Paper:
Challinor, AJ, Wheeler, TR, Craufurd, P and Slingo, JM (2005) *Simulation of the impact of high temperature stress on annual crop yields.* Agricultural and Forest Meteorology, 135 (1-4). 180 - 189. ISSN 0168-1923
http://dx.doi.org/10.1016/j.agrformet.2005.11.015

Simulation of the impact of high temperature stress on annual crop yields

A. J. Challinor (`ajc@met.rdg.ac.uk`)
CGAM, Department of Meteorology, University of Reading, Reading RG66BB

T. R. Wheeler (`t.r.wheeler@reading.ac.uk`) and P. Q. Craufurd
Department of Agriculture, The University of Reading, PO box 236, Earley Gate, Reading RG6 6AT, U.K.

J. M. Slingo
CGAM, Department of Meteorology, University of Reading, Reading RG66BB

Abstract.

Brief periods of high temperature which occur near flowering can severely reduce the yield of annual crops such as wheat and groundnut. A parameterisation of this well–documented effect is presented for groundnut (i.e. peanut; *Arachis hypogaea* L.). This parameterisation was combined with an existing crop model, allowing the impact of season–mean temperature, and of brief high–temperature episodes at various times near flowering, to be both independently and jointly examined. The extended crop model was tested with independent data from controlled environment experiments and field experiments. The impact of total crop duration was captured, with simulated duration being within 5% of observations for the range of season–mean temperatures used (20 to 28 degrees Celsius). In simulations across nine differently timed high temperature events, eight of the absolute differences between observed and simulated yield were less than 10% of the control (no-stress) yield. The parameterisation of high temperature stress also allows the simulation of heat tolerance across different genotypes. Three parameter sets, representing tolerant, moderately–sensitive and sensitive genotypes were developed and assessed. The new parameterisation can be used in climate change studies to estimate the impact of heat stress on yield. It can also be used to assess the potential for adaptation of cropping systems to increased temperature threshold exceedance via the choice of genotype characteristics.

Keywords: high temperature stress, crop simulation models, climate change, groundnut, crop yield

1. Introduction

Temperature variability is an important determinant of the yield of annual crops, particularly when high temperature episodes coincide with flowering (Wheeler et al., 2000). The response of crops to high temperature stress has been studied in detail for groundnut (e.g. Prasad et al., 2000), wheat (e.g. Ferris et al., 1998), cowpea (e.g. Ismail and Hall, 1999) and rice (e.g. Matsui et al., 2001). Under climate change an increase in the frequency of such episodes may occur (IPCC, 2001). Hence temperature variability could become a major yield–determining factor for some regions in the decades to come (Trnka et al., 2004). The magnitude of the impact will depend upon the level of heat stress tolerance in the genotypes grown (e.g. Craufurd et al., 2003).

This study develops and tests a parameterisation of the impact of high temperature episodes on crop yield. Since the impact of high temperature stress has been particularly well–quantified in groundnut (i.e. peanut; *Arachis hypogaea* L.), this is the crop used in this study. The parameterisation is designed for use over large spatial scales and this has implications for the level of complexity of the model (see also section 2.1): rather than parameterise specific genotypes, the equations simulate the characteristics of broader groups of genotypes. The principle aim of this study is to develop three parameter sets which can be used to simulate the impact of heat stress on tolerant, moderately sensitive and sensitive genotypes. These parameter sets are based on the response of particular genotypes which are identified as falling into one of these three categories. Further genotypes can be characterised, using published studies, in much the same way (e.g. Ntare et al., 2001).

Two principle mechanisms for temperature to impact yield are examined in this study. Mean temperature affects yield by determining the duration of developmental stages; sub– and super– optimal temperatures both increase duration. The impact of high temperatures, particularly near flowering, is primarily on the setting of fruit or grain. The crop model used for this study is GLAM (section 2.1). The impact of temperature on duration is already simulated by the published version of this model (Challinor et al., 2004). The impact of high temperature stress is a new addition to the model, and this is described in section 2.3.

2. Method: modelling high temperature stress

2.1. The General Large–Area Model for annual crops

The General Large–Area Model for annual crops (GLAM; Challinor et al., 2004) was developed following the methodology of Challinor et al. (2003) in order to to simulate crop yield on spatial scales far exceeding the farm or plot level. For this reason the parameterisations are relatively simple, whilst being complex enough to capture variability in yield. Where there is a climate signal in the observed yields, GLAM can be used to simulate yields over large areas using observed gridded weather data (Challinor et al., 2004) and General Circulation Model output using either deterministic (Challinor et al., 2005b) or probabilistic (Challinor et al., 2005a) methods.

GLAM–groundnut simulates four developmental stages, the first between sowing and onset of flowering, the second between onset of flowering and pod–initiation, the third between pod–initiation and maximum leaf area index (LAI) and the last between maximum LAI and maturity. The timing of these stages is determined by parameters which describe the cardinal temperatures for rates of development and corresponding thermal durations for each of the stages. GLAM uses a maximum rate of change of LAI, modified by water stress, to determine transpiration. A fixed transpiration efficiency, modified by vapour pressure deficit, then determines biomass. Finally, a fixed rate of change of harvest index during the pod–filling period (stages three and four) is used to partition to yield. The methods used to simulate water stress are not discussed here, since the simulations and experiments referred to in this study are not water–limited.

All use of the name GLAM in this paper refers to GLAM–groundnut as fully described in Challinor et al. (2004). The addition of the –HTS suffix refers to properties of and/or results from GLAM that are specific to the high temperature stress module described in the following section. This modification acts by modelling in greater detail the flowering stage and using the resulting information on pod–set (fraction of flowers that produce setting pods) to modify the rate of change of harvest index in the subsequent pod–filling period.

2.2. Observations of high temperature stress and crop duration

There have been a number of controlled environment experiments that quantify the impact of temperature on crop growth (e.g. Hall, 1990). Field experiments designed to quantify high temperature stress are much more rare. This section briefly summarises the experiments used in this study. Experiments have been used in one of two ways: (i) for the development of the high temperature stress (HTS) parameterisation presented in section 2.3, and (ii) for the evaluation of GLAM–HTS.

The parameterisation of high temperature stress is based on numerous studies (Craufurd et al., 2003; Prasad et al., 2000; Prasad et al., 2001; Craufurd et al., 2000; Kakani et al., 2002). These studies have quantified by experiment the impact on groundnut flowers, and their associated pegs and pods, of high temperatures at and near the time of anthesis (flower opening). These data show that high temperatures between six days prior to anthesis and twelve days after can reduce subsequent pod–set. These data also show that pre– and post–anthesis impacts are different due to the different processes affected (Prasad et al., 2001).

Data from three controlled environment experiments (CE1, CE2 and CE3) and one field environment experiment (FE1) were used to evaluate the performance of GLAM–HTS. CE1 and CE2 were conducted in polyethylene covered tunnels in Reading, UK. CE3 was conducted in walk–in growth chambers in North Carolina, USA. FE1 was conducted at a field site in Hyderabad, India. All of these data are for non–water–limiting conditions. The data have been published by Kakani (2001) (CE1, FE1), Prasad (1999) (CE2; see also Prasad et al., 1999) and Nigam et al. (1994) (CE3). CE1 and CE2 involve high temperature episodes sufficiently short ($\leq$ 10 days) as not to impact duration; CE3 uses season–long treatments of temperatures (with daily means of 20, 24 and 28 °C) that impact duration but are sufficiently low as not to impact pod–set; FE1 involves treatments which impact both pod–set and duration (see below). Hence the data were used to evaluate the response of GLAM-HTS to the impact of temperature on pod–set alone (CE1 and CE2), duration alone (CE3) and both duration and pod–set (FE1).

Experiment CE2 had nine sub–treatments created by varying the timing, but not the duration, of the high temperature stress. Experiment FE1 consisted of two sub–experiments created by using two different cultivars, one (ICGS11) more tolerant than the other (TMV2). Experiments CE1 and CE2 both used the same genotype (ICGV86015).

The three high temperature stress experiments (CE1, CE2 and FE1) each have a control–temperature treatment and a high–temperature treatment. For the two CE experiments the control temperatures chosen were those optimal for groundnut growth and development. For FE1, ambient conditions determined the control temperatures with the high temperature treatment imposed by the use of ventilated plastic tunnels. Both the ambient and high temperature treatments were affected by high temperature stress. A further experiment (referred to as FE1–Early) conducted at an earlier time at the same site and under ambient conditions showed no impact of high temperature stress. FE1–Early has no corresponding high temperature treatment and it was used only as a comparison for the FE1 ambient experiment. In FE1–Early the crop matured thirteen days later than in the other two FE1 experiments. The results from all these experiments are presented alongside the results of the simulations (section 3).

2.3. PARAMETERISATION OF HIGH TEMPERATURE STRESS

For GLAM to simulate the impacts of high temperature stress an appropriate level of complexity must be chosen; as GLAM is not a plot–scale model, detailed simulation of individual flowers is neither plausible or desirable. However, the model equations should be sufficiently detailed that tolerance to heat stress can be simulated. Hence the following parameterisation of tolerance retains a level of generality which is appropriate to a model such as GLAM, whilst retaining enough detail to distinguish the characteristics of heat stress tolerance.

The first stage of the simulation of high temperature stress is the identification of episodes of high temperature. This is done by comparing the mean 8am to 2pm (solar time) temperature (T_{AM}) to a pre-defined critical value (T_{cr}^{min}). From this, all high temperature episodes are identified and characterised by their duration (d) and the centred time at which they occur. Even–numbered durations are defined (arbitrarily) as being centred on the earliest of the two possible days. Since each of these episodes has a different timing relative to each of the days in the flowering stage, the number of possible discrete events impacting on pod–set is the number of episodes multiplied by the number of days in the flowering stage. Flowers occuring after the simulated flowering stage are not considered as these are not usually associated with setting pods that contribute to yield.

The critical temperature above which the pod–set begins to be affected (T_{cr}) and the temperature at zero pod–set (T_{lim}) are defined for each of these discrete events as follows:

$$\left.\begin{array}{l} T_{cr}(t) = \min\left[T_{cr}^{min}, 36 + S_c(t-6)\right] \\ T_{lim}(t) = 60 + S_l(t-6) \end{array}\right\} -6 \leq t \leq 0 \tag{1}$$

$$\left.\begin{array}{l} T_{cr}(t,d) = \min\left[T_{cr}^{min}, 37.8 + 1.8t - 3d\right] \\ T_{lim}(t,d) = T_{ia} + 0.75t - 1.5d \end{array}\right\} 0 < t \leq 12 \tag{2}$$

where t is the time of the high temperature episode (in days) relative to the day of anthesis. This is negative if the episode is centred prior to that day. S_c, S_l and T_{ia} are parameters which can be chosen in order to simulate varying degrees of sensitivity to high temperature stress during flowering. Equations 1 characterise pre-anthesis effects using parameter values determined by visual comparison with the data. Equations 2, which parameterise post-anthesis effects, have a dependency on two variables. Hence values for these parameters were determined by linear regression of the data.

The two temperatures defined in equations 1 and 2 are used to determine pod–set: pod–set at T_{cr} is not subject to modification (it is 100% of the non–stressed value), pod–set at T_{lim} is zero, and pod–set at intermediate temperatures is determined by linear interpolation, so that

$$P(i) = 1 - \frac{T_{AM} - T_{cr}}{T_{lim} - T_{cr}} \quad \text{for } T_{AM} > T_{cr} \tag{3}$$

where i is the time in days relative to the start of the pod–filling period. The reduction in the total pod–set is then given for each high temperature episode as a sum of the impact of that episode on each of the days during the flowering developmental stage (N_F). Hence for each episode the fractional pod–set is given by

$$P_{tot} = \sum_{i=1}^{i=N_F} P(i) F_f(i) \tag{4}$$

where the flowering distribution $F_f(i)$ prescribes the fraction of total flowers opening on day i. F_f is given by a cumulative normal distribution (see e.g. Press et al., 1994) which is consistent with observations (e.g. Ndoye and Smith, 1992). Values for the width and offset of the distribution can be used to give a range of plausible flowering time series (figure 1).

Equations 1—4 result in a value of P_{tot} for each identified high temperature episode. The lowest of these values is then used to modify the rate of change of harvest index as follows:

$$\frac{\partial H_I}{\partial t} = \left(\frac{\partial H_I}{\partial t}\right)_0 - \frac{P_{cr} - P_{tot}}{P_{cr}} \tag{5}$$

where P_{cr} is the critical fractional pod–set below which the rate of change of harvest index (left hand side of equation) begins to be reduced from its non–stressed value (subscript 0). The equation is based on the data of Chatzialioglou (1995) and Craufurd et al. (2001) which suggests a value of P_{cr} in the range 0.6–0.8.

2.4. DESCRIPTION OF SIMULATIONS

Experiments CE1, CE2, CE3 and FE1 (see section 2.2) were used to evaluate GLAM–HTS. CE1, CE2 and FE1 provide a total of twelve independent measurements of the impact of high temperature stress on yield. Using GLAM–HTS with these measurements, three HTS parameter sets were developed, each simulating a different degree of tolerance to high temperature stress: sensitive (SEN), moderately sensitive (MOD), and tolerant (TOL). None of the evaluation data were used in the derivation of GLAM–HTS (equations 1—5). Experiment CE3 was used to evaluate the impact of temperature on total crop duration in GLAM; no high temperature stress was observed or simulated for this experiment.

The input weather data and evaluation data used for the simulations are those recorded at the time (see table I). For FE1, observations of T_{AM} were not available; instead it was estimated from the maximum and minimum daily temperatures (T_{max} and T_{min}) by assuming sinusoidal diurnal cycle of temperature from sunrise to sunset. This cycle lags the solar cycle by two hours (Lüdeke et al., 1994) so that T_{max} occurs at 2pm (solar time). The resulting definite integral can be solved analytically and is a function of location and time of year, which together determine sunrise and sunset, and the amplitude of the diurnal cycle ($T_{max} - T_{min}$).

For CE1, CE2 and FE1, observations of the timing of the crop developmental stages were used to calibrate the GLAM development parameters determining both the time from emergence to onset of flowering and the time from onset of flowering to pod–initiation. For CE1 and CE2 the observed timing of these stages did not depend on temperature. For FE1 there was some observed dependence on temperature and GLAM was calibrated to simulate the development stages of the high temperature treatments since this was crucial to simulating the impact of high temperature stress on yields.

The flowering distributions (F_f) for simulations of CE1, CE2 and FE1 were chosen from figure 1 by assessing by eye which most closely approximated observations. Simulations using flowering distributions which agreed less with observation were also carried out, as a sensitivity study.

For CE1 and CE2 the harvest date was determined by the GLAM development parameters which govern time from the pod–initiation to maturity. These parameters (GCPFLM and GCLMHA) took the same values as in the study of Challinor et al. (2004). The FE1 simulation was terminated on the observed day of harvest for the field experiment: 87 DAP for the control and high temperature experiments and 100 DAP for FE–Early.

For CE3, observations of the timing of development stages were not used, since it is the ability of GLAM to simulate the impact of temperature on total crop duration that was being tested by this simulation. Observations of F_f were not needed for this simulation, since there was no impact of high temperature stress in this experiment. The parameter values used for this simulation were the calibrated values from each of CE1, CE2 and FE1. This resulted in three simulations for each single experimental temperature treatment.

The procedure adopted to determine parameter values was based on consistency and accuracy: different parameter sets should not be used to simulate the same genotype; yields and, where possible, pod–set, should match observations. Since experiments CE1 and CE2 both used the same genotype (table I), a single parameter set (SEN) was sought to describe the response of the crop to temperature for those experiments. That set of parameters was then used with the weather data for FE1. Two further parameter sets (MOD and TOL) were then developed to simulate the behaviour of the ICGS11 and TMV2 genotypes in FE1. All the experiments simulated are summarised in table I.

The parameters, which are relatively numerous (section 2.3), were not constrained enough by the data to allow rigorous testing of statistical significance. Instead, a sensitivity analysis was performed after the parameter sets had been developed, in order to gain insight into the relative impact of the choice of parameter values on pod–set. Experiment CE2 was chosen for this analysis because it showed a large impact of high temperature stress without having an impact on duration. One parameter at a time was varied from its baseline (SEN or MOD) value, across the full range of values used in the three developed parameter sets (TOL, MOD and SEN).

2.5. Analysis methods

The three high temperature stress experiments (CE1, CE2 and FE1) were each assessed in two ways: (i) comparing the simulated and observed reduction in pods between the control and high temperature treatments, and (ii) comparing the simulated and observed values of normalised rate of change of harvest index (all reference to normalised quantities in this study refer to high temperature values normalised by control values). For the GLAM formulation, this second comparison is equivalent to the use of the two simulated yields, providing neither the transpiration nor the dates of occurrence of the developmental stages are altered. GLAM transpiration was physiologically, rather than environmentally, limited for all three high temperature stress experiments. Hence transpiration was not greatly impacted by temperature. For the two CE experiments the high temperature treatments were sufficiently short (see table I) that duration was not affected. Hence where fractional differences in simulated yields are referred to for CE1 and CE2, they are derived from fractional differences in the rate of change of harvest index.

For FE1 the timing of the developmental stages was affected by temperature. Since simulated yields are affected by differences in the duration of developmental stages, they were used as an additional evaluation variable for this field experiment. For FE1, then, the normalised rate of change of harvest index measures the impact on yield due to high temperature stress alone (i.e. no impact of development rate or changes in biomass).

The impact of the high temperature treatments on pods can be assessed in a number of ways: the pod–set (fraction of flowers that produce setting pods) from the model can be compared directly to observed pod–set. Alternatively, since GLAM does not simulate flower number explicitly, the normalised simulated pod–set can be compared to the normalised observed pod number per plant. Where possible both of these comparisons have been carried out. Where data on pods was not available, data on peg number was used.

For CE3 none of the above evaluation variables were used: only the simulated impact of temperature on the total duration of the crop was evaluated.

3. Results

Table II lists the three parameter sets that were developed and tested using the procedure outlined above. Values lie within the ranges suggested by the data used to derive the HTS parameterisation (section 2.3). The exception to this is P_{cr}, which had to be increased for simulations of the CE2 experiment in order to match the observed value of $P_{cr} = 0.95$. The SEN parameter set is used to simulate two of the controlled environment experiments (section 3.1) and all three parameter sets are used to simulate the field experiment (section 3.3).

3.1. IMPACT OF HIGH TEMPERATURE STRESS (CE1 AND CE2)

Kakani (2001) reported no significant impact of high temperature on pod number or weight in CE1. Pod–set in the high temperature experiment was 109% of the control value and for pod weight the figure was 96%. GLAM-HTS with the SEN parameterisation, using the six flowering distributions in figure 1, resulted in pod–set in the range 89–91% of the control and pod weights in the range 94–96%. Hence the results were relatively insensitive to the choice of flowering distribution; however, flowering distributions F5 and F6, which were closest to observations, produced the least impact on crop yield. The control GLAM-HTS simulation showed no impact on pod–set or yield, as expected.

Prasad (1999) reported a significant impact of high temperature on pod–set and pod weight for some of the treatments in CE2. These results are summarised, and compared with the results from GLAM-HTS with the SEN parameterisation, in figure 2. The choice of input flowering distribution significantly affects the simulations; use of flowering distributions consistent with observations does not always produce the most accurate results. The impact of timing — greater yield reduction when a high temperature episode is towards the middle of the flowering period — is captured. Most of the absolute differences between simulated and observed yields are less than 10% of the control yield. As with CE1, the control GLAM-HTS simulation showed no impact on pod–set or yield.

The results of the sensitivity analysis (see section 2.4) are presented in figure 3. In order to ensure that the analysis was manageable, it was limited to one flowering distribution (F3) and one sub–experiment (high temperatures applied twelve days after the onset of anthesis). This combination was chosen since it produced the largest impact on pod–

set (figure 2). The results show that the impact of parameter changes depends upon the baseline parameter set; this is most evident with T_{ia}, where the range of values of pod–set in the MOD case is over double that of the SEN case. The parameter with the largest impact on pod–set across both MOD and SEN simulations (31% change from the baseline value) is T_{cr}^{min}. The parameter with the smallest impact (4.7% change) is S_c. This small change suggests that this parameter could be given a constant value across all three parameter sets. However, this suggestion may not be correct, since the sensitivity analysis performed was not extensive: it varied parameters one at a time, and therefore only sampled some of the sensitivity to parameter choice; furthermore, the analysis was carried out on only one flowering distribution, and only one high temperature event.

3.2. Impact of temperature on total crop duration (CE3)

Figure 4 shows the simulated and observed impact of seasonal mean temperature on total duration. The simulations, which were calibrated independently (section 2.4), show that GLAM is capable of reproducing the observed impacts of temperature on duration. The mean simulated duration (across three simulations) is within 5% of observed values (across three genotypes) at all three temperatures. The mean simulated change in duration from 20°C to either 24 or 28°C is within 8% of the observed mean change (5 days in absolute terms).

3.3. Impact of both high temperature stress and duration (FE1)

The majority of the results presented in this section compare the control (ambient) and high temperature treatments of field experiment FE1 (Kakani, 2001), described in section 2.2. Since the control experiment showed some impact of high temperature stress, this section then concludes with a comparison of the control treatment to a third, earlier–sown experiment (FE1–Early) which showed no heat stress impacts.

The pod–set, harvest index and yield of the high temperature treatment, normalised by the values from ambient conditions, are presented in figure 5. This figure also shows the results from the simulations using all three GLAM-HTS parameter sets: SEN, MOD and TOL. The general form of the differences between the two genotypes is captured by the simulations. The apparent exception is normalised pod–set which is higher in the TOL simulation than in the MOD simulation, with the data showing the converse. However, when normalised observed pod number rather than pod set is used (see section 2.5), the disparity between simulation and observation is reduced. This is because the field data show a reduction in flower number at high temperatures which increases pod–set in the moderately sensitive genotype despite two of the three replicates showing a fall in pod number.

The MOD and TOL parameter sets produce values of yield and harvest index which are in agreement with the spread of the data for TMV2 and ICGS11 respectively. If normalised pod number is chosen as the data for comparison then the model pod–set is slightly under–estimated. This slight over–estimation of the impact of high temperatures carries through into the harvest index and yield. The result contrasts with those of simulation CE2 where the simulated impact of high temperatures was comparable to and above (depending on the flowering distribution) observations (figure 2).

The choice of flowering distribution (F1, F5, F6 compared to F2–F4) in FE1 results in yield differences of between 3 and 92%. This impact of flowering distribution becomes more pronounced with increased sensitivity to high temperature stress. The flowering distributions which are closest to those observed for this experiment (F1, F5, F6) are not those that produce the values of harvest index and yield that best agree with observations. Given that GLAM normalised pod–set agrees more closely with observed normalised pod number than observed normalised pod–set (which includes information on the number of flowers), this is not surprising.

An impact of high mean temperatures on harvest index, and subsequently on yield, is simulated by GLAM–HTS. This can be seen in the difference between the impacts of high temperature measured using yields and the impacts measured using rates of change of harvest index (figure 5): yield shows the greater reduction under high temperature since in GLAM the time to pod–initiation is increased by the super–optimal temperatures. Since the harvest date is fixed in this experiment, this results in a shorter pod–filling period and therefore a lower harvest index (see Challinor et al., 2004).

GLAM-HTS simulates no impact of high temperature stress on yield for the ambient temperature experiment. An impact on pod–set of between 4 and 21% is simulated by the MOD and SEN parameter sets. Appropriate adjustment of P_{cr} would result in this having an impact on yield. Kakani (2001) reported a significant impact, measured relative to the earlier–sown experiment (FE1–Early), of high temperature on pods: a 37% decrease in both pod–set and pod number for TMV2, and an increase in both these quantities for ICGS11, were observed. Similarly, impacts on pod yield were observed: a 64% reduction for TMV2 and a 28% reduction for ICGS11. GLAM simulates 29% lower yields in the control experiment than in FE1–Early, because of the longer duration of the earlier–sown crop. The tolerance of ICGS11 to high temperature stress, together with this result, suggests that a significant fraction of the impact on yield in this experiment is due to the shorter duration at higher temperatures (see section 2.2). The remaining observed impact on the TMV2 crop, however, remains unaccounted for by GLAM–HTS.

4. Concluding remarks

A parameterisation of the impacts of high temperature stress on the yield of groundnut has been developed. This parameterisation has been presented as an extension to the GLAM crop model. The ability of GLAM-HTS to simulate three levels of tolerance to heat stress has been demonstrated. The ability of GLAM to simulate the impact of temperature on duration has also been investigated, thus allowing an assessment of the impacts of the mean and variability of seasonal temperature on yield.

The form and magnitude of the response of simulated yield to high temperature stress (section 3.1) and mean temperature changes (section 3.2) for the controlled environments is satisfactory: most errors are less than 10% of the control yield. The field experiment (section 3.3) combines both the stress and duration effect of temperature. The results of this experiment show a relatively large degree of variability across replicates (figure 5). The form of the response of yield to temperature is captured in the simulations of this experiment. However, the impact of heat stress is slightly over–estimated in the FE1 high temperature treatment, and underestimated in the FE1 ambient temperature TMV2 case. Overall, the results suggest that GLAM-HTS is able to simulate the relative magnitudes of the duration and heat stress effects. Further, GLAM-HTS lends itself to integrated studies of crop responses to climate, as it can also assess the impact of changes in rainfall and atmospheric carbon dioxide.

The new high temperature stress parameterisation can be used in studies of current and future climates to assess the impact of high temperature stress events relative to mean temperature effects. Parameterisations for annual crops other than groundnut could have a similar or even identical functional form, hence enabling estimates of the vulnerability of crop yield to heat stress. The representation of genotype properties using a relatively small number of parameters minimises unnecessary complexity and allows assessment of the potential for adaptation to climate change via heat tolerance characteristics. The sensitivity analysis, which was necessarily limited in scope, highlights an important point: more data on the impact of high temperatures on pod–set and yield are needed in order to further constrain parameterisations of high temperature stress.

Acknowledgements

The authors wish to thank all the researchers who published the experimental data that was used in this study. We are also grateful to the reviewers for their insightful comments.

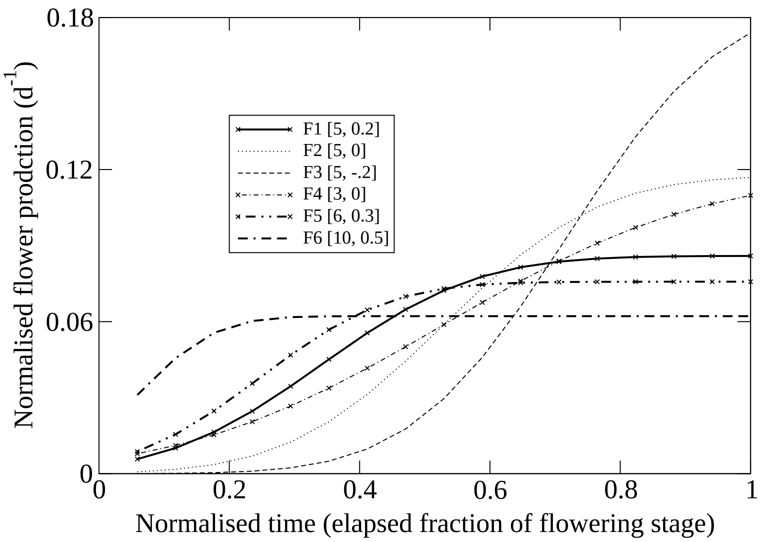

Figure 1. Flowering distributions used in the simulations, which follow a cumulative normal distribution. Thick lines (F1, F5, F6) show parameterisations consistent with the data of Kakani (2001) and crosses (F4, F5) indicate parameterisations consistent with the data of Prasad (1999). The remaining two curves (FE2, FE3) show distributions which are consistent with the data of Ndoye and Smith (1992). Values in brackets show the [width, offset] parameter pairs from the cumulative normal distribution.

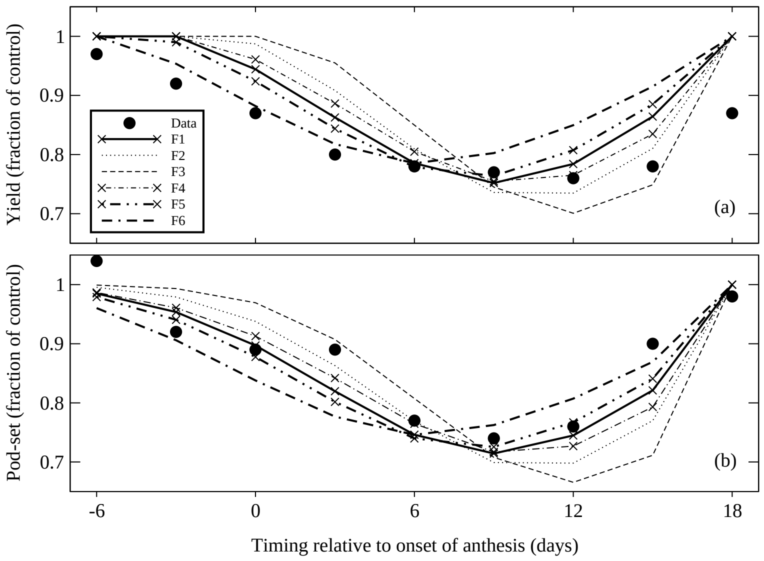

Figure 2. Observed and simulated (a) yields and (b) pod–set, as a fraction of the control (i.e. no high temperature impact) for experiment CE2. The observations in (b) show normalised peg number, since this was the only data available. The x–axis indicates the timing of the start of the six–day high temperature episode. Six flowering distributions, corresponding to those of figure 1, are shown; three of these (F1, F4, F5, with data points marked by crosses) are in closer agreement with observed distributions than the rest.

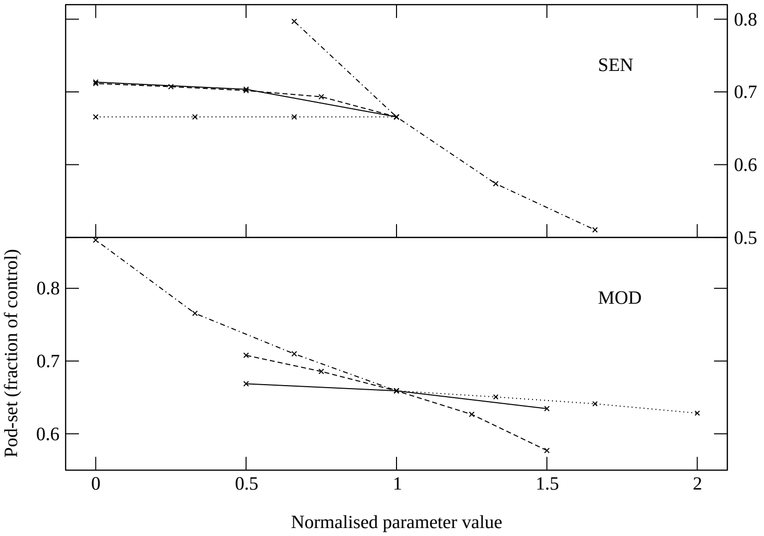

Figure 3. The sensitivity of pod–set to variation in parameter values for one of the sub–treatments of experiment CE2 (high temperatures applied twelve days after the onset of anthesis). Flowering distribution F3 was used for these simulations. In order to present all parameter variations in one graph, values have been normalised such that: (i) the range of values corresponds to the range used across all three parameter sets (TOL, MOD, SEN), with positive values corresponding to increased impact on pod–set; and (ii) a value of 1 corresponds to the baseline value. Baseline values were either SEN (upper panel) or MOD (lower panel). Hence in the upper panel normalised parameter values of 1 correspond to the point x=12 in figure 2. Normalised values can be converted to absolute values by examining the ranges in table II; appendix A presents the absolute values used in the SEN case. All model parameters that impact pod–set are shown: S_l (solid line), S_c (dotted line), T_{ia} (dashed line), and T_{cr}^{min} (dot-dashed line).

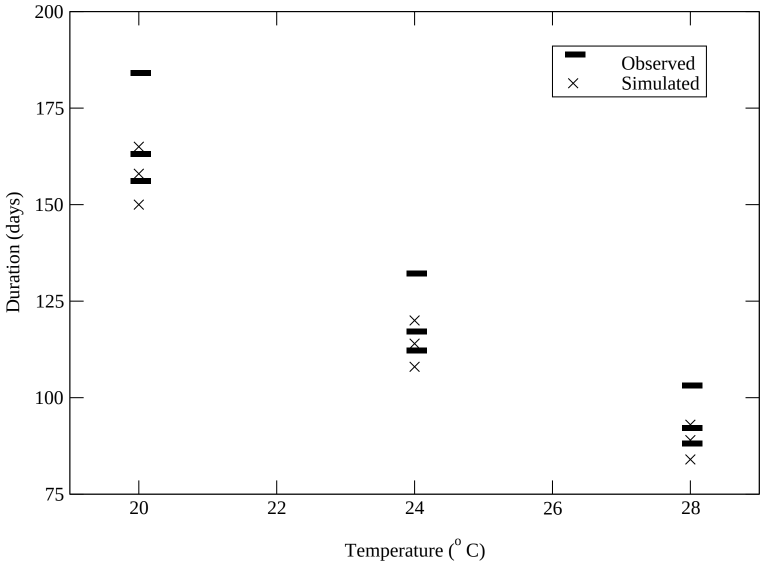

Figure 4. The simulated and observed impact of seasonal mean temperature on total crop duration for the controlled environment experiment CE3. The ranking (shortest to longest duration) remains constant with temperature for both the observations and simulations. The observations are taken from Nigam et al., 1994 (see table I). Simulated values are from the GLAM–HTS simulations described in section 2.4.

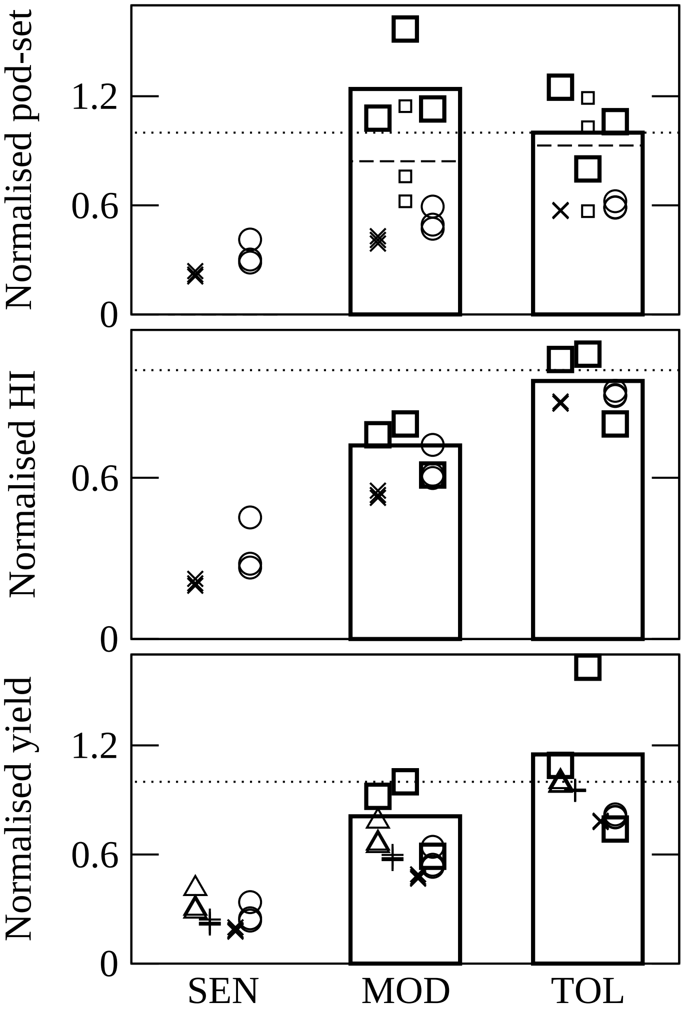

Figure 5. Results of SEN, MOD and TOL simulations with data from the two field experiment (FE1) genotypes: TMV2 (moderately sensitive: MOD) and ICGS11 (tolerant: TOL). All results are for the high temperature treatment normalised by the control treatment (ambient conditions). Bars show the mean across three replicates and bold squares show the three individual replicates. Crosses show GLAM-HTS simulations using flowering distributions F1, F5 and F6 (those in closest agreement with observations). Circles show the remaining three flowering distributions (F2, F3 and F4). Also shown are the normalised observed pod number per plant (small squares) and the normalised simulated rate of change of harvest index (pluses for F1, F5 and F6 and triangles for F2, F3 and F4). The dotted line show unity. Section 2.5 contains the rationale for these comparisons.

Table I. Summary of the experiments simulated. Cultivars in square brackets behaved similarly in terms of their response to heat stress (i.e. no temperature x cultivar interaction) and so were not treated separately in the analysis. Timing refers to the start of the high temperature episode. DRO indicates days relative to onset of flowering. T_{WD} refers to the mean 8am–8pm (whole day) temperature during the simulated flowering stage. Since T_{AM} spans a subset of this period (8am–2pm) and since diurnal variability in the controlled environment experiments (CE1 and CE2) was low, $T_{AM} = T_{WD}$ was assumed for these experiments. T_{max} refers to the daily maximum temperature during the simulated flowering stage. The corresponding calculated value of T_{AM} for the field experiment (FE1) is 37.6°C. Data sources are coded as follows: K2001 (Kakani, 2001), P1999 (Prasad, 1999), N1994 (Nigam et al., 1994). Evaluation data is of three types: P denotes data on pod number, Y denotes yield data and D denotes data on duration. Also shown are the model parameters. SEN, MOD and TOL refer to the values in table II and the flowering–curve codes correspond to the curves in figure 1.

Expt.	Cultivars	Sub– treatments or experiments	Timing	Duration (days)	Temperature °C	Data source	Eval. data	Model parameters
CE1	[ICGV86015, ICG796]	None	At 50% anthesis	10	$T_{WD} = 37$	K2001	P, Y	SEN; F1, F5, F6
CE2	[ICGV86015, ICGV87282]	9 timings	−6 – +18 DRO	6	$T_{WD} = 38$	P1999	P, Y	SEN; F1, F4, F5
CE3	TMV2, NCAc17090, VA81B	3 temperatures	— Whole season —		$T_{max} \leq 30.0$	N1994	D	—
FE1	TMV2, ICGS11	2 cultivars	At 50% anthesis	20	$T_{max} \leq 47$	K2001	P, Y	SEN,MOD,TOL; F1,5,6

Table II. Parameter values used in the simulation of tolerant (TOL), moderately sensitive (MOD) and sensitive (SEN) genotypes.

Parameter	Reference	units	TOL	MOD	SEN
T_{cr}^{min}	Eqn. 1 & 2	°C	37.0	34.0	36.0
S_c	Eqn. 1	$^\circ$C d^{-1}	0.3	0.0	0.3
S_l	Eqn. 1	$^\circ$C d^{-1}	2.0	2.5	3.0
T_{ia}	Eqn. 2	°C	53.0	51.0	48.8
P_{cr}	Eqn. 5	–	0.60	0.60	0.95

Appendix

A. Parameter values used in the sensitivity analysis

Table III. Maximum and minimum normalised parameter values, with the SEN parameter set as the baseline, that were used in the sensitivity analysis. Also shown are the corresponding absolute values. Normalised values correspond to the x–axis of the upper panel in figure 3. Also shown is the impact of each parameter: pre– and/or post– anthesis high temperature events.

Parameter	Impact	Min		Max	
		Normalised	Absolute	Norm.	Abs.
T_{cr}^{min}	Pre & Post	0.66	37	1.66	34
S_c	Pre	0.00	0	1.00	0.3
S_l	Pre	0.00	2	1.00	3
T_{ia}	Post	0.00	53	1.00	48.8

List of symbols

Symbol	Description	Units
d	Duration of episode	days
$F_f(i)$	Flowering distribution: the fraction of total flowers that open on day i	–
N_F	Duration of flowering stage	days
P_{cr}	Critical pod fraction	–
$P(i)$	The fraction of pods from day i which set	–
P_{tot}	The fraction of total yield–determining pods which set	–
S_c	Sensitivity of T_{cr} to timing (t) for negative t	°C day^{-1}
S_l	Sensitivity of T_{lim} to timing (t) for negative t	°C day^{-1}
t	Time of episode relative to day of anthesis	days
$T_{cr}(t)$	Critical temperature	°C
T_{cr}^{min}	Minimum value of T_{cr}	°C
T_{ia}	Intercept of post-anthesis T_{lim} parameterisation (eqn. 2)	°C
$T_{lim}(t)$	Temperature at zero pod–set	°C
T_{WD}	Mean whole day (8am–8pm) temperature	°C
T_{AM}	Mean 8am–2pm temperature	°C
T_{max}, T_{min}	Maximum and minimum daily temperatures	°C
$\left(\frac{\partial H_I}{\partial t}\right)$	Rate of change of harvest index	day^{-1}
$\left(\frac{\partial H_I}{\partial t}\right)_0$	Non-stressed rate of change of harvest index	day^{-1}

List of abbreviations

CE	Controlled environment
F	Flowering distribution
FE	Field environment
GLAM	General Large–Area Model for annual crops
HTS	High temperature stress
LAI	Leaf area index
MOD	Moderately sensitive to HTS
SEN	Sensitive to HTS
TOL	Tolerant to HTS

References

Challinor, A. J., J. M. Slingo, T. R. Wheeler, P. Q. Craufurd, and D. I. F. Grimes: 2003, 'Towards a combined seasonal weather and crop productivity forecasting system: Determination of the spatial correlation scale'. *J. Appl. Meteorol.* **42**, 175–192.

Challinor, A. J., J. M. Slingo, T. R. Wheeler, and F. J. Doblas-Reyes: 2005a, 'Probabilistic hindcasts of crop yield over western India'. *Tellus A.* In press.

Challinor, A. J., T. R. Wheeler, J. M. Slingo, P. Q. Craufurd, and D. I. F. Grimes: 2004, 'Design and optimisation of a large–area process–based model for annual crops'. *Agric. For. Meteorol.* **124**, 99–120.

Challinor, A. J., T. R. Wheeler, J. M. Slingo, P. Q. Craufurd, and D. I. F. Grimes: 2005b, 'Simulation of crop yields using the ERA40 re-analysis: limits to skill and non-stationarity in weather–yield relationships.'. *J. Appl. Meteorol.* In Press.

Chatzialioglou, A.: 1995, 'Effects of high temperature stress on dry matter partitioning in two genotypes of groundnut (*Arachis Hypogaea* L.'. Master's thesis, University of Reading, U.K.

Craufurd, P. Q., P. V. V. Prasad, G. Kakani, T. R. Wheeler, and S. N. Nigam: 2003, 'Heat tolerance in groundnut'. *Field Crops Research* **80**, 63–77.

Craufurd, P. Q., P. V. V. Prasad, and R. J. Summerfield: 2001, 'Dry matter production and rate of change of harvest index at high temperature in peanut'. *Crop Science* **42**, 146–151.

Craufurd, P. Q., T. R. Wheeler, R. H. Ellis, and P. V. V. Prasad: 2000, 'Escape and tolerance to high temperature at flowering in groundnut (*Arachis hypogaea* L.)'. *J. Agric. Sci.* **135**, 371–378.

Ferris, R., R. H. Ellis, T. R. Wheeler, and P. Hadley: 1998, 'Effect of high temperature stress at anthesis on grain yield and biomass of field–grown crops of wheat'. *Annals of Botany* **82**, 631–639.

Hall, A. E.: 1990, 'Breeding for heat tolerance — An approach based on whole–plant physiology'. *Hortscience* **25**(1), 17–19.

IPCC: 2001, *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press. 881 pp.

Ismail, A. M. and A. E. Hall: 1999, 'Reproductive stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea'. *Crop Science* **39**, 1762–1768.

Kakani, V. G.: 2001, 'Quantifying the effects of high temperature and water stress in Groundnut'. Ph.D. thesis, University of Reading, U.K.

Kakani, V. G., P. V. V. Prasad, P. Q. Craufurd, and T. R. Wheeler: 2002, 'Response of *in vitro* pollen germination and pollen tube growth of groundnut (*Arachis hypogaea* L.) genotypes to temperature'. *Plant, Cell and Environment* **25**, 1651–1661.

Lüdeke, M. K. B., F.-W. Badeck, R. D. Otto, C. Häger, S. Dönges, J. Kindermann, G. Würth, T. Lang, U. Jäkel, A. Klaudius, P. Ramge, S. Habermehl, and G. H. Kohlmaier: 1994, 'The Frankfurt biosphere model: a global process-oriented model for the seasonal and longterm CO_2 exchange between terrestrial ecosystems and the atmosphere. Part I: model description and illustrative results for cold deciduous and boreal forests'. *Climate Research* **4**, 143–166.

Matsui, T., K. Omasa, and T. Horie: 2001, 'The difference in sterility due to high temperatures during the flowering period among japonica rice varieties'. *Plant Production Science* **4**, 90–93.

Ndoye, O. and O. D. Smith: 1992, 'Flowering pattern and fruiting characteristics of 5 short growth duration peanut lines'. *Oleagineux* **47**, 235–240.

Nigam, S. N., R. C. N. Rao, J. C. Wynne, J. H. Williams, M. Fitzner, and G. V. S. Nagabhushanam: 1994, 'Effect and interaction of temperature and photoperiod on growth and partitioning in 3 groundnut (*Arachis Hypogaea* L. genotypes'. *Ann. Appl. Biol* **125**, 541–552.

Ntare, B. R., J. H. Williams, and F. Dougbedji: 2001, 'Evaluation of groundnut genotypes for heat tolerance under field conditions in a Sahelian environment using a simple physiological model for yield'. *J. Agric. Sci.* **136**, 81–88.

Prasad, P. V. V.: 1999, 'The effect of heat stress on fruit-set and fruit yield of groundnut (*Arachis hypogaea* L.)'. Ph.D. thesis, Department of Agriculture, University of Reading, Earley Gate, P.O. Box 236, Reading RG6 6AT, U.K.

Prasad, P. V. V., P. Q. Craufurd, V. G. Kakani, T. R. Wheeler, and K. J. Boote: 2001, 'Influence of high temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in peanut'. *Australian Journal of Plant Physiology* **28**, 233.

Prasad, P. V. V., P. Q. Craufurd, and R. J. Summerfield: 1999, 'Sensitivity of peanut to timing of heat stress during reproductive development'. *Crop Science* **39**(5), 1352–1357.

Prasad, P. V. V., P. Q. Craufurd, R. J. Summerfield, and T. R. Wheeler: 2000, 'Effects of short episodes of heat stress on flower production and fruit-set of groundnut *Arachis hypogaea* L.'. *Journal of Experimental Botany* **51**(345), 777–784.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery: 1994, *Numerical recipes in Fortran: The Art of Scientific Computing*. Cambridge University press.

Trnka, M., M. Dubrovský, D. Semerádová, and Z. Žalud: 2004, 'Projections of uncertainties in climate change scenarios into expected winter wheat yields'. *Theor. Appl. Climatol.* **77**, 229–249.

Wheeler, T. R., P. Q. Craufurd, R. H. Ellis, J. R. Porter, and P. V. V. Prasad: 2000, 'Temperature variability and the annual yield of crops'. *Agric. Ecosyst. Environ.* **82**, 159–167.