

Adaptation of US maize to temperature variations

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High temperatures are associated with reduced crop yields^{1,2}, and predictions for future warming³ have raised concerns regarding future productivity and food security⁴⁻⁸. However, the extent to which adaptation can mitigate such heat-related losses remains unclear⁹⁻¹³. Here we empirically demonstrate how maize is locally adapted to hot temperatures across US counties. Using this spatial adaptation as a surrogate for future adaptation, we find that losses to average US maize yields from a 2 °C 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 adaptation¹⁴⁻¹⁸, 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.

Global maize yields are forecast to decline in response to increasing temperature, particularly as the upper range of growing season temperatures become hotter^{1,2,4-7,19}. The sensitivity of crop yields to increased temperature is often estimated through analysis of variability in annual yield and growing season temperature^{1,2,7,19}, 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, US corn hybrids have a product half-life of about 4 years¹¹, suggesting sufficiently rapid turnover to adapt to decadal changes in climate. To explore the adaptability of maize production to long-term differences in climate, we analyse 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 US because relatively high-quality data and a highly adapted and managed agricultural demographic can be assumed. Yield data are available from more than 1,600 counties between 1981 and 2008 from the United States Department of Agriculture/National Agriculture Statistics Service²⁰ in the Eastern US, and daily temperature is estimated for each county using a network of 534 weather stations²¹ for which daily minimum and maximum surface air temperature is available.

The influence of temperature on 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^{1,15,22,23}, 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^{1,15}, but we use a new approach to define the growing season using average planting and harvest dates reported for each state on each year²⁰, 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^{1,2,19}. Whereas GDDs are indicative of higher yields (for example, by enabling a longer period of grain development), KDDs decrease yield (for example, by accelerating the plant through grain development or directly damaging plant tissue or enzymes^{24,25}). Note that although 29 °C is a low threshold for the initiation of damage²⁶, stressed maize plants have been shown to experience higher temperatures than the air measured above the crop canopy²⁷.

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,

$$Y = \beta_0 + \beta_1 t + \beta_2 GDD' + \beta_3 KDD' + \epsilon \quad (1)$$

A prime indicates that the sample mean is removed. The β coefficients are fitted 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 equation (1) to each county results in an average squared cross-correlation between predictions and observations of $R^2 = 0.65$ (Supplementary Fig. S1). For comparison, other recent empirical fits to maize data obtained an R^2 of 0.47 with four adjustable parameters⁶ and 0.77 using about 20 adjustable parameters¹. An F -test is then used to determine whether the full model of equation (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 more than 1,600 to a subset of 1,013 counties showing a statistically significant relationship with temperature variations (Supplementary Fig. S2), although a similar result is obtained when using the full sample. See the Methods for a further description of the model and the Supplementary Information for a more detailed case study.

The sensitivity of yield to GDD has values of 0.15 (bushels per acre)/GDD in cool northwestern regions of the study domain and trends to values near zero in the hotter southeastern regions (Fig. 1a). Yield sensitivity to KDDs (Fig. 1b) is nearly orthogonal to that of GDDs, trending from more negative than -0.5 (bushels per acre)/KDD in northeastern regions towards less negative than -0.2 (bushels per 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 climates²⁵.

Our focus will be on KDD regional variation in sensitivity and the consequences of a warming climate. Field trials on cultivars planted in different regions of the US have demonstrated a pattern

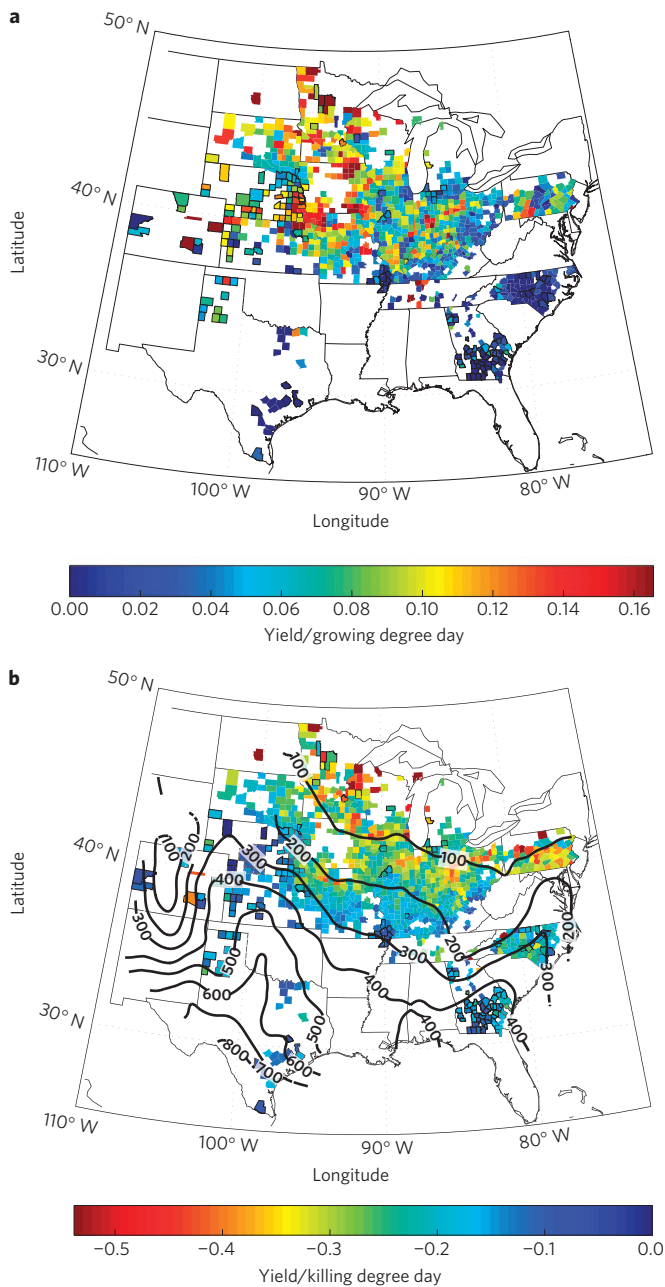


Figure 1 | Sensitivity of maize yield to temperature variations. a, Yield sensitivity to GDDs. **b,** Yield sensitivity to KDDs (shading) and the climatological average of KDDs (contours). Counties with at least 10% of their crop area irrigated are indicated by black borders.

of heat tolerance⁹ 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, osmotic adjustment and membrane structures that confer drought resistance^{9–11}. Although 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 study¹ 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 (see the Supplementary Information).

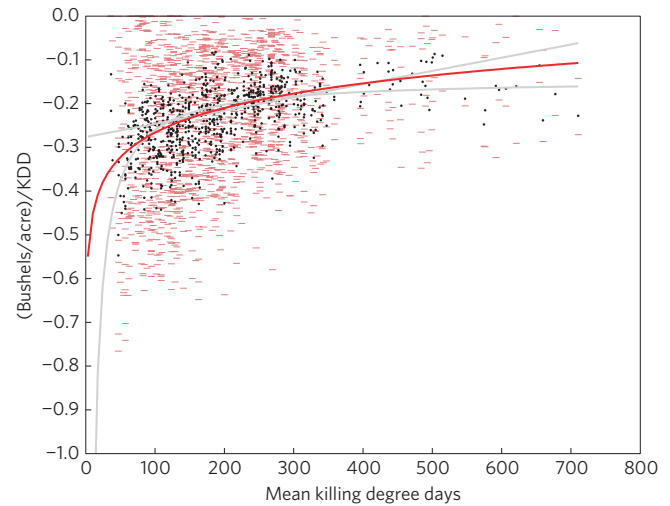


Figure 2 | The climatological average KDDs versus the sensitivity of yield to KDDs for individual US counties. A logarithmic fit provides a functional relationship between climatology and sensitivity (red line, equation (2)). For reference, linear and inverse fits are also included (grey lines) and would 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 per acre)/KDD are not shown as they have little influence on the weighted fit.

We interpret the varied spatial sensitivity to KDDs diagnosed across US 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. 2) and irrigated crops (Supplementary Fig. S3) that can be approximated using a logarithmic relationship,

$$\beta_3 = \alpha_0 + \alpha \ln(\overline{KDD}) + \eta \tag{2}$$

Equation (2) is fitted 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 $\alpha_0 = -0.64$ (bushels per acre)/KDD (with a bootstrapped 95% confidence interval (c.i.) of -0.69 to -0.59) and an adaptation factor of $\alpha = 0.08$ (bushels per acre)/(KDD $\ln(\overline{KDD})$) for unirrigated crops (95% c.i., 0.07 – 0.09). For irrigated crops the base sensitivity is much lower, $\alpha_0 = -0.38$ (95% c.i., -0.47 to -0.28), and adaptation is weaker, $\alpha = 0.04$ (95% c.i., 0.02 – 0.06).

Essentially, equation (2) states that hotter counties are less sensitive to yield losses from heat but that differences in sensitivity asymptote to zero towards 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 on extrapolation. Furthermore, when we consider a 2°C warming scenario (Supplementary Fig. S5), 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 per acre)/KDD, whereas the domain average is 0.05 (bushels per acre)/KDD. Exclusion of these 18 counties would have no influence on yield statistics at the reported precision level.

Equation (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 an open

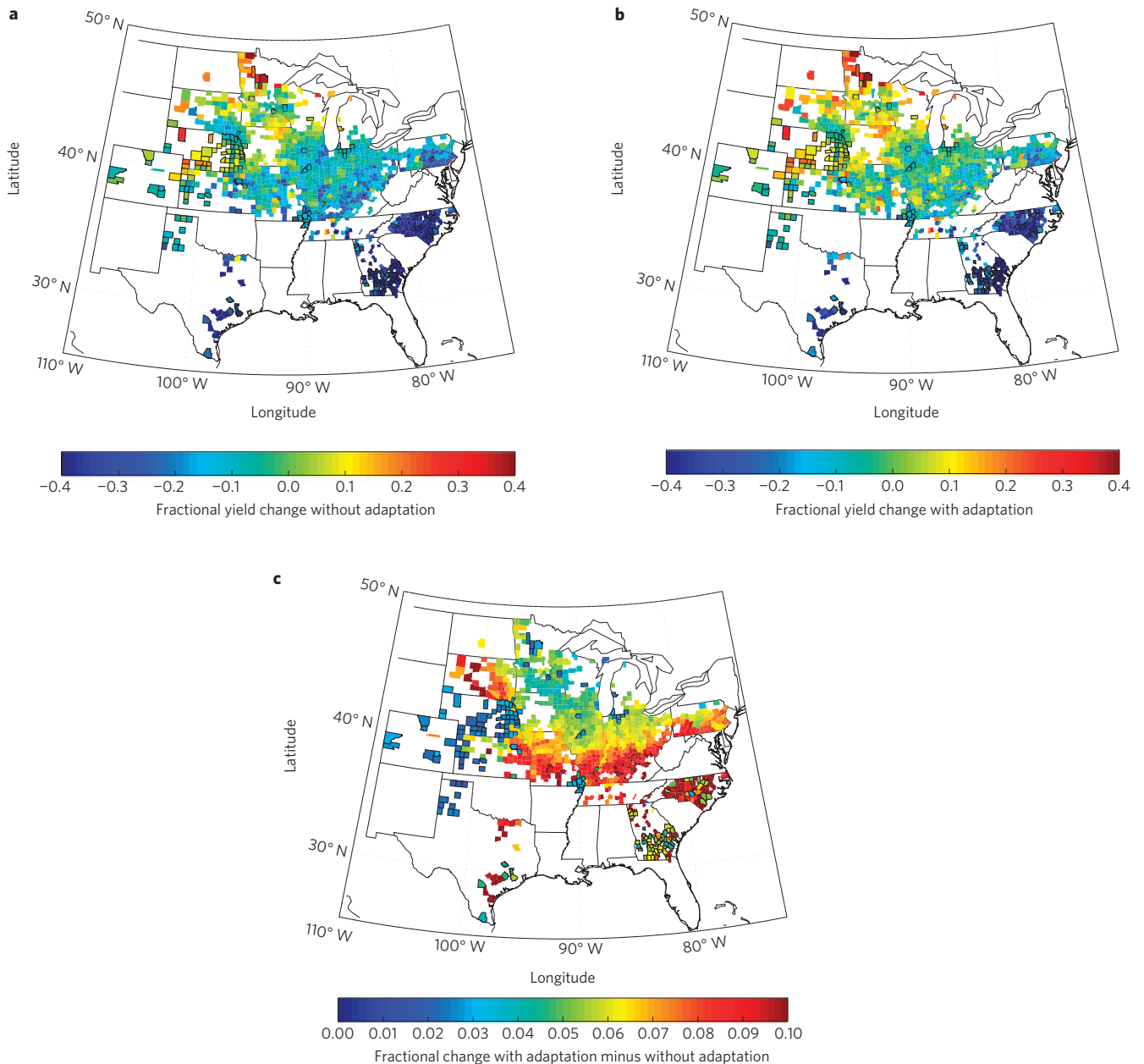


Figure 3 | Changes in yield from a 2°C warming. **a**, Without adaptation warming causes yield to decrease by 14% on average, although counties in the deep south lose more than 50% of their yield, whereas those in the northwest increase by as much as 30%. The colour bar saturates at $\pm 40\%$ to highlight 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 colour bar saturates at 10% to highlight variation across most counties. As in Fig. 1, black borders indicate irrigated counties.

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.

To explore the implications of the observed spatial adaptation to KDDs for the sensitivity of yield to warming, we redefine β_3 in equation (1) to follow the adaptation function given by equation (2),

$$Y = \beta_0 + \beta_1 t + \beta_2 GDD' + (\alpha_0 + \alpha \ln(\overline{KDD}) + \eta) KDD' + \epsilon \quad (3)$$

In equation (3), as climatological KDDs increase with greater warming, it is assumed that cultivar selection and management practices are adjusted in keeping with the extant adaptation observed across the US. Yield is solved for each county and each

year using the β , ϵ , α and η terms from equations (1) and (2) such that, in the absence of any change in temperature, the original yield data are recovered.

To illustrate the differences between non-adapted (equation (1)) and adapted (equation (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 warming²⁸. 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. 3a). Furthermore, warm regions will gain KDDs more rapidly in response to uniform warming because they have more days that already exceed the 29° threshold. The (unweighted) average yield decrease across all counties is 14% for a 2°C warming without adaptation.

This result is generally consistent with foregoing estimates, although comparisons are limited by the fact that different spatial averages are considered. One study⁶ found a 17% decline in global average yields in response to a 2°C warming. Another study¹ found a 15% decline in an area-weighted average of eastern US 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 US 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. 3b,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 last regions are already well above the optimal temperature for present US 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 with the corn belt, and one consequence of increased temperature could be migration of maize production towards 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.

The adaptation function that we have empirically estimated for a theoretical warming is consistent both with extant regional adaptation and field trials of differing cultivars⁹, 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 yields¹⁶. To further explore the issue of trade-offs, we extend equation (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 (Supplementary Figs S6 and S7). 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-alone 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 specific changes. Furthermore, there are also potential benefits to warming that we have not included in our model, such as greater flexibility in planting times¹⁵, a longer growing season and opportunities for cultivating new regions²⁹. Finally, note that most, if not all, of these forms of adaptation can be implemented only in a warmer climate, explaining why farmers that we expect to benefit from adaptation have not yet made such changes.

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 per acre)/KDD smaller than neighbouring counties without irrigation, a difference that is highly significant ($P < 0.01$, using a one-sided t -test, see Fig. 1b) and is in qualitative agreement with other findings^{14,18}. Prize-winning yields from the 2010 to 2011 National Corn Yield Contest also point to the importance of irrigation. For unirrigated crops, the median prize-winning yields increase from 216 bushels per acre in the south, to 247 in the centre and 266 in the north of the US (regional groupings follow that of a previous study¹). For irrigated crops, however, median southern yields are 260 bushels per acre, central yields are 267 and northern ones are 247. The highest yields come from Texas with 370 bushels per 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 temperature³⁰ but probably 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 (Supplementary Fig. S8), 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 fitted adaptation function partially accounts for the expectation that warming will cause dry regions to become drier³¹, although further explicit examination of the influences of water availability on yield is necessary.

Losses to US maize yield from increased temperature are almost certainly overestimated if adaptation is not accounted for^{1,7}, and here we have shown that adaptation could decrease the average fractional losses in the Eastern US by roughly a factor of 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 on 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.

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. 2) 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 fitted ($P < 0.05$) by equation (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 equation (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°C 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 (Supplementary Fig. S9). We found no clear spatial pattern in optimal threshold values and, for consistency, selected the same threshold of 29 °C used in previous studies^{1,19}. Calculating GDDs after capping daily maximum temperatures at 29 °C to exclude overlap with KDDs also had little overall effect.

Inclusion of a freezing degree day term in equation (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, to minimize the influence from trends and regional differences in yield^{1,2}. Repeating our analysis using logarithmically transformed yields gave a similar relationship between climatological KDDs and the sensitivity to KDDs (compare Supplementary Fig. S10 and Fig. 2) and lower yield losses of 11% without adaptation and 2% with adaptation.

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.

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Author contributions

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Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to E.E.B.

Competing financial interests

The authors declare no competing financial interests.