Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures

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Abstract

The importance of temperature in the determination of the yield of an annual crop (groundnut; *Arachis hypogaea* L. in India) was assessed. Simulations from a regional climate model (PRECIS) were used with a crop model (GLAM) to examine crop growth under simulated current (1961–1990) and future (2071–2100) climates. Two processes were examined: the response of crop duration to mean temperature and the response of seed-set to extremes of temperature. The relative importance of, and interaction between, these two processes was examined for a number of genotypic characteristics, which were represented by using different values of crop model parameters derived from experiments.

The impact of mean and extreme temperatures varied geographically, and depended upon the simulated genotypic properties. High temperature stress was not a major determinant of simulated yields in the current climate, but affected the mean and variability of yield under climate change in two regions which had contrasting statistics of daily maximum temperature. Changes in mean temperature had a similar impact on mean yield to that of high temperature stress in some locations and its effects were more widespread. Where the optimal temperature for development was exceeded, the resulting increase in duration in some simulations fully mitigated the negative impacts of extreme temperatures when sufficient water was available for the extended growing period. For some simulations the reduction in mean yield between the current and future climates was as large as 70%, indicating the importance of genotypic adaptation to changes in both means and extremes of temperature under climate change.
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1. Introduction

Under climate change, increases in both the mean and extremes of temperature are expected for many parts of the globe (IPCC, 2001a). These changes can impact the growth and development of crops in a number of ways. Temperature is a key determinant of evaporative and transpirative demand, particularly in tropical regions (e.g. Priestley and Taylor, 1972). Sustained temperature increases over the season will change the duration (from sowing to maturity) of the crop (e.g. Roberts and Summerfield, 1987) whilst short episodes of high temperature at critical stages of crop development can impact yield independently of any substantial changes in mean temperature (e.g. Wheeler et al., 2000; McKeown et al., 2005).

High temperature stress is perhaps the most complex and least accurately quantified of the processes described above. Threshold temperatures for flower production and seed abortion have begun to be identified by field and controlled environment studies for a number of crops, including wheat, rice, maize and groundnut (see e.g. Ferris et al., 1998; Rötter and van de Geijn, 1999; Ismail and Hall, 1999; Matsui et al., 2001). This has enabled crop simulation models to begin to simulate the impact of heat stress (e.g. Matthews et al., 1995; Challinor et al., 2005c). This means that some crop models

can be used to explore the various pathways through which temperature impacts crop yield.

A full assessment of the impacts of changes in temperature involves an analysis of the socio-economic impacts resulting from the biophysical processes. For this reason, integrated assessments of the impacts of climate change often simulate crop yield, land-use change and world food trade. The treatment of crop growth and development in these assessments tends to be based on empirical methods. For example, Parry et al. (2004) used parameterisations of crop model functions, whilst Fischer et al. (2002) used observed statistical relationships based on those of Doorenbos and Kassam (1979). These methods are pragmatic advances, but they do not account for the possible impacts of high temperature stress. In some cases intra-seasonal variability in weather is accounted for at only the coarsest temporal resolution (i.e. monthly).

Changes in atmospheric carbon dioxide concentration and in the seasonal cycle may mean that statistical relationships between weather and crop yield developed under the current climate are not valid under climate change (Challinor et al., 2005b). The increasing recognition of the importance of weather extremes, intra-seasonal variability and climate thresholds is reflected in crop modelling studies (e.g. Semenov and Porter, 1995; Easterling et al., 1996; Semenov and Barrow, 1997; Hansen and Jones, 2000; Challinor et al., 2005c; Porter and Semenov, 2005). Used in conjunction with weather inputs, process-based crop models provide a method for the quantification of the impact of the causative pathways between weather and yield, and the interaction between these pathways and plant characteristics (e.g. Sinclair and Muchow, 2001). Weather stations are one possible source of data for crop simulation models (e.g. Sultan et al., 2005). However, if yields are to be simulated over large areas or for future climate scenarios then alternative sources of data are needed. Weather inputs over large areas commonly come from gridded climate model output of the kind used by Challinor et al. (2005a,b).

This study uses regional climate modelling simulations for the current climate and one future climate scenario, together with a process-based crop model, to quantify the impact of temperature changes on the crop. The impacts are examined using a number of sets of crop parameter values, representing different crop responses to the mean and extremes of temperature. Two key responses in particular are analysed: the impact of mean temperature on duration, and the impact of extremes of temperature at a critical stage of crop development (flowering). The primary objective of the study is to explore the importance of genotypic selection in response to changes in the mean and extremes of temperature. This includes assessment of the relative importance of, and interaction between, these processes for the case of groundnut (Arachis hypogaea L.) in India. The secondary objective is to highlight regions within India that are at risk from the changes in temperature statistics that are expected under climate change. Since only one climate change scenario is used no attempt is made to make firm projections regarding crop productivity changes.

2. Materials and methods

2.1. Crop and climate models

Two climate simulations from the joint Indo-UK program (IITM, 2004) on climate change were used in this study. As part of this program the PRECIS regional climate model (http://www.metoffice.com/research/hadleycentre/models/PRECIS.html) was used to simulate present-day and future climates. For the present-day (baseline) case the HadAM3 general circulation model (GCM) was run with observed sea surface temperatures in order to produce the boundary conditions for PRECIS. For the future climate simulations a coupled GCM (HadCM3) was used to simulate changes in climate and these changes were added to the baseline values in order to produce the boundary conditions. Availability of the data at the time of the present study limited the scenarios used to a baseline 1961–1990 simulation, and a 2071–2100 A2 simulation, both without sulphur. The A2 scenario is one of the most extreme scenarios, with emissions rising monotonically from present-day values (<10 Gt of carbon) to over 25 Gt of carbon in 2100 (IPCC, 2001b).

The crop model used in this study is the General Large-Area Model for annual crops (GLAM; Challinor et al., 2004, 2005c). This was designed in order to capitalise on the predictability that is suggested by large-area relationships between weather and climate (Challinor et al., 2003). The model is sufficiently complex as to allow mechanistic simulation of crop-climate processes, and sufficiently simple for use over large areas, without the need to parameterise sub-regional variability. GLAM has been used to simulate groundnut pod yields with observed gridded data (Challinor et al., 2004), reanalysis data (Challinor et al., 2005a,b) and probabilistic seasonal forecast data (Challinor et al., 2005b). In this way, understanding of processes (such as the role of intra-seasonal variability) and confidence in simulation results for climate change has been developed using simulation in the current climate (see e.g. Stooksbury and Michaels, 1994). On the whole these studies show that mean yields are simulated well by the model, with the standard deviation being too small over most of India and too large in parts of the southern Indian peninsula. The pattern of inter-annual variability in these studies (as measured by the correlation coefficient between observed and simulated yields) is simulated well in the northwest of India, and with variable accuracy in other regions.

The parameter values used in this study were those for groundnut developed by Challinor et al. (2004), since this has been tested extensively (Challinor et al., 2004, 2005a,b,c). The one exception to this is that since net radiation input data is used the surface albedo in the crop model is set to zero. The parameterisation of high temperature stress, which was not

included in Challinor et al. (2004), follows Challinor et al. (2005c); (hereafter GLAM-HTS—high temperature stress). The parameterisation of water stress near anthesis follows Challinor et al. (2006). One further modification to the GLAM-HTS parameterisation was made: a minimum value of 40 °C (suggested by the data of Vara Prasad, 1999 and Kakani, 2001) for one of the critical temperatures (T_{lim}) was introduced, since the standard parameterisation produced some unrealistically low values when used with the climate data in this study.

2.2. Calibration methods

GLAM is calibrated by varying the yield gap parameter (YGP) and choosing the value that minimises the difference between observed and simulated yields. YGP simply multiplies the potential maximum rate of change of leaf area index in order to give a value that is limited by non-climatic factors such as pests, diseases and nutrients. In practice YGP can also act to correct bias in the input weather data (Challinor et al., 2005b). The yield data for calibration are from the district-level database of agricultural returns compiled by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. The time series of pod yield (1966–1989) for each individual district was linearly detrended to 1966 levels in order to remove the influence of improved varieties and management methods. Each grid cell was assigned uniquely to a district (one-to-many mapping) according to the location of its centre. The yield data include both the monsoon (rainfed) season and winter (irrigated) season. Fig. 1 presents the mean and standard deviation of the yield data. Challinor et al. (2003, 2004) have more discussion on these data.

In developing calibration methods for the present study, two separate methods were developed. Appendix A describes these methods and the resulting choice of calibration method for the remainder of the study. The use of YGP values calibrated using the baseline climate in projections of future climates raises an important issue: will changes in YGP between the two time periods be greater than the climate-induced changes in yield? Challinor et al. (2005b) showed that providing the technology trend has been removed, fluctuations in the calibrated value of YGP on decadal timescales are small, at least between the 1960s and the 1990s.

2.3. Crop simulation experiments

Six crop simulation experiments, with varying crop parameter values, were carried out. Parameters were varied in order to simulate different genotypic responses to two key processes: (i) the impact of high temperatures near flowering, and (ii) the impact of mean temperature on crop duration. The crop model is formulated such that the choice of parameter values for each of these processes does not affect the response of the crop to the other process. All simulations used the same sowing window (Reddy, 1988); the crop is sown on the first day in which the soil moisture exceeds a specified threshold (see Challinor et al., 2004).

Following GLAM-HTS, the parameters used to determine the critical temperatures (step (i) above) and/or the response of harvest index to P_{tot} were changed in order to simulate a sensitive (SEN), moderately sensitive (MOD) and tolerant (TOL) crop genotype. The simulations of GLAM-HTS showed that the impact of high temperatures near anthesis (flowering) in GLAM can be heavily dependent on
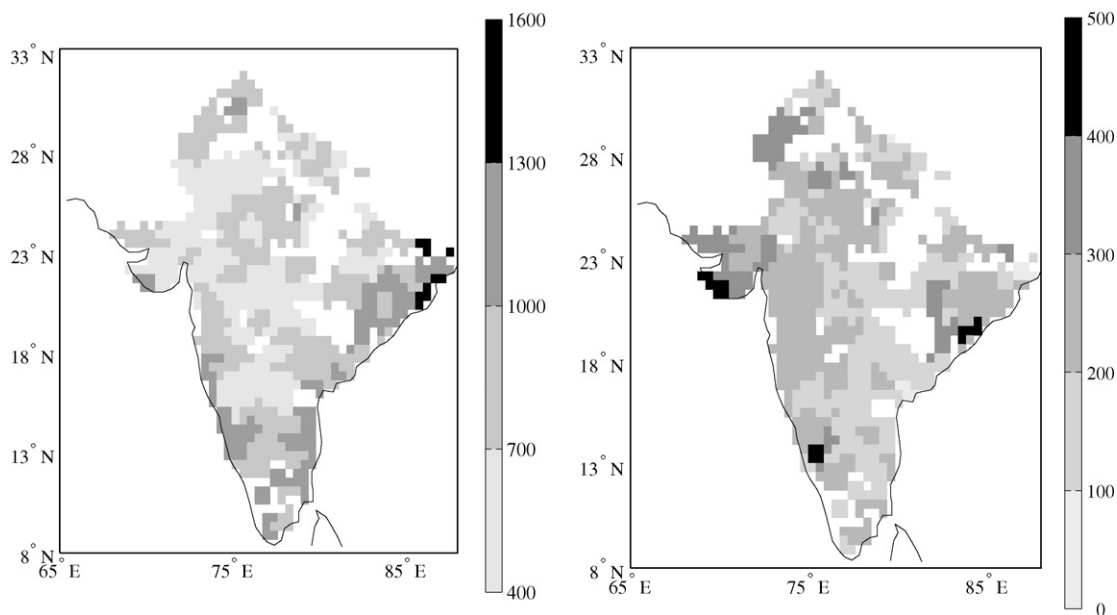

Fig. 1. Mean (left panel) and standard deviation of observed yields, in kg/ha, over the time period 1966–1989. Data have been linearly detrended to 1966 levels, and are presented on the grid used for modelling.

the temporal pattern of flowering (i.e. the fraction of total flowers associated with yield that form each day). This temporal pattern is determined by the choice of flowering distribution, F. For the present study, the choice of tolerant or sensitive crop parameter values was found to provide greater variability in yield than the choice of F within crop genotype. Hence a single flowering distribution (F3 from GLAM-HTS) was used for all the simulations reported.

Simulations for the baseline climate were carried out using the MOD parameter set; there is little difference between this simulation and a simulation using either TOL or SEN. The results presented for the future climate scenario are for the TOL and SEN cases. The response of crop development rate to mean temperature was varied using the optimal temperature (T_{opt}): one set of simulations used $T_{opt} = 28\ °C$, which is at the lower end of the observed range, and is the calibrated value used in previous GLAM-groundnut studies over India. A second set of simulations used $T_{opt} = 36\ °C$; this is at the high end of the observed range for groundnut (Ong, 1986). Hence the six simulations carried out consist of three for each value of T_{opt}: a baseline (current climate) simulation, and two 2071–2100 simulations (TOL, SEN). The baseline $T_{opt} = 36\ °C$ simulation was only used to assess percentage changes from the 2071 to 2100 projection; the $T_{opt} = 28\ °C$ baseline run was used for assessing the skill of the simulations. Simulations for 2071–2100 are referred to using the high temperature stress parameter set, followed by the value of the optimal temperature for development (e.g. SEN-28).

The six simulations were repeated with the high temperature stress parameterisation switched off. Together with an analysis of the impact of high temperatures on the rate of change of harvest index, this allowed quantification of the sensitivity of yield changes (between the baseline period and the projection) to processes associated with mean and extreme temperatures. The results of this analysis are presented in Section 4. The simulations are listed, together with the figures in which they are presented, in Table 1.

Since the uncertainty associated with the CO_2 fertilisation effect, both simulated and actual, is substantial (Kimball et al., 2002; Challinor et al., 2005d; Ainsworth and Long, 2005) this process is not examined in this study; the transpiration efficiency and water-use characteristics of the

crop are held constant between the two time periods studied. This means that whilst one contribution to the uncertainty in yield simulation is avoided, caution in needed in any direct interpretation of yield projections. Note, however, that despite accounting for the beneficial effects of carbon dioxide, Mall et al. (2004) projected decreases in soybean yields across India under doubled CO_2. Whilst this projected decrease is not necessarily a consensus result, there is some evidence that projected increases in crop yield under elevated CO_2 may, due to high temperature stress, result in no increase in yield (Vara Prasad et al., 2002; Sivakumar et al., 2005). There is also some evidence that the beneficial impacts of CO_2 may not be as large as previously thought (Long et al., 2005). These observations are merely suggestive, however; there may be an interaction between high CO_2 and high temperature stress that, if parameterised, would produce different results. This is clearly an area for future work.

2.4. Analysis methods

In order to examine the changes in climate between the two time slices, differences in the mean and standard deviation of climate variables were calculated. In addition, the number of days in July (when the crop usually flowers) with temperatures exceeding a given threshold was computed by analysing daily maximum temperature (T_{max}). Differences in this statistic between the two time slices indicate regions where the risk of high temperature stress increases. This statistic can also be adjusted in order to determine the extent to which changes in exceedance rates in a grid cell are due to changes in the mean of T_{max}, both the mean and the variance, or the shape of the probability distribution function (Ferro et al., 2005; Appendix B). This analysis can begin to distinguish the impacts of different types of change in the PDF of temperature: changes in the mean affect crop duration (see e.g. GLAM-HTS) and changes in variance can have a greater impact on extreme temperatures (e.g. Katz and Brown, 1992). The contribution of changes in the mean, variance and shape of the temperature distributions to changes in temperature threshold exceedance is assessed using this method in Section 3.2.

The choice of threshold temperature for the analysis described above was 34 °C. A sensitive groundnut variety would show some impacts of high temperature stress for mean 8 a.m. to 2 p.m. temperatures above this value during flowering. Hence this choice corresponds to the onset of heat sensitivity in a groundnut crop (Vara Prasad et al., 2001). More importantly, it is a temperature above which other crops are likely to be affected by heat stress: threshold temperatures for wheat, rice and maize are estimated to be in the region 30–36 °C, and durations of the order of hours can be enough to impact the crop (Rötter and van de Geijn, 1999). Note that threshold temperatures for temperate crops may be lower than those of tropical crops (Wheeler et al., 1996; Matthews and Wassmann, 2003); McKeown et al.

Table 1
List of simulations carried out and figures where corresponding results appear

Period	Parameter set	Figures
1961–1990	MOD-28	Figs. 1, 5, 6, 7, 8
1961–1990	MOD-36	Figs. 6, 8
2071–2100	SEN-28	Figs. 2, 3, 5, 6, 8
2071–2100	SEN-36	Figs. 6, 8
2071–2100	TOL-28	Figs. 2, 3, 5, 6, 7, 8
2071–2100	TOL-36	Figs. 2, 6, 8

Numbers in italics refer to figures with percentage changes across both time series.

(2005) used a threshold of 30 °C to explain the impacts of high temperatures on annual horticultural crops.

A number of yield-related quantities were analysed: final pod yields and the percentage of pods setting are direct model output. Percentage changes in yield between current and projected climates always use simulations with the same value of T_{opt} (28 or 36 °C). The fraction of pods setting due to temperature stress only was calculated by discounting the impact of water stress on pod-set in the model. In some years in some regions the seasonal cycle of temperature is such that the thermal time requirement of the crop is not met. These crop seasons are not included in the analysis.

3. Results

3.1. Baseline climate

The accuracy of GLAM in simulating the mean and standard deviation of yield is shown in Fig. 2. Over most of India, mean yields are simulated well and the standard deviation (σ_s) is underestimated. The main exception to this is the central and eastern parts of the southern peninsula, where simulated mean yields are too low and σ_s is too high. This is also the region where simulated rainfall is too low (see IITM, 2004) with mean values being between 100 and 400 mm over most of this region. These low values are likely to contribute to the poor simulation of yields in this region. Another contributing factor may be the lack of simulation of the irrigated crop; when averaged over the 1966–1989 period, the area under irrigation accounts for up to 25% of total growing area over this region. Simulation of yields in this part of India has been improved by bias correction of

seasonal total rainfall towards observations, and by use of a later planting window, in at least one study (Challinor et al., 2005a). The results for the simulation of yields in the baseline climate are broadly similar to those of previous studies (see Section 2.1).

3.2. Climate change scenario

The climate projection for 2071–2100 shows various changes in climate that are relevant to crop growth and development. The mean of cumulative precipitation during the simulated growing season increases over most of India (by up to 60%) and the standard deviation also increases in most regions (by up to 20%). Mean growing-season temperature increases everywhere from its baseline values (mostly 24–28 °C), most markedly in the north-west (increases of up to 5 °C). The variability of mean temperature increases over most of India (by up to 0.5 °C).

The response of the crop to changes in precipitation and temperature is that, over most of India, the mean and variability of yield fall between the two simulation periods (Fig. 3). Since precipitation over most of India increases between the two periods, this is not the cause of the yield decreases. Rather, it is changes in crop duration across India, and incidence of high temperature stress in parts of the north and south, that cause the changes in yield. These causes are examined in more detail below.

3.2.1. High temperature stress

An indication of likely crop responses to high temperatures comes from examining the increase, between the two time slices, in the mean number of July days with $T_{max} > 34$ °C. The analysis is based on daily maximum

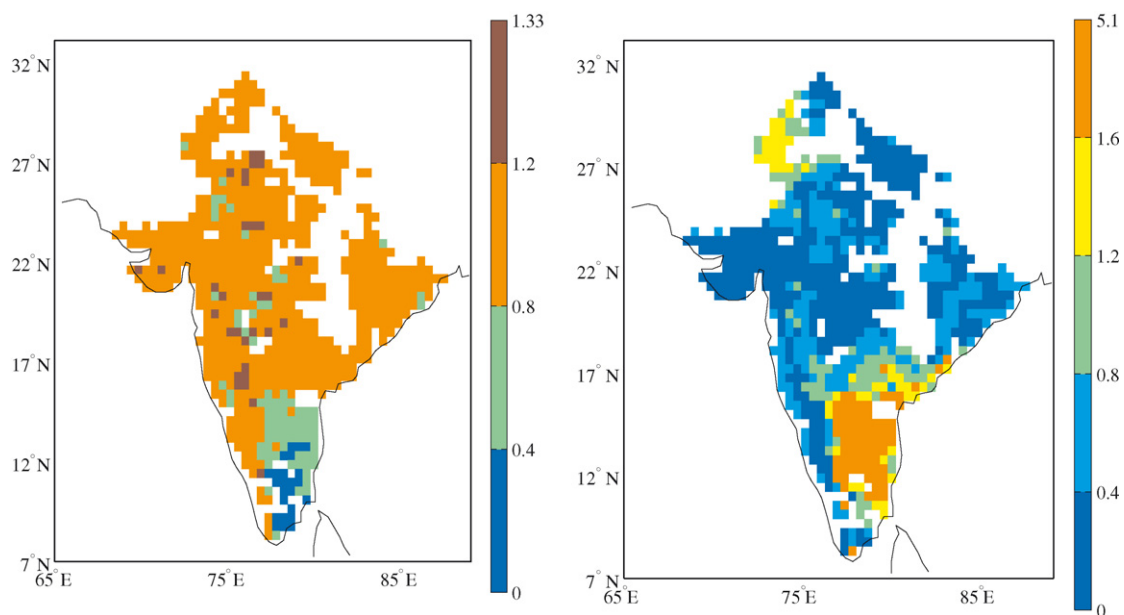Fig. 2. Ratio of simulated to observed mean (left panel) and standard deviation (right panel) of yield for the baseline simulation with $T_{opt} = 28$ °C. Only grid cells with at least 5 years of completed simulations are shown.
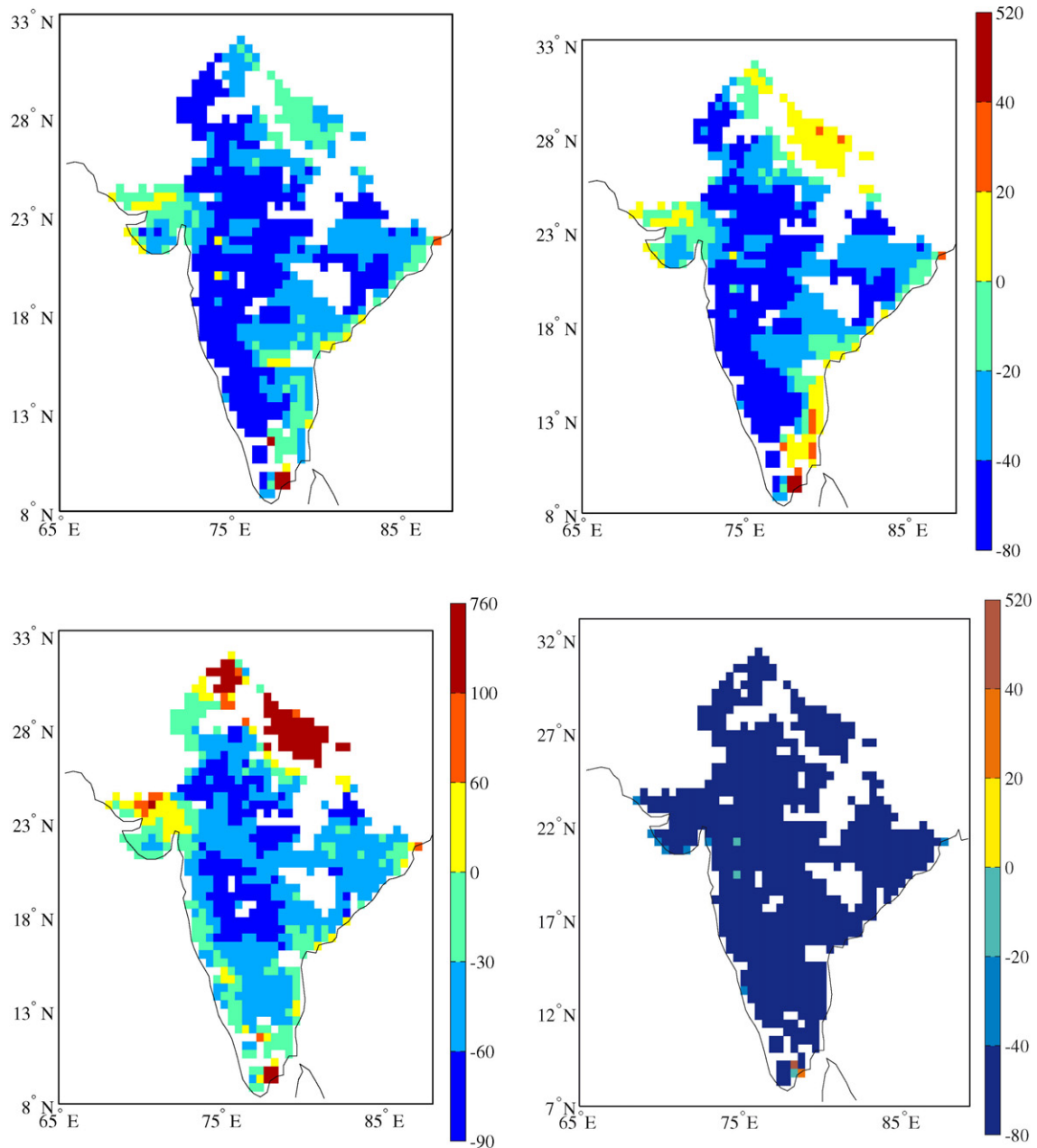
Fig. 3. Percentage change in the mean yield for 2071–2100 simulations relative to the respective baseline simulation: SEN-28 (top left panel), TOL-28 (top right) and TOL-36 (bottom right). The corresponding plot of SEN-36 (not shown) is very similar to TOL-36. The percentage change in the standard deviation of TOL-28 is also shown (bottom left).

temperatures with the annual cycle and inter-annual trend removed (see Appendix B). Increases of over 10 days are simulated in the north and southeast, resulting in an expansion of the areas experiencing long-term temperature stress (see below). When the increase in temperature exceedance is adjusted for changes in the mean and variance, a difference between the high temperatures in the north and the south emerges: the increase in exceedance in the south is due primarily to a change in the mean, whereas an additional change in variance contributes significantly to the increase in the north. The former behaviour is typical of the response of sea-surface temperatures (e.g. Ferro et al., 2005) with which

land temperatures in the southeast are associated. These features are exemplified in Fig. 4 by the frequency distributions of temperatures from two grid points representative of the northern and southeastern regions. Variances in the northern region increase more than two-fold (not shown explicitly), amplifying the frequencies of high temperatures.

The duration of high-temperature events (number of consecutive days with temperature exceeding 34 °C) also has an impact on crop yield (GLAM-HTS). The simulated change in the mean duration of these events between the baseline and scenario run shows increases of up to 10 days in the north and increases of more than 15 days in the southeast.
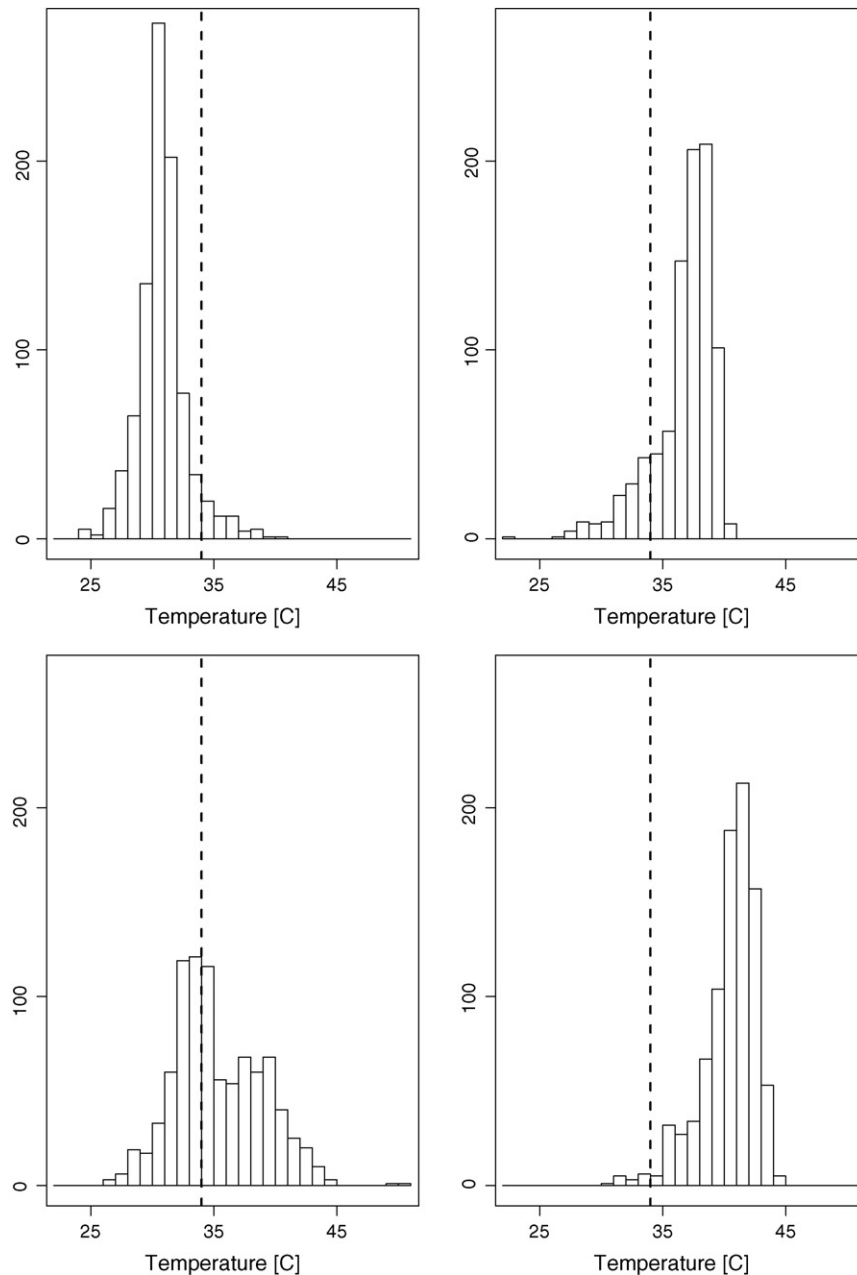
Fig. 4. Frequency distributions of daily maximum temperatures for two grid cells, one in the north (left) and one in the southeast (right) for the baseline (top) and scenario (bottom). The dashed lines indicate the 34 °C threshold. Both grid cells are at 78.90°E and their latitudes are 27.61 and 10.80°E.

Analysis of lagged temperatures using autocorrelations, and of lagged temperature extremes using scatter plots (not shown), reveal that there is little change between the baseline and projected climates in the serial dependence of temperature. Hence the increases in the duration of high temperature events can be explained by the changes in temperature means and, for the north, variances mentioned previously.

It is not possible to examine impacts on yield using analysis of weather fields alone, since the precise timing of weather events relative to the development of the crop is a key determinant of yield (Wheeler et al., 2000). Hence we now move on to look at output from the crop model.

Temperature stress near anthesis is significant in the climate projection, but not in the baseline simulation (Fig. 5). The differences between the SEN-28 and TOL-28 varieties are also significant. In particular, in the north SEN-28 produces a decrease in mean yields, whilst TOL-28 results in an increase in mean yields. Yield increases in the TOL-28 case are mediated via a change in duration (see below).

Regions where the variability of yield increases between the two time slices (Fig. 3) tend to have unrealistically low values of standard deviation in the baseline simulation (Fig. 2). Hence another method for examining the interannual variability is needed; an indication of the extent of risk of crop failure induced by temperature stress is given
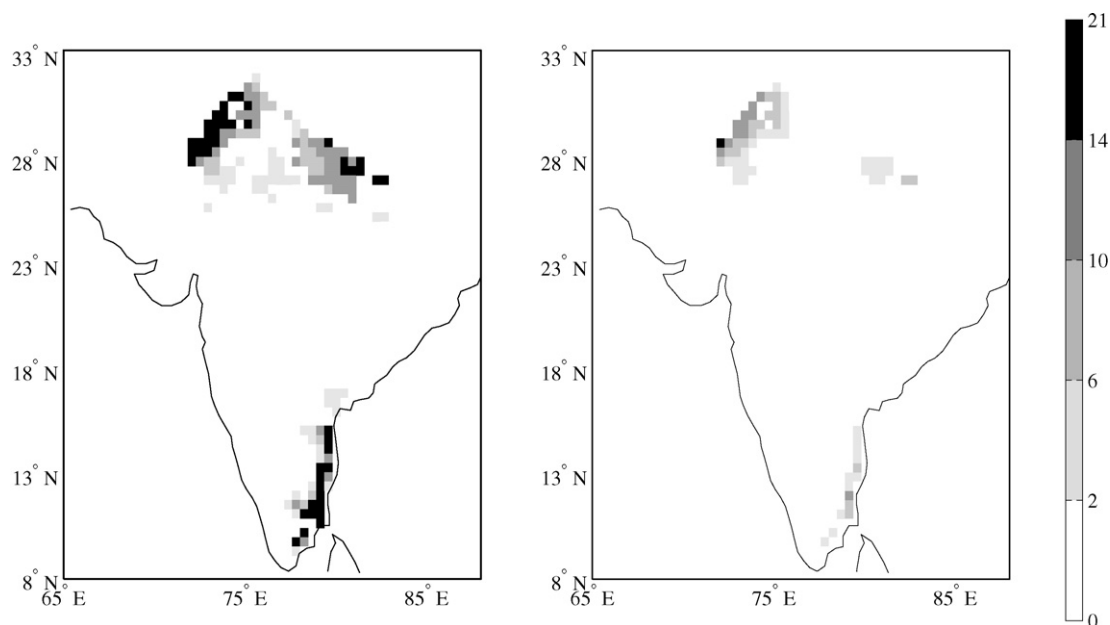
Fig. 5. Number of years (from the sample 2071–2100) when the total number of pods setting is below 60% for SEN-28 (left) and TOL-28 (right). This percentage corresponds to the value below which harvest index begins to be reduced in the TOL-28 parameter set. The corresponding plot for the current climate has only two non-zero grid cells (in the north) of value 2.

by the number of years when the total number of pods setting is below a threshold value. For parts of India, failure events, defined using a pod-set threshold of 60%, occurs less than once in 30 years in the baseline simulation, and become a one in 21 (TOL-28) or one in 10 (SEN-28) year event in the 2071–2100 projection (Fig. 5).

Correlations between yield and the fraction of pods setting (Fig. 6) show the regions where high temperature stress and/or water stress is a significant determinant of yield. There is a marked difference between SEN-28 and TOL-28, most of which is due to temperature, as opposed to water, stress. The baseline and SEN-28 simulations are also markedly different. The TOL-28 simulations, however, look more like the baseline simulation.

3.2.2. Duration

Increases in mean daily temperature can either decrease or increase the duration of the crop, depending on whether the temperature exceeds that which is optimal for the rate of crop development, T_{opt}. The contrast in behaviour between the two chosen values of T_{opt} is illustrated in Fig. 7, which shows the statistics of the changes in duration between the two time slices. Simulations with $T_{opt} = 36\,^{\circ}C$ show decreases in mean duration, across all of India, of between 10 and 35 days. Simulations with $T_{opt} = 28\,^{\circ}C$ show similar decreases in some regions, but show lengthening duration of up to 20 days in some regions.

Correlations between simulated duration and yield (Fig. 8, left panels) show where duration is a significant determinant of yield. These correlations change sign between the two simulation periods. Positive correlations are easily understood: the longer the duration of the crop, the

greater the accumulated biomass. Negative correlations are less trivially explained. Correlations are negative mostly in regions where duration and vapour pressure deficit (VPD) are positively correlated (Fig. 8, right panels); the increase in the number of these positive correlations between the two simulation periods is associated with co-located increases in negative correlations between yield and duration. The relationship between these two correlations is explained as follows: increases in crop duration are associated with temperature increases. Increases tend to be greater in maximum daily temperature than in minimum daily temperature (not shown), and this leads to an increase in the amplitude of the diurnal cycle. This in turn results in an increase in the estimated daily mean values of VPD (calculated using the parameterisation of Tanner and Sinclair, 1983). In GLAM, as in observations (e.g. Zwart and Bastiaanssen, 2004), higher VPD is associated with lower yields because it reduces transpiration efficiency.

4. Sensitivity analysis

The results presented above show that the impact of changes in the mean and extremes of temperature varies geographically. The contrasting yields obtained when different responses to changes in the mean and extremes of temperature are prescribed (Fig. 3) show that both reproductive and developmental processes are important in determining the nature of this response. The following analysis focuses on the relative importance of, and interaction between, these two processes. The analysis centres on the 153 grid cells north of 25°N.
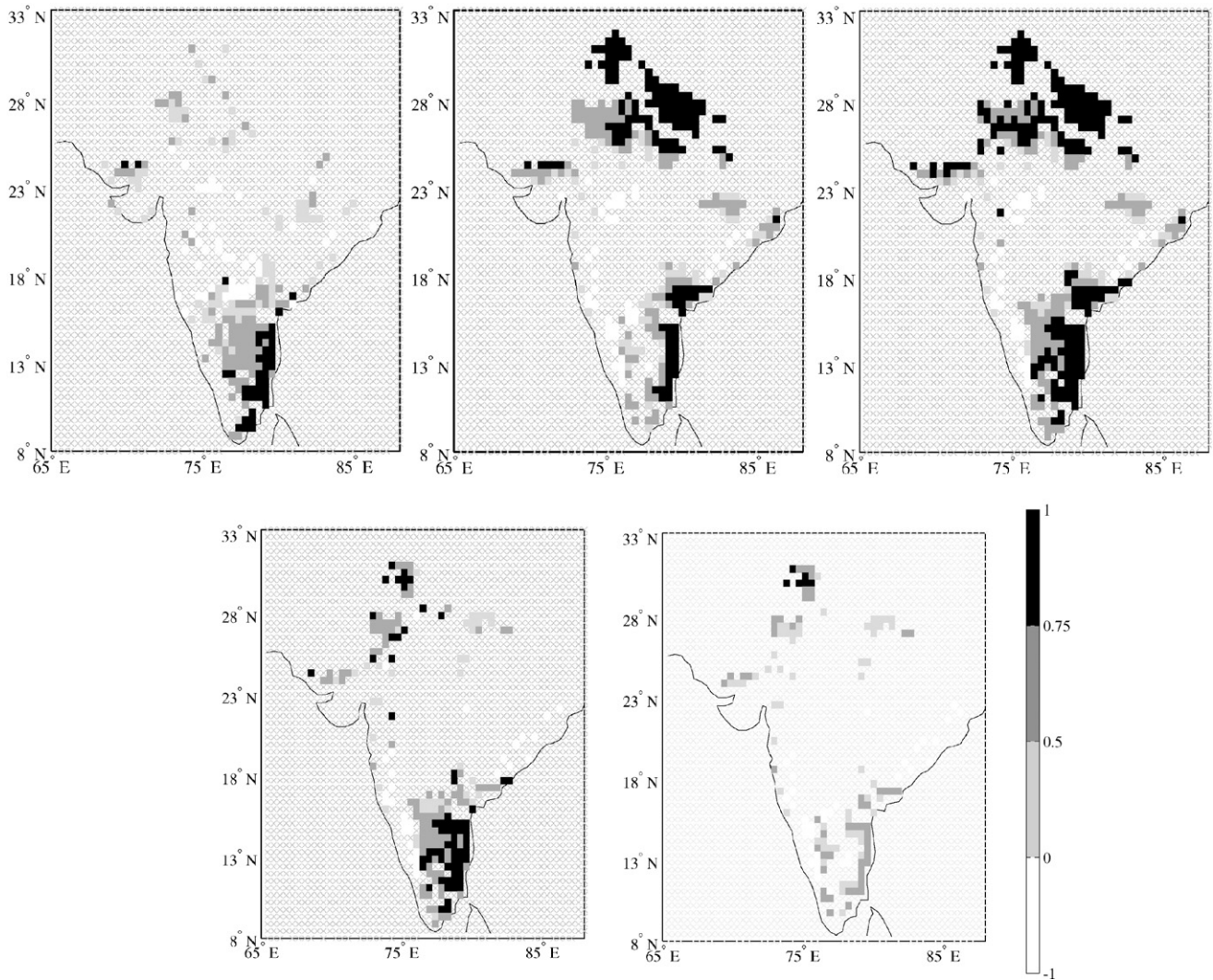
Fig. 6. Correlations between simulated percentage pods and simulated yield for: (i) the baseline simulation (i.e. 1961–1990 MOD-28; top left) and (ii) the 2071–2100 simulations: SEN-28 (top middle) and TOL-28 (bottom left). The temperature only impact is also shown for the future climate period for SEN-28 (top right) and TOL-28 (bottom right). Only correlations that are statistically significant at the 95% ($r = 0.37$ in this case) level are shown.

Three sets of simulation data, each one quantifying the impact on yield of a different set of processes, are examined. Firstly, the impact of high temperature stress alone was estimated by taking the impact of temperature on the fraction of pods setting (see Section 2.4) and using the GLAM-HTS equations to calculate the impact on the rate of change of harvest index, and hence yield (see Challinor et al., 2005c). Secondly, yields from the simulations with the high temperature stress parameterisation turned off (see Section 2.3) were examined. Finally, the impact on yield of all simulated crop processes was examined by using the simulations presented in Section 3. Each of these three sets of simulation data consists of four genotypic parameters sets, SEN-28, TOL-28, SEN-36 and TOL-36, as used in Section 3.

The impact of the projected climate on yield for each of the 12 simulations is presented in Fig. 9. From left to right, the first four boxes show the results when high temperature

stress is not considered. Here the impact of seasonal mean temperature can be seen. Where T_{opt} is exceeded less often or not at all (as in the 36 °C case) mean yields fall significantly due to a shortening of crop duration. The same process is evident in the simulations with all parameterisations switched on (the last four boxes in Fig. 9); here, the impact of seasonal mean temperature on yield is greater than that of tolerance to high temperatures. The last four boxes also show the result seen in Fig. 3: for $T_{opt} = 28$ °C, the degree of tolerance to high temperatures can affect the sign of the change in yield.

The middle four boxes of Fig. 9 show the impact of high temperature stress only. These can be used to assess the relative importance of the timing of flowering (which is different for different values of T_{opt}) and the degree of tolerance to high temperature stress. The greatest similarity in impact is across T_{opt} rather than across tolerance, showing that for this particular case, the degree of tolerance is a
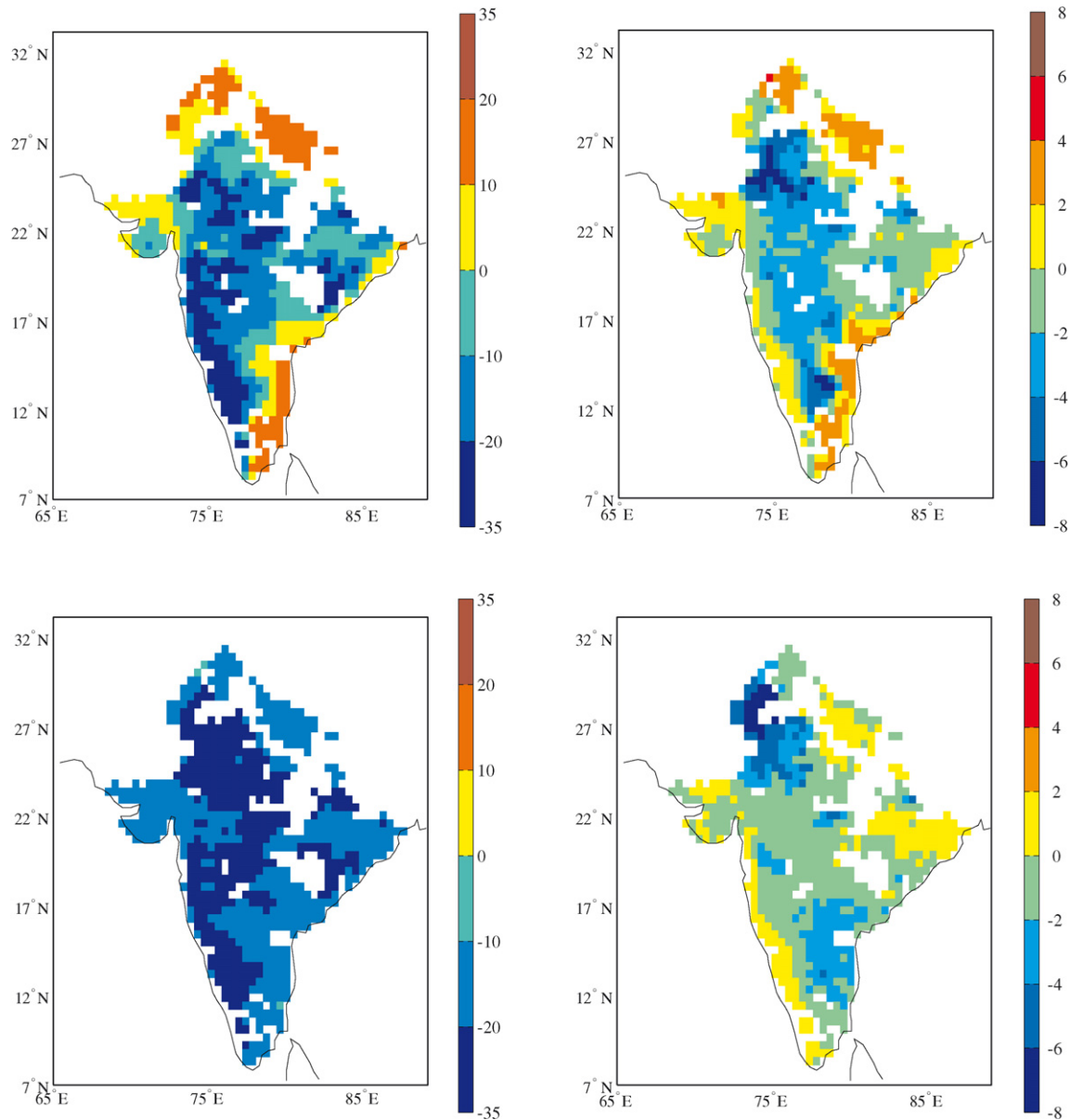
Fig. 7. Change in the mean (left) and standard deviation (right) of crop duration (in days) for simulations with T_{opt} = 28 °C (left) and T_{opt} = 36 °C (right), relative to the respective baseline simulation. Note that crop duration is unaffected by the choice of SEN/TOL parameter values.

greater determinant of yield than the timing of flowering. Note, however, that we have only sampled two possible flowering periods, which is far from comprehensive. The degree of tolerance affects not only mean yield, but also yield variability: the SEN parameter set has a greater range of values than TOL. Hence the degree of tolerance influences the response of the crop to interannual variability in temperature extremes during flowering.

Comparing the three different SEN-28 simulations shows that the simulation of high temperature stress only produces results that are closer to the all-processes simulation than the simulation without high temperature stress; hence this genotypic parameter set is dominated by high temperature stress. In contrast, TOL-28 is dominated by the impact of changes in seasonal mean temperatures (i.e. the second and

tenth bars are similar). For T_{opt} = 36 °C, seasonal mean temperature dominates in both the SEN and TOL case.

5. Discussion

This study set out to examine the importance of the mean and extremes of temperature in the determination of the yield of an annual crop in India. Mean temperature affects duration, which is an important determinant of yield in the current climate simulations, and less important in the climate projection (Fig. 8). However, this result depends on the choice of optimal temperature for crop development, which is not well constrained. Challinor et al. (2005d) found that uncertainty in the value of the optimum temperature for
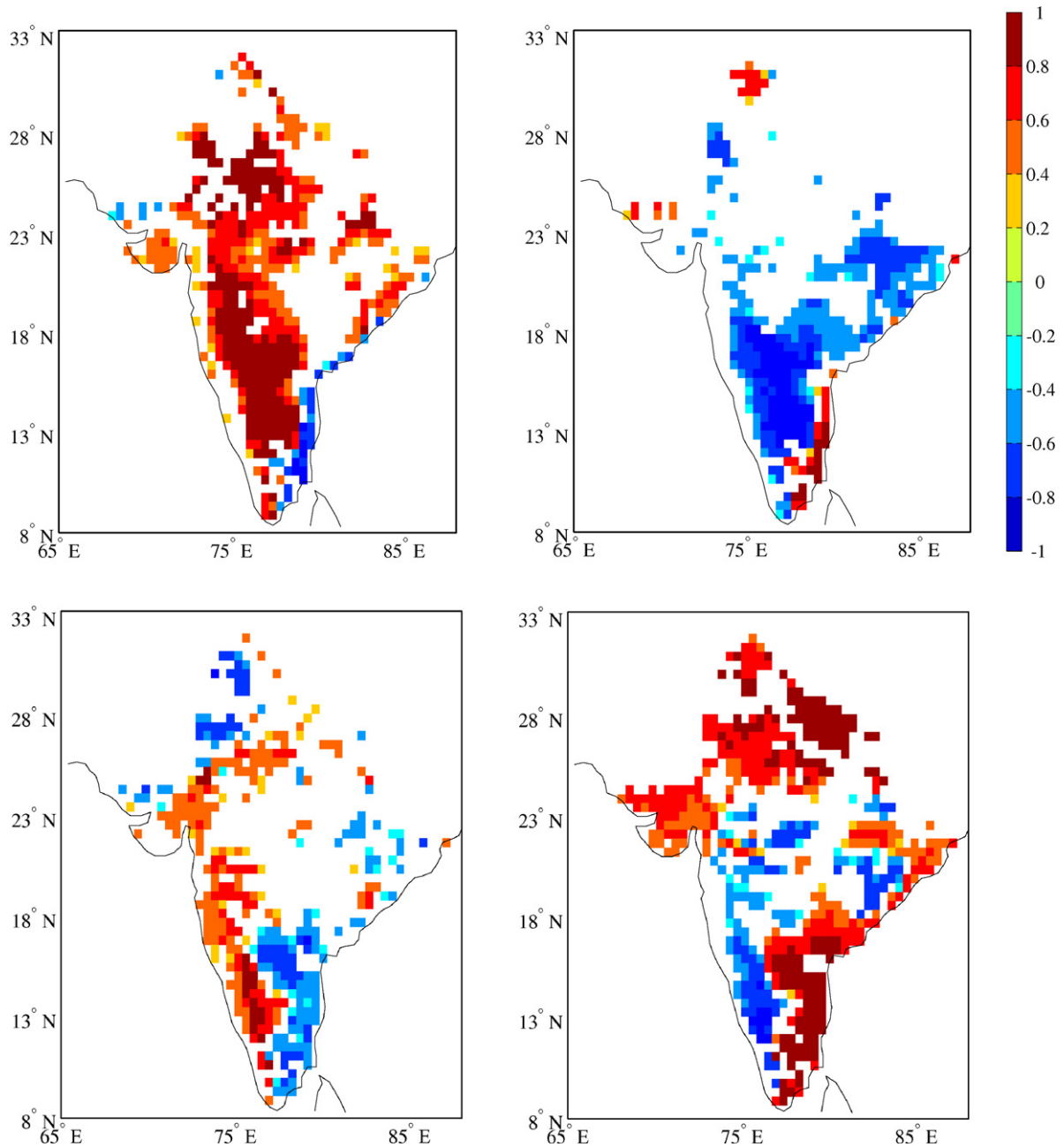
Fig. 8. Correlations between simulated duration and: (i) simulated yield (left panels), (ii) VPD (right panels). Upper panels: baseline simulation. Lower panels: TOL-28 future climate simulation. Only correlations that are statistically significant at the 95% ($r = 0.37$ in this case) level are shown.

development is an important component of the total (climate plus crop) uncertainty in a climate change projection.

High temperature stress is not a major determinant of yield in the current climate simulations, but becomes important in parts of the north and south under climate change with the parameter sets used in this study (Figs. 4 and 5). Increases in the magnitude and duration of high temperature events in northern and south-eastern growing regions are due to increases in the means and, for the north, variances of temperature frequency distributions (Fig. 4). Whilst groundnut is not a major crop in northern regions (see e.g. Challinor et al., 2003), this result is a first indicator of

the risk to other short-duration annual crops, many of which have a similar response to mean and extreme temperatures (Section 2.4). The regions in the north of India which show increased risk to crop production coincide with the regions of continued and/or increased climate sensitivity under doubled CO_2 calculated by O'Brien et al. (2004). Work on the quantification of the impacts of high temperature stress on crop yield based on future climate projections is at an early stage. Whilst there are few published studies in this area, there is some qualitative evidence of increased risk to crop production, similar to that seen in the current study, in parts of Africa (Huntingford et al., 2005).
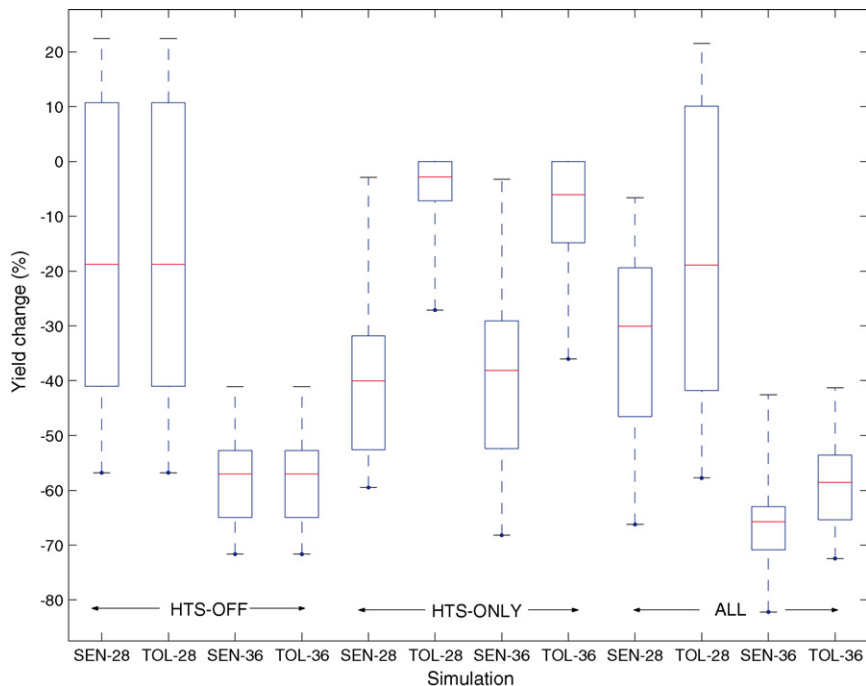
Fig. 9. Boxplots (the box shows the upper and lower quartiles, the line within shows the median and the whiskers show the full extent of the data) of the percentage change in yield, between the baseline and projection climates, for the 153 grid cells north of 25°N in which groundnut is grown. Twelve simulations are shown, consisting of four genotypic parameter sets and three processes: 'HTS-OFF' denotes simulations with the high temperature stress parameterisation turned off; 'HTS-ONLY' denotes the calculation of the impact of high temperature stress only; 'ALL' denotes the simulation of all the processes that are parameterised in GLAM.

Genotypic differences in tolerance to high temperature stress have been documented in many annual crops (Wheeler et al., 2000). In groundnut, Craufurd et al. (2003) screened 22 genotypes using controlled environments in order to identify genotypes that were tolerant or sensitive to high temperature stress at flowering or at microsporogenesis (3 days before flowering). They listed 6 groundnut genotypes, of diverse origin, that were heat tolerant at these stages. The modelling approach demonstrated in the current study can be used with the detailed information from such genotype screens in order to properly investigate the extent of genotypic adaptation to high temperature stress associated with climate change within current crop germplasm. Equally, the potential for crop adaptation to climate change through breeding for improved tolerance to high temperatures can be explored in a robust manner within this modelling framework.

The relative importance of mean and extremes of temperature varies geographically, and depends upon the genotypic parameters (Section 4). The impact on yield of changes in duration resulting from seasonal mean temperature changes can have a greater magnitude than that of high temperature stress (Fig. 9) and its effects can be more widespread (Fig. 3). Where the optimal temperature for development is exceeded the resulting increase in duration can mitigate and even counteract the negative impacts of reproductive temperature threshold exceedance on yield, provided that there is sufficient water for the crop to benefit from the extended duration. The magnitude and sign of this effect depends on the degree of tolerance of the crop to temperature extremes; hence yields are particularly threatened when water availability and/or mean temperature shorten the duration of a crop which experiences and is sensitive to high temperatures during flowering. The degree of sensitivity determines the response of not only mean yields, but also the magnitude of interannual variability (Fig. 9).

Increases in maximum temperature between the two time periods studied are associated with increases in the diurnal temperature range and hence in VPD (Section 3.2). Due to the high temperatures involved, the regions where this occurs will tend to be co-located with regions where reproductive temperature thresholds are being exceeded. Hence, as well as the impact of mean temperatures on the rate of development, which are linear for $T < T_{opt}$, there is a non-linear response to diurnal temperature amplitude, of the kind described by Porter and Semenov (2005).

6. Conclusions

Methods like those employed here can be used to quantify the impact of high temperature threshold exceedance on crops. The results from this study suggest that temperature extremes could be an important determinant of the yield of annual crops, specifically in parts of northern and southern India. Changes in mean temperature, through their impact on development rates, may have a more

widespread impact on yield. The magnitude of that impact could be greater than that of heat stress in this climate scenario; this depends upon the cardinal temperatures and thermal time requirements of the varieties grown. The magnitude of the impacts is large – yield reductions of up to 70% – and this illustrates the importance of genotypic adaptation to changes in the mean and extremes of temperature. Repeating this kind of study with crop models designed for use at the field scale, which tend to parameterise more processes than GLAM, would provide a useful perspective on the current study.

Once this work has been extended to other crops and other climate and emissions scenarios, a more consolidated picture will emerge. Genotypic adaptation to changes in both the mean and extremes of temperature will be important, as is evident from the large differences in the results between the different crop parameter sets used in this study. Changes in thermal time requirement and tolerance to heat stress are two key adaptive methods. Other adaptive methods may include a change in planting date, crop type or management practices (particularly irrigation). When quantifying the benefits of these methods it is important to consider adaptive capacity (see O'Brien et al., 2004 for appropriate methods). This study has focussed more on processes than on the provision of yield estimates. In beginning to quantify the risk of future climates to cropping systems, it is clear that an associated quantification of uncertainty is important (e.g. Challinor et al., 2005d). In particular, since the timing of heat stress is critical, there is considerable uncertainty associated with it. The model used in this study, and those used in most other studies, simulate the impact of heat stress deterministically. A probabilistic approach, which takes into account uncertainty in the timing of heat stress events relative to anthesis, may provide more realistic estimates of the impacts of extreme temperatures.

Acknowledgements

Appendix A. Crop model calibration

The calibration procedure varied YGP in steps of 0.05 between 0.05 and 1. Studies of crop yield under the current climate using GLAM have used cross-validation to obtain two values of YGP for each location. Since in the present study the focus is on simulation of the impacts of changes in climate, the full yield time series was used to find a single value of YGP for each location.

Two methods of minimising the difference between observed and simulated yields were tested. The first method minimises the difference between time-mean observed and simulated yields (and ignores inter-annual variability). The second method uses both the mean and the standard deviation of yield over time. The basis for this method is a decomposition of mean square error in yield (MSE) into systematic bias (in the mean), bias in the standard deviation (σ) and a remaining term that depends upon correlation coefficient (see e.g. Taylor, 2001):

$$MSE = (\bar{o} - \bar{s})^2 + (\sigma_o - \sigma_s)^2 + 2\sigma_o\sigma_s(1 - r) \tag{1}$$

where o are observed yields, s the simulated yields, bars indicate time-averages and r (which cannot be calculated) is the correlation coefficient between o and s. By setting $r = 1$ in the above equation, a value of RMSE of a perfectly correlated time series can be calculated. This value of RMSE is used to determine YGP. The following analysis shows that whilst the assumption of perfect correlation can seriously underestimate RMSE, it is unlikely to seriously bias the resulting values of YGP.

Calibration of the Yield Gap Parameter on climate data corrects for some of the bias in the climate data, and on the whole GLAM simulates mean yields well (Challinor et al., 2005a,b). Hence this analysis ignores mean bias and focuses on the relationship between σ and r. For a given value of r there is a value of σ_s that minimises RMSE. Call this value σ_{sm}. Only for $r = 1$ will $\sigma_{sm} = \sigma_o$. Hence by including σ_o in the calibration, and nudging the model towards correct simulation of standard deviation, RMSE will be increased. If this increase in RMSE is within tolerable limits, then the assumption of perfect correlation is acceptable.

A polar coordinate plot of correlation coefficient and standard deviation (Taylor, 2001) and the law of cosines, or, less trivially, manipulation of Eq. (2), can be used to find the ratio of the RMSE associated with σ_{sm}, and the RMSE associated with $\sigma_s = \sigma_o$. The relationship between this ratio (A) and r is as follows:

$$r = \frac{90 - \cos^{-1}(2A^2 - 1)}{90} \tag{2}$$

If we are willing to accept that correct simulation of the standard deviation of yield results in a RMSE which would be improved upon by 10% by reducing σ_s, then we set $A = 0.9$, and find that $r = 0.43$; only below this value is $A < 0.9$. For $A = 0.71$, $r = 0$. Hence the perfect correlation method has the potential advantage of reducing errors in the standard deviation without increasing significantly the RMSE. Whether or not this potential is realised depends upon the simulation results.

Tests were carried out using both calibration methods in order to decide upon one method for the remainder of the study. For the baseline simulations, the perfect correlation method lowers the maximum error in standard deviation by

up to 15% without significantly altering the error in the mean. Hence this method was adopted.

Appendix B. Adjusted temperatures

The mean-adjusted baseline temperatures are $T_{max} - \bar{T}_{max} + \bar{T}'_{max}$, where bars indicated time-averages, primes indicate the future climate scenario, and no superscript indicates the baseline simulation. Thus, if the difference between the current and future climate distributions is only a shift in mean from $\bar{T}_{max}$ to $\bar{T}'_{max}$, then the distributions of the mean-adjusted temperatures and T'_{max} will be identical. Furthermore, the differences between any properties of these two distributions, such as the frequency with which a high temperature threshold is exceeded, will be zero. The equivalent mean-and-variance-adjusted temperatures are $(T_{max} - \bar{T}_{max}) \times s'/s + \bar{T}'_{max}$, where s and s' are the standard deviations in T_{max} and T'_{max}.

Due to the transient nature of the climate forcing (Section 2.1), the two adjusted temperatures described above, if based on raw values of T_{max}, will not be computed from a stationary climate. Seasonal and interannual variability means that temperature values are not taken from a single statistical distribution. This may lead to errors in the attribution of the role of changes in the mean, variance, and the shape of the probability density function (PDF). For example, the sample variance will over-estimate the variability of the temperatures around the trend or cycle. For this reason, the annual cycles and the inter-annual trends were removed from the temperatures prior to the analysis: if $T(i,j)$ is the temperature on the jth day of the ith July at a single grid point in either the baseline or scenario run then the adjusted temperatures $T(i,j) - T(i,o) + T(1,o) - T(o,j) + T(o,1)$, where 'o' denotes averaging over an index, are representative of the climate at that location on the first day of the first year of the run.

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