Charles, D., Heald, C. L., & Fung, I. Y. (2009). Biogenic carbon and anthropogenic pollutants combine to form a cooling haze over the southeastern United States. *Proc. Natl. Acad. Sci. USA*, 106(22), 8835–8840.

[61] Gourdji, S., Sibley, A., & Lobell, D. (2013). Global crop exposure to critical high temperatures in the reproductive period: historical trends and future predictions. *Environ. Res. Lett.*, 8, 10pp.

[62] Guanter, L., Zhang, Y., Jung, M., Joiner, J., Voigt, M., Berry, J. A., Frankenberg, C., Huete, A. R., Zarco-Tejada, P., Lee, J.-E., Moran, M. S., Ponce-Campos, G., Beer, C., Camps-Valls, G., Buchmann, N., Gianelle, D., Klumpp, K., Cescatti, A., Baker, J. M., & Griffis, T. J. (2014). Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. *Proceedings of the National Academy of Sciences*, 111(14), E1327–E1333.

[63] Guimarães, P. d. S., Bernini, C. S., Pedroso, F. K., & Paterniani, M. E. (2014). Characterizing corn hybrids (*Zea Mays* L) for water shortage by principal components analysis. *Maydica*, 59, 72–79.

[64] Gunset, G. & Arndt, M. (1993). Flooding expected to put major dent in crop yields.

[65] Hawkins, E., Fricker, T., Challinor, A., Ferro, C., Ho, C., & Osborne, T. (2013). Increasing influence of heat stress on French maize yields from the 1960s to the 2030s. *Global Change Biology*, 19, 937–947.

[66] Hay, R. & Porter, J. R. (2006). *The Physiology of Crop Yield*. Blackwell Publishing, second edition.

[67] He, Y., Theakstone, Wilfred, H., Zhonglin, Z., Dian, Z., Tandong, Y., Tuo, C., Yongping, S., & Hongxi, P. (2004). Asynchronous Holocene climatic changes across China. *Quaternary Research*, 61, 52–63.

[68] Held, I. & Soden, B. (2006). Robust response of the hydrological cycle to global warming. *J. Climate*, 19, 5686–5699.

[69] Huybers, P., McKinnon, K., Rhines, A., & Tingley, M. (2014). U.S. daily temperatures: the meaning of extremes in the context of non-normality. *Journal of Climate*, in press, doi:10.1175/JCLI–D–14–00216.1.

[70] Jones, M., Hunt, H., Lightfoot, E., Lister, D., Liu, X., & Motuzaite-Matuzeviciute, G. (2011). Food globalization in prehistory. *World Archeology*, 43(4), 665–675, DOI: 10.1080/00438243.2011.624764.

[71] Jones, R., Ouattar, S., & Crookston, R. K. (1984). Thermal environment during endosperm cell division and grain filling in maize: Effects on kernel growth and development in vitro. *Crop Sci.*, 2(133-137).

[72] Kienast, M., Steinke, S., Stattegger, K., & Calvert, S. (2001). Synchronous Tropical South China Sea SST Change and Greenland Warming During Deglaciation. *Science*, 291, 2132–2134.

[73] Kirtman, B., Power, S., Adedoyin, J., Boer, G., Bojariu, R., Camilloni, I., Doblas-Reyes, F., Fiore, A., Kimoto, M., Meehl, G., Prather, M., Sarr, A., Schär, C., Sutton, R., van Oldenborgh, G., Vecchi, G., & Wang, H. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, chapter Near-term Climate Change: Projections and Predictability. Cambridge University Press: Cambridge, United Kingdom and New York, NY, USA.

[74] Kubota, Y., Katsunori, K., Tada, R., Oda, H., Yokoyama, Y., & Matsuzaki, H. (2010). Variations of East Asian summer monsoon since the last deglaciation based on Mg/Ca and oxygen isotope of planktic foraminifera in the northern East China Sea. *Paleoceanography*, 25, PA4205, doi:10.1029/2009PA001891.

[75] Kucharik, C. (2006). A Multidecadal Trend of Earlier Corn Planting in the Central USA. *Agron. J.*, 98, 1544–1550.

[76] Kucharik, C. J. (2008). Contribution of Planting Date Trends to Increased Maize Yields in the Central United States. *Agron. J.*, 100(2), 328–336.

[77] Lau, N.-C. & Nath, M. J. (2012). A Model Study of Heat Waves over North America: Meteorological Aspects and Projections for the Twenty-First Century. *Journal of Climate*, 25, 4761–4784.

[78] Li, X., Wang, L., Chen, D., Yang, K., Xue, B., & Sun, L. (2011). Near-surface air temperature lapse rates in the mainland China during 1962-2011. *J. of Geophys. Res. Atmos.*, 118, 7505–7515, doi:10.1002/jgrd.50553.

[79] Lobell, D. (2014). Climate change adaptation in crop production: Beware of illusions. *Global Food Security*, http://dx.doi.org/10.1016/j.gfs.2014.05.002i.

[80] Lobell, D. & Asner, G. P. (2003). Climate and Management Contributions to Recent Trends in U.S. Agricultural Yields. *Science*, 299, 1032.

[81] Lobell, D. & Burke, M. (2010). *Climate Change and Food Security: Adapting Agriculture to a Warmer World*, volume 37. Springer.

[82] Lobell, D. & Field, C. (2007). Global scale climate-crop yield relationships and the impacts of recent warming. *Environ. Res. Lett.*, (pp. 7pp).

[83] Lobell, D., Roberts, M., Schlenker, W., Braun, N., Little, B., Rejesus, R., & Hammer, G. (2014). Greater Sensitivity to Drought Accompanies Maize Yield Increase in the U.S. Midwest. *Science*, 344, 516–519.

[84] Lobell, D. & Tebaldi, C. (2014). Getting caught with our plants down: the risks of a global crop yield slowdown from climate trends in the next two decades. *Environ. Res. Lett.*, 9.

[85] Lobell, D. B., Bänziger, M., Magorokosho, C., & Vivek, B. (2011). Nonlinear heat effects on African maize as evidenced by historical yield trials. *Nature Clim. Change*, 1, 42–45.

[86] Lobell, D. B., Burke, Marshall, B., Tebaldi, C., Mastrandea, Michael, D., Falcon, Walter, P., & Naylor, R. L. (2008). Prioritizing climate change adaptation needs for food security in 2030. *Science*, 319, 607–610.

[87] Lobell, D. B. & Burke, M. B. (2008). Why are agricultural impacts of climate change so uncertain? The importance of temperature relative to precipitation. *Environ. Res. Lett.*, 3, 034007.

[88] Lobell, D. B., Hammer, G., McLean, G., Messina, C., Roberts, M., & Schlenker, W. (2013a). The critical role of extreme heat for maize production in the United States. *Nature Clim. Change*, 3, 497–501.

[89] Lobell, D. B., Ortiz-Monasterio, J. I., Sibley, A. M., & Sohu, V. S. (2013b). Satellite detection of earlier wheat sowing in India and implications for yield trends. *Agricultural Systems*, 115(0), 137–143.

[90] Maddonni, G., Otegui, M., & Bonhomme, R. (1998). Grain yield components in maize II. postsilking growth and kernel weight. *Field Crops Research*, 56, 257–264.

[91] Mann, C. C. (2005). *1491*. New York: Random House.

[92] Marcott, S., Shakun, J., Clark, P., & Mix, A. (2013). A reconstruction of regional and global temperature for the past 11,300 years. *Science*, 339, 1198–1201.

[93] McMaster, G. S., Edmunds, D., Wilhelm, W., Nielsen, D., Prasad, P., & Ascough II, J. (2011). Phenologymms: A program to simulate phenological responses to water stress. *Computers and Electronics in Agriculture*, 77, 118–125.

[94] McMaster, G. S. & Wilhelm, W. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology*, 87, 291–300.

[95] McWilliam, J. & Naylor, A. (1967). Temperature and plant adaptation. I. interaction of temperature and light in the synthesis of chlorophyll in corn. *Plant Physiol.*, 42, 1711–1715.

[96] Mearns, L. O., Katz, R. W., & Schneider, S. H. (1984). Extreme high-temperature events: Changes in their probabilities with changes in mean temperature. *Journal of Climate and Applied Meteorology*, (pp. 1601–1613).

[97] Meehl, G. A. & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, 305, 994–997.

[98] Meehl, G.A., et al. (2007). *Climate Change 2007: The Physical Science Basis. Contributions of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, chapter Global Climate Projections. Cambridge University Press.

[99] Meerburg, B.G., et al. (2009). Do nonlinear temperature effects indicate severe damages to us crop yields under climate change? *Proc. Natl. Acad. Sci. USA*, 106(E120).

[100] Menne, M., Durre, I., Vose, R., Gleason, B., & Houston, T. (2012). An overview of the global historical climatology network-daily database. *Journal of Atmospheric and Oceanic Technology*, 29, 897–910.

[101] Menne, M., Williams, C.N., J., & Vose, R. (2014). *United States Historical Climatology Network Daily Temperature, Precipitation, and Snow Data*. Technical report, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

[102] Menzel, A., von Vopelius, J., Estrella, N., Schleip, C., & Dose, V. (2006). Farmers' annual activities are not tracking the speed of climate change. *Clim. Res.*, 32, 201–207.

[103] Menzel, A., et al. (2006). European phenological response to climate change matches the warming pattern. *Glob. Ch. Biol.*, 12, 1969–1976.

[104] Miller-Rushing, A. J. & Primack, R. B. (2008). Global warming and flowering times in thoreau's concord: A community perspective. *Ecology*, 89(2), 332–341.

[105] Morisette, J. T., Richardson, A. D., Knapp, A. K., Fisher, J. I., Graham, E. A., Abatzoglou, J., Wilson, B. E., Breshears, D. D., Henebry, G. M., Hanes, J. M., & Liang, L. (2009). Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Front. Ecol. Environ.*, 7(5), 253–260.

[106] Muchow, R., Sinclair, T., & Bennett, J. (1990). Temperature and solar radiation effects on potential maize yield across locations. *Agron. J.*, 82, 338–343.

[107] Mueller, N. D., Butler, E., Holbrook, N., & Huybers, P. (in prep.). Cropland intensification cools us midwest extreme summer temperatures.

[108] Mueller, N. D., Gerber, J. S., Johnston, M., Ray, D. K., Ramankutty, N., & Foley, J. A. (2012). Closing yield gaps through nutrient and water management. *Nature*, 490(7419), 254–257.

[109] NCDC (1993). *Local Climatological Data. Environmental Information Summary (C-2)*. Technical report, National Climatic Data Center, NOAA-NCDC, Asheville, NC.

[110] Neild, R. (1982). Temperature and rainfall influences on the phenology and yield of grain sorghum and maize: a comparison*. *Agric. Meteorol.*, 27, 79–88.

[111] Nelson, G.C., et al. (2009). Climate change: Impact on agriculture and costs of adaptation. *Int. Food Policy Res. Inst., Washington, DC.*

[112] NOAA (1988). *Data Announcement 88-MGG-02, Digital Relief of the Surface of the Earth.* Boulder, CO, NOAA, National Geophysical Data Center.

[113] O'Gorman, P. A. (2012). Sensitivity of tropical precipitation extremes to climate change. *Nature Geoscience*, 5, 697–700.

[114] O'Gorman, P. A. & Schneider, T. (2009). The physical basis for increases in precipitation extremes in simulations of 21st century climate change. *Proc. Natl. Acad. Sci. USA*, 106(35), 14773–14777.

[115] Ortiz-Bobea, A. (2011). Improving agronomic structure in econometric models of climate change impacts. Presented at the Agricultural and Applied Economics Association's 2011 AAEA and NAREA Joint Annual Meeting.

[116] Ortiz-Bobea, A. & Just, R. (2012). Modeling the structure of adaptation in climate change impact assessment. *Amer. J. Agr. Econ.*, 95(2), 244–251.

[117] Pan, Z., Arritt, R. W., Takle, E. S., Gutkowski, W. J. J., Anderson, C. J., & Segal, M. (2004). Altered hydrologic feedback in a warming climate introduces a "warming hold". *Geophys. Res. Lett.*, 31, L17109, doi:10.1029/2004GL020528.

[118] Parmesan, C. & Yohe, G. (2003). A global coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

[119] Parry, M., Duinker, P., Morison, J., Porter, J., J.Reilly, & Wright, L. (1990). *Climate Change: The IPCC Impacts Assessment*, chapter Agriculture and forestry. Australian Government Publishing Service.

[120] Pelejero, C., Grimalt, J., Heilig, S., Kienast, M., & Wang, L. (1999). High Resolution UK 37 temperature reconstructions in the South China Sea over the past 220 kyr. *Paleoceanography*, 14(2), 224–231, doi:10.1029/1998PA900015.

[121] Porter, J. R., Xie, L., Challinor, A., Cochrane, K., Howden, M., Iqbal, M., Lobell, D., & Travasso, M. (2014). *Volume 1: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, chapter Food Security and Food Production Systems. Climate Change 2014: Impacts, Adaptation and Vulnerability. Cambridge University Press: Cambridge, United Kingdom and New York, NY, USA.

[122] Portmann, R. W., Solomon, S., & Hegerl, G. C. (2009). Spatial and seasonal patterns in climate change, temperatures, and precipitation across the United States. *Proc. Natl. Acad. Sci. USA*, 106(18), 7324–7329.

[123] Quick Stats 2.0 (2014). United states department of agriculture/national agriculture statistics service.

[124] Ramankutty, N., Evan, A., Monfreda, C., & Foley, J. A. (2008). Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochem. Cycles*, 22(GB10003), doi:10.1029/2007GB002952.

[125] Ramankutty, N., Foley, J., Norman, J., & McSweeney, K. (2002). The global distribution of cultivable land: current patterns and sensitivity to possible climate change. *Global Ecol. Biogeogr*, 11, 377–392.

[126] Rattalino Edreira, J. & Otegui, M. (2012a). Heat stress in temperate and tropical maize hybrids: A novel approach for assessing sources of kernel loss in field conditions. *Field Crops Research*, 142, 58–67.

[127] Rattalino Edreira, J. & Otegui, M. (2012b). Heat stress in temperate and tropical maize hybrids: Differences in crop growth biomass partitioning and reserves use. *Field Crops Research*, 130, 97–98.

[128] Rezaei, E., Siebert, S., & Ewert, F. (2015). Intensity of heat stress in winter wheat-phenology compensates for the adverse effect of global warming. *Environ. Res. Lett.*, 10(doi:10.1088/1748-9326/10/2/024012).

[129] Richardson, K. et al. (2009). *Synthesis Report from Climate Change: Global Risks, Challenges, and Decisions*. Technical report, University of Copenhagen, Copenhagen, Denmark.

[130] Ristic, Z., Williams, G., Yang, G., Martin, B., & Fullerton, S. (1996). Dehydration, Damage to Cellular Membranes, and Heat-Shock Proteins in Maize Hybrids from Different Climates. *J. Plant Physiol*, 149, 424–432.

[131] Roberts, M. & Schlenker, W. (2011). *The Economics of Climate Change, Adaptations Past and Present*, chapter The Evolution of Heat Tolerance of Corn: Implications for Climate Change. University of Chicago Press.

[132] Rosenzweig, C., Elliott, J., Deryng, D., Müller, C., Arneth, A., Boote, Kenneth, J., Folberth, C., Glotter, M., Khabarov, N., Neumann, K., Piontek, F., Pugh, Thomas, A., Schmid, E., Stehfest, E., Yang, H., & Jones, James, W. (2013). Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. *Proc. Natl. Acad. Sci. USA*, 111(9), 3268–3273.

[133] Rosenzweig, C. & Parry, M. (1994). Potential impact of climate change on world food supply. *Nature*, 367, 133–138.

[134] Rowley-Conwy, P. (2004). How the West was lost: a reconsideration of agricultural origins in Britain, Ireland, and southern Scandinavia. *Current anthropology*, 45, 83–113.

[135] Ruane, A. C., Major, D. C., Yu, W. H., Alam, M., Hussain, S. G., Khan, A. S., Hassan, A., Hossain, B. M. T. A., Goldberg, R., Horton, R. M., & Rosenzweig, C. (2013). Multi-factor impact analysis of agricultural production in Bangladesh with climate change. *Global Environmental Change*, 23(1), 338–350.

[136] Sacks, W. J. & Kucharik, C. J. (2011). Crop management and phenology trends in the U.S. Corn Belt: Impacts on yields, evapotranspiration and energy balance. *Agricultural and Forest Meteorology*, 151, 882–894.

[137] Sage, R. & Kubien, D. (2007). The temperature response of C_3 and C_4 photosynthesis. *Plant, Cell and Env.*, 30, 1086–1106.

[138] Sánchez, B., Rasmussen, A., & Porter, J. (2014). Temperature and the growth and development of maize and rice: A review. *Glob. Ch. Biol.*, XX.

[139] Schlenker, W. & Roberts, M. (2006). Nonlinear effects of weather on corn yields. *Rev. Ag. Econ.*, 28, 391–398.

[140] Schlenker, W. & Roberts, M. (2009a). Nonlinear temperature effects indicate severe damage to U.S. crop yields under climate change. *Proc. Natl. Acad. Sci. USA*, 106, 15594–15598.

[141] Schlenker, W. & Roberts, M. (2009b). Reply to Meerburg et al.: Growing areas in Brazil and the United States with similar exposure to extreme heat have similar yields. *Proc. Natl. Acad. Sci. USA*, 106, E121.

[142] Schlenker, W., Roberts, M., & Lobell, D. (2013). US maize adaptability. *Nature Clim. Change*, 3, 690–691.

[143] Schwartz, M. D., Ahas, R., & Aasa, A. (2006). Onset of spring starting earlier across the northern hemisphere. *Glob. Ch. Biol.*, 12, 343–351.

[144] Semenov, M. A. & Shewry, P. R. (2011). Modeling predicts that heat stress, not drought, will increase vulnerability of wheat in europe. *Nature Scientific Reports*, (pp. DOI: 10.1038/srep00066).

[145] Siebert, S., Burke, J., Faures, J., Frenken, K., Hoogeveen, J., Döll, P., & Portmann, F. (2010). Groundwater use for irrigation - a global inventory. *Hydrol. Earth Syst. Sci.*, 14, 1863–1880.

[146] Sinclair, T. (2011). Challenges in breeding for yield increase for drought. *Trends Plant Sci.*, 16, 289–293.

[147] Singletary, G., Banisadr, R., & Keeling, P. (1994). Heat stress during grain filling in maize: Effects on carbohydrate storage and metabolism. *Aust. J. Plant Physiol.*, 21, 829–841.

[148] Smil, V. (2001). *Enriching the Earth*. Cambridge, Massachusetts: MIT Press.

[149] Smith, W. (1914). The Effect of Weather upon the Yield of Corn. *Monthly Weather Review*, 42, 78–94.

[150] Steinke, S., Kienast, M., Groeneveld, J., Lin, L.-C., Chen, M.-T., & Rendle-Bühring, R. (2008). Proxy dependence of the temporal pattern of deglacial warming in the tropical South China Sea: toward resolving seasonality. *Quaternary Science Reviews*, 27, 688–700.

[151] Stine, A., Huybers, P., & Fung, I. (2009). Changes in the phase of the annual cycle of surface temperatures. *Nature*, 457, 435–440.

[152] Stott, L., Timmerman, A., & Thunell, R. (2007). Southern hemisphere and deep-sea warming led deglacial atmospheric CO2 rise and tropical warming. *Science*, 318, 435–438.

[153] Sun, Y., Oppo, D., Xiang, R., Liu, W., & Gao, S. (2005). Last deglaciation in the Okinawa Trough: Subtropical northwest Pacific link to Northern Hemisphere and tropical climate. *Paleoceanography*, 20, PA4005, doi:10.1029/2004PA001061.

[154] Tack, J., Singh, R. K., Nalley, Lawton, L., Viraktamath, B. C., Krishnamurty, S. L., Lyman, N., & Jagadish, Krishna, S. (2015). High vapor pressure deficit drives salt-stress-induced rice yield losses in India. *Global Change Biology*, (pp. doi: 10.1111/gcb.12803).

[155] Tai, A. P., Val Martin, M., & Heald, C. L. (2014). Threat to future global food security from climate change and ozone air pollution. *Nature Clim. Change*, 4, 817–821.

[156] Taiz, L. & Zeiger, E. (2002). *Plant Physiology*. Sinauer Associates, third edition edition.

[157] Thompson, L. (1975). Weather Variability, Climatic Change, and Grain Production. *Science*, 188, 535–541.

[158] Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, 108(50), 20260–20264.

[159] Tollenaar, M. & Bruulesma, T. (1988). Effects of Temperature on Rate and Duration of Kernel Dry Matter Accumulation of Maize. *Can. J. Plant Sci.*, 68, 935–940.

[160] Tollenaar, M. & Wu, J. (1999). Yield Improvement in Temperate Maize is Attributable to Greater Stress Tolerance. *Crop Sci.*, 39, 1597–1604.

[161] Ummenhofer, C., Xu, H., Twine, T., Girvetz, E., McCarthy, H., Chhetri, N., & Nicholas, K. (2015). How Climate Change Affects Extremes in Maize and Wheat Yield in Two Cropping Regions. *J. Climate*, in press(doi:10.1175/JCLI-D-13-00326.1).

[162] UN (2013). *World Population Prospects: The 2012 Revision*. New York: Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat, United Nations.

[163] USDA (2015). *Grain: World Markets and Trade, February*. Technical report, Foreign Agricultural Service/USDA.

[164] Wahid, A., Gelani, S., Ashraf, M., & Foolad, M. (2007). Heat tolerance in plants: An overview. *Environ. Exp. Bot.*, 61, 199–223.

[165] Wallace, H. (1920). Mathematical Inquiry into the Effect of Weather on Corn Yield in the Eight Corn Belt States. *Monthly Weather Review*, 48, 439–446.

[166] Wang, J. (1960). A Critique of the Heat Unit Approach to Plant Response Studies. *Ecology*, 41(4), 785–790.

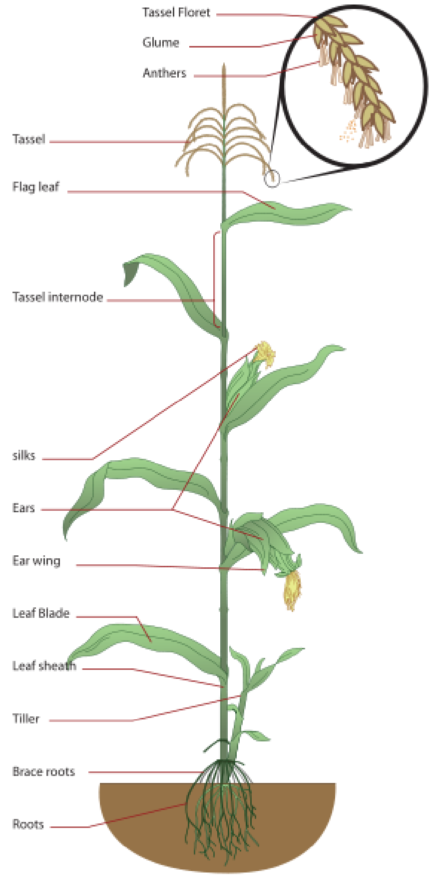
[167] Wilhelm, E., Mullen, R., Keeling, P., & Singletary, G. (1999). Heat Stress during Grain Filling in Maize: Effects on Kernel Growth and Metabolism. *Crop Sci.*, 39, 1733–1741.

[168] Xu, J., Holbourn, A., Kuhnt, W., Jian, Z., & Kawamura, H. (2008). Changes in the thermocline structure of the Indonesian outflow during Terminations I and II. *Earth and Planetary Science Letters*, 273(1–2), 152–162.

[169] Yan, W. & Hunt, L. A. (1999). An Equation for Modelling the Temperature Response of Plants using only the Cardinal Temperatures. *Ann. Bot*, 84, 607–614.

[170] York, D., Evensen, N. M., Martínez, M. L., & Delgado, J. D. B. (2004). Unified equations for the slope, intercept, and standard errors of the best straight line. *Am. J. Phys.*, 72(3), 367–375.

[171] Zaitchik, B. F., Macalady, A. K., Bonneau, L. R., & Smith, R. B. (2006). Europe's 2003 heat wave: A satellite view of impacts and land-atmosphere feedbacks. *Int. J. Climatol.*, 26, 743–769.



This thesis was typeset using LaTeX, originally developed by Leslie Lamport and based on Donald Knuth's TeX. The figure above can be found on the Wikimedia commons at commons.wikimedia.org/wiki/Maize-plant. A template that can be used to format a PhD thesis with this look and feel has been released under the permissive MIT (X11) license, and can be found online at github.com/suchow/Dissertate or from its author, Jordan Suchow, at suchow@post.harvard.edu.