



ELSEVIER

Agriculture, Ecosystems and Environment 82 (2000) 159–167

**Agriculture  
Ecosystems &  
Environment**

www.elsevier.com/locate/agee

## Temperature variability and the yield of annual crops

Timothy R. Wheeler<sup>a,\*</sup>, Peter Q. Craufurd<sup>a</sup>, Richard H. Ellis<sup>a</sup>,  
John R. Porter<sup>b</sup>, P.V. Vara Prasad<sup>a</sup>

<sup>a</sup> Department of Agriculture, The University of Reading, Earley Gate, PO Box 236, Reading RG6 6AT, UK

<sup>b</sup> Department of Agricultural Sciences, The Royal Agricultural and Veterinary University, Agrovej 10, 2630 Taasnuup, Denmark

### Abstract

Global production of annual crops will be affected by the increases in mean temperatures of 2–4°C expected towards the end of the 21st century. Within temperate regions, current cultivars of determinate annual crops will mature earlier, and hence yields will decline in response to warmer temperatures. Nevertheless, this negative effect of warmer temperatures should be countered by the increased rate of crop growth at elevated atmospheric CO<sub>2</sub> concentrations, at least when there is sufficient water. Of more importance for the yield of annual seed crops may be changes in the frequency of hot (or cold) temperatures which are associated with warmer mean climates. The objectives of this paper are to review evidence for the importance of variability in temperature for annual crop yields, and to consider how the impacts of these events may be predicted. Evidence is presented for the importance of variability in temperature, independent of any substantial changes in mean seasonal temperature, for the yield of annual crops. Seed yields are particularly sensitive to brief episodes of hot temperatures if these coincide with critical stages of crop development. Hot temperatures at the time of flowering can reduce the potential number of seeds or grains that subsequently contribute to the crop yield. Three research needs are identified in order to provide a framework for predicting the impact of episodes of hot temperatures on the yields of annual crops: reliable seasonal weather forecasts, robust predictions of crop development, and crop simulation models which are able to quantify the effects of brief episodes of hot temperatures on seed yield. © 2000 Elsevier Science B.V. All rights reserved.

**Keywords:** Temperature; Temperature variability; Crop yields; Climate change

### 1. Introduction

Temperature is central to how climate influences the growth and yield of crops. The rate of many growth and development processes of crop plants is controlled by air or soil temperature. Over the last decade or so, the interests of the scientific community in the response of crops to temperature has been renewed as the evidence of a warming of global mean temperatures due to human activities (e.g. Kattenberg et al., 1995) becomes more persuasive.

Many studies have investigated how the warmer temperatures and elevated atmospheric CO<sub>2</sub> concentrations expected under climate change scenarios affect crop plants (reviewed in Morison and Lawlor, 1999). In general, an increase in mean seasonal temperature of 2–4°C reduces the yield of annual crops of determinate growth habit, such as wheat (*Triticum aestivum* L.) (Wheeler et al., 1996a; Batts et al., 1997), grown in well-watered conditions. Much of this decline in yield is due to shorter crop durations at these warmer temperatures. Nevertheless, this decline is expected to be countered by the enhancement of the rate of photosynthesis under future conditions of elevated atmospheric CO<sub>2</sub> concentrations. For example, a

\* Corresponding author. Fax: +44-118-9316747.  
E-mail address: t.r.wheeler@reading.ac.uk (T.R. Wheeler).

decline of wheat yield due to mean seasonal temperatures of 4.5°C (Goudriaan and Unsworth, 1990) and 1.8°C (Wheeler et al., 1996a) warmer were entirely offset by a doubling of atmospheric CO<sub>2</sub> concentration. In addition, reductions in the yield of determinate crops due to shorter crop durations could be countered by changing to a cultivar which has a longer crop duration in future climates through different sensitivities to temperature and/or photoperiod. Thus, the combined impact of warmer mean seasonal temperatures of 2–4°C and elevated atmospheric CO<sub>2</sub> concentrations of about 700 ppm at the end of the 21st century on the yield of current cultivars of annual crops grown in environments with sufficient water may not be great.

The effects of differences in mean seasonal temperature on crops are better understood than those of the fluctuating temperatures of many natural environments. For example, the rate of many development processes is a positive linear function of temperature between a base temperature (at and below which the rate of a particular process is zero) and an optimum temperature, and a negative linear function of temperature between this optimum and a ceiling temperature (Roberts and Summerfield, 1987). Many development processes of crop plants conform to these relationships. For example, the rate of seed germination (Garcia-Huidobro et al., 1982; Covell et al., 1986), the rate of flowering of photoperiod insensitive crop genotypes and photoperiod sensitive genotypes continuously grown in inductive photoperiods (Hadley et al., 1983; Roberts and Summerfield, 1987), and the rate of grain filling of cereals (Slafer and Rawson, 1994; Wheeler et al., 1996b). Thus, the response of these processes to changes in mean seasonal temperature can be easily quantified provided that the base or optimum temperatures are not transgressed for substantial periods of time.

Nevertheless, the effects of variability in temperature on crops may also be important. First, the effects of weather variables on crops are often non-linear because of the ways in which many crop processes respond to environment (Semenov and Porter, 1995). Second, fluctuations of extreme temperatures may affect the survival of crop plants or plant organs. The lethal temperatures for many growth and development processes of wheat have been clearly defined (Porter and Gawith, 1999). Under such extreme conditions, crop plants are loosely defined as under tempera-

ture or thermal stress. Recognition of the effects of temperature stress implies a comparison with plant performance under optimal conditions of temperature. Accordingly, resistance of crop plants to temperature stress has been defined as the maintenance of economic value where the crop is exposed to temperature stress (Mahan et al., 1995). Such definition does not consider the mechanisms responsible for temperature stress. Alternatively, 'stress' temperatures are more simply defined as those hotter (or colder) than a specific temperature. For example, Srinivasan et al. (1996) defined hot temperatures as those >30°C, and then identified regions where tolerance to hot temperatures would be a useful attribute for both vegetative growth and flowering of four grain legumes. Regardless of a precise definition, it is clear that the impact of temperature variability on crops is likely to include tolerance of crops to episodes of stress temperatures.

The objectives of this paper are to review evidence for the importance of variability in temperature for annual crop yields, and consider how episodes of hot temperatures affect the yield of annual crops which are grown for seed or grain, and how the impact of these events may be predicted. Episodes of hot temperatures are concentrated on for two reasons. First, although it is uncertain whether future global climates of warmer temperatures will be more variable or not (Nicholls et al., 1996), current warm temperature stress events will be more frequent for a given location even if the amplitude of temperature remains the same. Inter-daily climatic variability is thought to be of principal importance for the impact of climate change on the yield of annual crops (Porter and Semenov, 1999). Hence, brief episodes of stress temperatures will be focused on. Second, changes of temperature on a seasonal and daily basis are important for the adaptation of crop plants to current climates. There are many regions of seasonally arid climates within the sub-tropics, and winter rainfall areas at higher latitudes, where hot temperatures are thought to constrain the current yield potential of crops. For example, rice (*Oryza sativa* L.) is particularly sensitive to hot temperature at anthesis — sterility of some cultivars occurs if temperatures exceed 35°C at anthesis and last for >1 h — and hot temperatures cause spikelet sterility in dry and monsoon season crops in parts of Asia, and in tropical Africa (Yoshida, 1981). Improved knowledge on how these hot temperatures

affect crop yields now, and in the future, should contribute to the current and future management of risk in cropping systems.

## 2. The importance of variability in temperature for annual crops

The importance of changes in variability of climate, as opposed to changes in mean climate, for the growth of annual crops has been shown by crop simulation studies and by experiment. Semenov and Porter (1995) coupled the AFRCWHEAT2 simulation model to a stochastic weather generator in order to investigate the effects of differences in mean seasonal temperature and the variability of temperature (for the whole season) on the grain yield of wheat. An increase in mean seasonal temperature of 2°C in simulations at Rothamsted, UK decreased grain yield by 7% (cv increased by 90%) (Fig. 1) largely due to a reduction in (mean) crop duration of 24 days. Doubling the standard deviation of temperature on a daily basis, whilst the mean seasonal temperature was kept the same, reduced grain yield to the same extent as a 2°C increase in mean seasonal temperature (Fig. 1). The combined effects of a warmer mean seasonal temperature (in this example, +4°C) and a doubling of variability were to reduce yields by 19%; more than the sum of these two factors separately (Fig. 1).

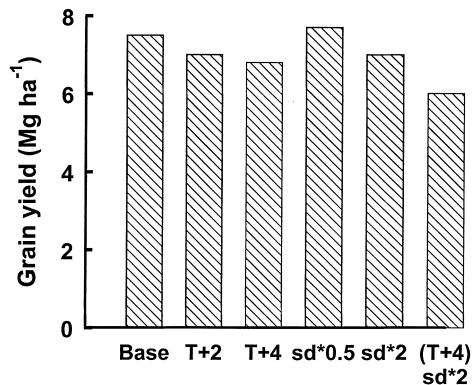


Fig. 1. Grain yield of winter wheat predicted using the AFR-CWheat3S crop simulation model for Rothamsted, UK with current climate (base), an increase in mean seasonal temperature ( $T + 2$ ,  $T + 4$ ), and a change in the variability of temperature (0.5S.D., 2S.D.) (redrawn from Semenov and Porter, 1995).

The processes within the model which were sensitive to these changes in variability were durations to double ridge stage (reduced due to exposure to more vernalising cold temperatures), and a delay in the time of anthesis and crop maturity (due to more frequent supra-optimal temperatures for these rates). Some of these simulated effects of increased variability of temperature were confirmed by a controlled environment experiment with wheat (Moot et al., 1996). A doubling of the standard deviation of daily temperature delayed the onset of grain filling, and reduced maximum crop leaf area. However, grain yields were not affected (Moot et al., 1996) possibly because fully vernalised plants were used.

Mearns et al. (1997) investigated the effects of variability in temperature during the whole season using the CERES-Wheat simulation model. An increase in mean temperature of 2°C reduced ( $P = 0.002$ ) predicted grain yield from 1266 kg ha<sup>-1</sup> (S.D. = 947) to 966 kg ha<sup>-1</sup> (S.D. = 815). Yields were predicted to fall further to 744 kg ha<sup>-1</sup> (S.D. = 741) when this warmer mean temperature was accompanied by a doubling of the variance of temperature. This effect of increasing variability of temperature was thought to be due to a greater proportion of winter kill (seedlings that did not survive the winter) at the colder extremes of temperature (Mearns et al., 1997). Riha et al. (1996) combined some functions of the CERES and EPIC models to investigate the effect of a doubling of temperature variability on soybean (*Glycine max* (L.) Merr.), wheat and maize (*Zea mays* L.). A doubling of temperature variability was predicted to reduce yields of all these crops by up to 50%. Most of this decrease was due to reduced rates of photosynthesis at cold temperatures. Thus, in all these simulations of wheat crops under increased temperature variability in temperate environments, exposure to cold temperatures accounted for most of the effect of variability of temperature during the season.

Evidence from crop experiments for the importance of variability in temperature was provided by one particular year's results in a series of wheat experiments (Batts et al., 1997) conducted within temperature-gradient chambers. This technique provides a field-based system to investigate how whole season CO<sub>2</sub> enrichment of crops interacts with differences in mean seasonal temperatures which vary from close to ambient temperature to +3 to +5°C (Hadley

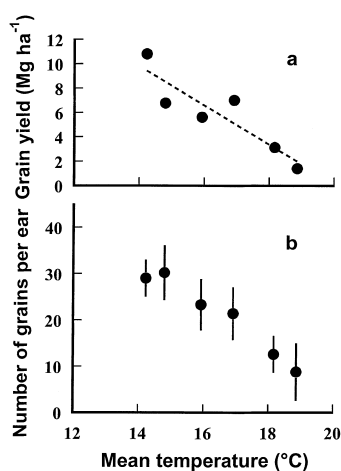


Fig. 2. Effects of differences in mean temperature from anthesis to harvest maturity on grain yield (a) and the number of grain per year (b) of winter wheat cv. Hereward grown at 350 ppm CO<sub>2</sub> within a temperature-gradient chamber. The vertical bars in (b) are ±1 S.D. (redrawn from Wheeler et al., 1996b).

et al., 1995). The 1992/1993 experiment in which winter wheat cv. Hereward was grown in these temperature gradient chambers is of interest to us here, and we will consider only those crops grown at ambient (350 ppm) CO<sub>2</sub>. As expected, in that experiment grain yield declined with an increase in mean temperature (Fig. 2a, but note that mean temperature is for the grain filling duration) due principally to more rapid crop development at warmer temperatures. However, the magnitude of this decline was far greater than in the other three seasons of experiments with the same cultivar of winter wheat. For a 1°C rise in mean seasonal temperature from sowing to harvest, grain yields declined by 4.09 Mg ha<sup>-1</sup> in 1992/1993 compared with 2.75, 0.26, and 1.43 Mg ha<sup>-1</sup> in 1991/1992, 1993/1994, and 1994/1995, respectively (Batts et al., 1997). The rapid decline in grain yields in 1992/1993 was associated with a reduction in the number of grains per year at the time of harvest maturity (Fig. 2b).

The number of grains in a wheat ear which develop can be reduced by hot temperatures (Al-Khatib and Paulsen, 1984; Thorne and Wood, 1987; Wardlaw et al., 1989) and low humidity (Tashiro and Wardlaw, 1990) at anthesis. Inspection of the daily temperatures for the wheat crops grown within the temperature gradient chambers in the 1992/1993 season at ambient CO<sub>2</sub> confirmed that unusually hot temperatures (for

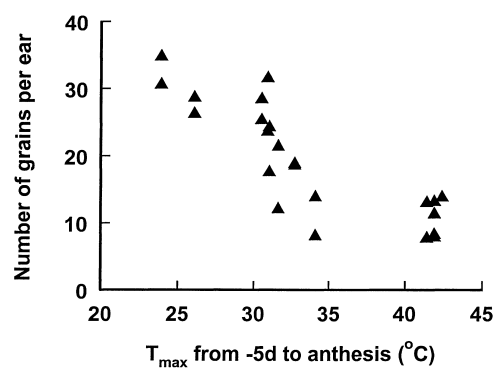


Fig. 3. Effects of differences in the maximum temperature ( $T_{\max}$ ) in the 5-day period ending at 50% anthesis on the number of grains per year at harvest maturity of winter wheat cv. Hereward grown at 350 ppm CO<sub>2</sub> within two temperature-gradient chambers (redrawn from Wheeler et al., 1996a).

Reading at 51°N) coincided with the period of anthesis (Wheeler et al., 1996a). Post-hoc analysis revealed that the number of grains per year was stable when maximum temperatures in the 5-day period ending at 50% anthesis (as defined by Porter et al., 1987) did not exceed 31°C (Fig. 3). However, the number of grains per year at harvest maturity declined rapidly when  $T_{\max}$  was greater than 31°C during this period. Hence grain yields were reduced by much more than would be expected from an advancement of crop development due to the warmer mean seasonal temperature. The effects of hot temperature episodes close to the time of anthesis were of more importance to the yield of these crops than the effects of the increase in mean seasonal temperature of about +2°C.

Further evidence for the importance of brief episodes of hot temperatures has been provided for spring wheat and for soybean. Ferris et al. (1998) imposed a range of hot temperatures (daily  $T_{\max}$  varied from <20 to 40°C) on a field-grown crop of spring wheat for a 12-day period starting 7–9 days before 50% anthesis. The crops were grown in a common environment before and after this period. Grain yield at harvest maturity varied from 3.7 to 9.5 Mg ha<sup>-1</sup> as a result of differences in temperature during this 12-day period. Some 97% of the variation in grain yield were explained by differences in grain number per square meter at harvest maturity. Furthermore, grain numbers were closely related to a maximum temperature during the 4-day period which encompassed 50% anthesis. Ferris et al. (1999) studied the effects of an

increase in temperature by 10°C for 8 days during the late flowering/early pod filling stage of soybean. Seed yields at harvest maturity were 29% less due to the high temperature episode. Of particular relevance to future climates of elevated CO<sub>2</sub> concentrations was the observation that the relative effects of the hot temperature episode on soybean yield was the same at both 350 and 700 ppm CO<sub>2</sub> (Ferris et al., 1999). Thus, it may be that once we understand the quantitative nature of the response to a temperature stress event under current CO<sub>2</sub> conditions, we may also use these responses for simulations in future climates of elevated CO<sub>2</sub>.

Variability in temperature can affect yield quality. The effects of episodes of hot temperatures on wheat grain quality for breadmaking are reasonably well documented. For example, grain nitrogen concentration of wheat varieties grown over 27 years in Australia was positively associated with the number of hours at temperatures >35°C during grain filling (Blumenthal et al., 1991), and temperatures >35°C are often associated with dough weakening (Blumenthal et al., 1993). Also, temperatures >32°C were negatively associated with sodium dodecyl sulphate (SDS) sedimentation volume (Graybosch et al., 1995), and with loaf volume (Finney and Fryer, 1958). In general, however, information on the effects of variability in temperature on the yield quality of annual crops is sparse and this subject requires further investigation.

These studies clearly demonstrate that variability in temperature affects the grain and seed yield of annual crops. Moreover, hot temperatures close to the time of flowering or anthesis appear to be particularly important to subsequent crop yield. Precisely when crop plants are most sensitive to hot temperature episodes, and how to quantify the effects of these hot temperature on yield will now be considered.

The time of flowering of many crop plants is sensitive to extremes of temperature. For example, in common beans (*Phaseolus vulgaris* L.) high temperature (32/27°C day/night temperature) during the period shortly before and at anthesis reduced pod set substantially (Gross and Kigel, 1994). No pods were set when high temperatures occurred at sporogenesis, or 10 days before anthesis, and pod set, pod abscission and seed set were all greatly reduced when high temperatures occurred near or at anthesis. Similarly, in cowpea

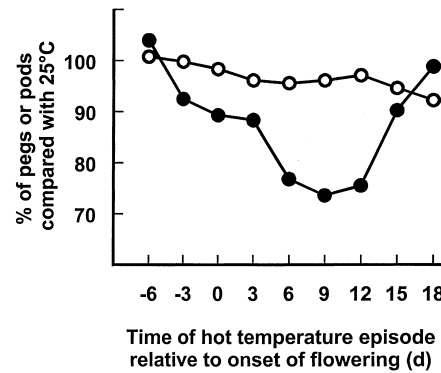


Fig. 4. Effect of a hot day temperature episode of +10°C above a control of 28°C for 6 days during flowering on the number of pods simulated using PNUTGRO for cv. TMV-2 (○) and the number of pods observed under the same growing conditions for cv. ICGV 86015 by Vara Prasad et al. (1999) (●).

(*Vigna unguiculata*) high temperatures for 6 days before anthesis substantially reduced pod set (Hall, 1992).

Vara Prasad et al. (1999) used reciprocal transfers of groundnut (*Arachis hypogaea* L.) plants from a near optimal day temperature (28°C) to a hot (38°C) temperature for 6-day periods to identify the period that fruit set (the production of pegs) was sensitive to hot temperatures. Transfers before 6 days prior to first flowering (R1 development stage of Boote, 1982) of the Spanish botanical type groundnut cv. ICGV 86015 did not affect the number of pegs subsequently produced. However, transfers to 38°C for 6 days during the period from 3 days prior to first flowering until 15 days after first flowering (3 days before the onset of seed growth, R3 development stage) reduced the number of pegs by up to 27% (Fig. 4). More precise transfers have subsequently shown two critical stages to hot temperature, 3–6 days before anthesis when microsporogenesis occurs, and at anthesis. Similarly, cowpea was sensitive to the effects of high night temperatures (30°C) during early bud development and at floral bud development; the most sensitive phase was 7–9 days prior to anthesis (Ahmed et al., 1992).

Two aspects of hot temperature episodes at sensitive stages of crop development need to be considered: the duration of the hot temperature episode, and its magnitude. The effects of the duration and magnitude of hot temperature on flower survival of groundnut are not independent. The peg numbers of groundnut

cv. ICGV 86015 (Spanish botanical type) declined from an average of 16.3 per plant at a day temperature of 28°C, to 5.0 (sed = 1.79) at 42°C (Vara Prasad et al., 2000). However, this average response was affected by an interaction between duration of exposure and temperature such that peg numbers exposed to a hot temperature were reduced to a greater extent as duration increased. This interaction between duration of exposure and temperature may simply result from a confounding of the underlying processes. Two processes determine successful fruit production in groundnut: the rate of flowering and fruit set. The number of flowers produced by groundnut cv. ICGV 86015 was a simple negative function of air temperature between 28 and 48°C (Vara Prasad et al., 2000). In contrast, fruit set is a more critical event response. The proportion of flowers which set fruit was not affected by air temperatures cooler than 37°C (equivalent to a bud temperature of 36°C, Vara Prasad et al., 2000). However, fruit set declined rapidly at >37°C until no fruit at all were set at 44°C. Hot temperatures in the morning (08:00–14:00 h) period of the day accounted for this response. A simple model of these processes quantified these effects of hot temperature episodes at flowering of groundnut (Vara Prasad et al., 2000).

Rice is also very sensitive to hot temperatures close to the time of anthesis, and most sensitive at about 9 days before anthesis (Yoshida, 1981). At anthesis, spikelet fertility is reduced from 90 to 20% by only 2 h exposure to 38°C, and to 0% by <1 h exposure to 41°C. The critical temperature for spikelet fertility (defined as when fertility exceed 80%) varies between genotypes, but is about 32–36°C. Similar to groundnuts, flowering in rice also occurs during the morning, and therefore models have to both accurately predict the day of flowering and the diurnal course of temperature if the effects of high temperature events are to be predicted.

### 3. Prediction of the impacts of hot temperature episodes on crop yield

The impacts of hot temperature episodes on crop yield which have been described represent a risk to production in some current climates, and in future climates given anthropogenic climate change. Three components are needed to provide a predictive system

to assess these risks: a forecast of seasonal weather, prediction of crop development, and a model of the effects of hot temperature episodes.

Analysis of historical weather provides an initial indication as to the probability of hot temperatures for a given location in the current climate. However, advances by climate scientists continue to improve the predictive skill of seasonal forecasts, and investigations of their use in crop management have begun (e.g. Hammer et al., 1996). One challenge to the use of these forecast ensembles to investigate the effects of variability of temperature on crops is the brief time resolution that is known to disrupt reproductive processes in crop plants.

Much effort has been invested into predicting the timing of crop development. The reason for this is twofold. First, the effects of environment (temperature and photoperiod) on crop development (phenology) are central to crop adaptation (Evans, 1993; Roberts et al., 1996). Second, the accuracy of the phenology sub-model of a crop simulation model is a sensitive step to the precise prediction of crop biomass and yield. Two separate, but related methods to predict the timing of flowering have been developed. In the first, the effects of temperature and photoperiod on the entire duration from sowing to flowering are quantified. These models often are used to predict the time of flowering of different crop genotypes for the purposes of examining crop adaptation to climate. Such models are usually an additive function of temperature and photoperiod (e.g. Hadley et al., 1983; Roberts and Summerfield, 1987), but other models include a multiplicative temperature $\times$ photoperiod interaction (e.g. Yan and Wallace, 1998). The important characteristic of these models is that for crop genotypes for which the durations of the pre- and post-inductive photoperiod insensitive phases are negligible, the duration from sowing to flowering is treated as a single phase. Crop simulation models which operate on daily time steps often treat each development stage separately and quantify the effects of environment on each. For example, the CERES-maize model divides the duration from sowing to tassel initiation into four stages, some of which are determined by temperature alone (germination to emergence, emergence to the end of the juvenile phase), others by photoperiod alone (end of juvenile phase to tassel initiation), and all are influenced by genetic coefficients (Jones and Kiniry, 1986).

A number of studies permit the precision of these methods of predicting the time of crop development to be assessed. The mean absolute deviation of observed time from sowing to flowering of rice cv. IR8 from that predicted using a beta function to describe the response of development rate to temperature was 9 days from durations that ranged from about 85 to 150 days (Yin et al., 1995). The average difference between observed duration from sowing to flowering of 12 cultivars of soybean and the duration predicted using additive functions of temperature and photoperiod to predict the rate of flowering ranged from <1 to 8.7 days (Summerfield et al., 1993). The accuracy of these predictions was better for the short duration cv. Fiskeby V (average difference of 0.3-day from observed duration of 31.5 days) than for the longer duration genotypes such as cv. Jupiter (average difference of 8.7 days from observed duration of 82.2 days). This decline in predictive ability with an increase in the duration of the development stage is a natural consequence of using the rate of flowering as a basis for modelling the effects of environment.

A comparison of three wheat simulation models compared the prediction of time of anthesis (Porter et al., 1993). The residual mean square deviation of prediction of anthesis date from the most accurate model was 4.5 days, but was >20 days for the least accurate. Model validation of the CERES-maize simulation model included a comparison of the prediction of date of silking of a range of maize cultivars (Jones and Kiniry, 1986). Average deviation between predicted and observed dates was small, e.g. -1.2 days for cv. Pioneer 3780, -3.7 days for cv. B73×Mo17, and +2.2 days for cv. H610. However, the variance of these deviations ranged from 4.3 to 5.7 days (Jones and Kiniry, 1986).

These examples demonstrate that crop phenology models are capable of predicting the time of flowering or anthesis to an accuracy of within, at worst, 10% of the duration of this developmental stage. However, the predictive skill of these phenology models will not always be good enough to examine whether or not the time of flowering coincides with a hot temperature event which may be of only 2–3 days duration.

Crop simulation models usually account for the effects of both sub- and supra-optimal temperatures on development processes, and on the rates of photosynthesis and respiration. However, it is less common for

crop simulation models to capture the effects of brief episodes of hot temperature which have only a minor effect on the rate of development, but substantially reduce yield potential by reducing the number of reproductive structures (Porter and Gawith, 1999). For example, the simulation model PNUTGRO (Boote et al., 1986) was used to simulate the effect of a 6-day hot temperature episode of +10°C (i.e. 38°C) each day, starting from -6 to +21 days from the time of first flowering of groundnut, on the number of pods of cv. TMV-2 (a Spanish botanical-type genotype similar to cv. ICGV 86015). This simulated response was compared with the response of the number of pegs of cv. ICGV 86015 to these hot temperature episodes observed by experiment (Vara Prasad et al., 1999). The response of peg and pod numbers to these brief hot temperature episodes was quantitatively and qualitatively different between the model output and those observed by experiment (Fig. 4). The decline in the proportion of pods (0.2–8.3%) predicted by the model was much less than that observed for pegs (7.6–27%) by experiment (Fig. 4). Thus, this crop simulation model does not at present capture the effects of brief hot temperature episodes on the number of reproductive structures of groundnut.

#### 4. Conclusion

It is clear that changes to the variability of temperature, separate to changes in mean seasonal temperature, affect the yield of annual crops. The effects of brief episodes of hot temperatures on the number of yield components can be particularly dramatic. However, the impact on crop yield cannot simply be predicted from the absolute temperature. Instead, it is reflected by the combination of the magnitude and duration of the hot temperature episode, and coincidence with the development stage of the crop.

A predictive system for the impacts of hot temperature variability may permit the risk of crop production to be estimated for different cropping regions, and for current and future climates. Such a system requires three components: a seasonal forecast of weather with the appropriate predictive skill on a relatively brief time resolution; robust models for prediction of crop development with a resolution which more closely matches the variability in natural temperatures; and

crop simulation models which model the processes of crop responses to hot temperature episodes. The basis of such a predictive system exists within the disciplines of meteorology and crop science. Two further challenges for research remain to develop the precision/robustness of the predictions of these three components to the appropriate resolution, and to integrate these components into a predictive system.

### Acknowledgements

We acknowledge the scientific contributions of our colleagues Prof. P. Hadley and R.J. Summerfield, Drs. J.I.L. Morison, G.R. Batts, R. Ferris and M.J. Gooding, and Mr. V.G. Kakani.

### References

- Ahmed, F.E., Hall, A.E., DeMason, D.A., 1992. Heat injury during floral development in cowpea (*Vigna unguiculata*, Fabaceae). *Am. J. Bot.* 79, 784–791.
- Al-Khatib, K., Paulsen, G.M., 1984. Mode of high temperature injury to wheat during grain development. *Physiol. Plant.* 61, 363–372.
- Batts, G.R., Morison, J.I.L., Ellis, R.H., Hadley, P., Wheeler, T.R., 1997. Effects of CO<sub>2</sub> and temperature on growth and yield of crops of winter wheat over four seasons. *Eur. J. Agron.* 7, 43–52.
- Blumenthal, C.S., Bekes, F., Batey, I.L., Wrigley, C.W., Moss, H.I., Mares, D.J., Barlow, E.W.R., 1991. Interpretation of grain quality results from wheat variety trials with reference to high temperature stress. *Aust. J. Agric. Res.* 42, 325–334.
- Blumenthal, C.S., Barlow, E.W.R., Wrigley, C.W., 1993. Growth environment and wheat quality: the effect of heat stress on dough properties and gluten proteins. *J. Cereal Sci.* 18, 3–21.
- Boote, K.J., 1982. Growth stages of peanut (*Arachis hypogaea* L.). *Peanut Sci.* 9, 35–39.
- Boote, K.J., Jones, J.W., Mishoe, J.W., Wilkerson, G.G., 1986. Simulating the growth and yield of Florunner peanut. In: *Proceedings of the American Peanut Research and Education Society*, Vol. 18, 38 pp.
- Covell, S., Ellis, R.H., Roberts, E.H., Summerfield, R.J., 1986. The influence of temperature on seed germination rate in grain legumes. I. A comparison of chickpea, lentil, soyabean and cowpea in constant temperatures. *J. Exp. Bot.* 37, 705–715.
- Evans, L.T., 1993. *Crop Evolution, Adaptation and Yield*. Cambridge University Press, Cambridge.
- Ferris, R., Ellis, R.H., Wheeler, T.R., Hadley, P., 1998. Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. *Ann. Bot.* 82, 631–639.
- Ferris, R., Wheeler, T.R., Ellis, R.H., Hadley, P., 1999. Seed yield after environmental stress in soybean grown under elevated CO<sub>2</sub>. *Crop Sci.* 39, 710–718.
- Finney, K.F., Fryer, H.C., 1958. Effect on loaf volume of high temperatures during the fruiting period of wheat. *Agron. J.* 50, 28–34.
- Garcia-Huidobro, J., Monteith, J.L., Squire, G.R., 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides*). I. Constant temperature. *J. Exp. Bot.* 33, 288–296.
- Goudriaan, J., Unsworth, M.H., 1990. Implications of increasing carbon dioxide and climate change for agricultural productivity and water resources. In: Kimball, B.A., Rosenberg, N.J., Allen, L.H. (Eds.), *Impact of Carbon Dioxide, Trace Gases, and Climate Change on Global Agriculture*. Special Publication No. 53. American Society of Agronomy, Madison, WI, pp. 111–130.
- Graybosch, R.A., Peterson, C.J., Baenziger, P.S., Shelton, D.R., 1995. Environmental modification of hard red winter wheat flour protein composition. *J. Cereal Sci.* 22, 45–51.
- Gross, Y., Kigel, J., 1994. Differential sensitivity to high temperature of stages in the reproductive development of common bean (*Phaseolus vulgaris* L.). *Field Crops Res.* 36, 112–201.
- Hadley, P., Roberts, E.H., Summerfield, R.J., Minchin, F.R., 1983. A quantitative model of reproductive development in cowpea (*Vigna unguiculata* (L.) Walp.) in relation to photoperiod and temperature, and implications for screening germplasm. *Ann. Bot.* 51, 531–543.
- Hadley, P., Batts, G.R., Ellis, R.H., Morison, J.I.L., Pearson, S., Wheeler, T.R., 1995. Temperature gradient chambers for research on global environment change. II. A twin-wall tunnel system for low stature, field-grown crops using a split heat pump: technical report. *Plant Cell Environ.* 18, 1055–1063.
- Hall, A.E., 1992. Breeding for heat tolerance. *Plant Breeding Rev.* 10, 129–167.
- Hammer, G.L., Holzworth, D.P., Stone, R., 1996. The value of skill in seasonal climate forecasting to wheat crop management in a region of high climatic variability. *Aust. J. Agric. Sci.* 47, 717–737.
- Jones, C.A., Kiniry, J.R., 1986. *CERES-maize: A Simulation Model of Maize Growth and Development*. Texas A & M University Press, College Station, TX.
- Kattenberg, A., Giorgi, F., Grassl, H., Meehl, G.A., Mitchell, J.F.B., Stouffer, R.J., Tokioka, T., Weaver, A.J., Wrigley, T.M.L., 1995. Climate models — projection of future climate. In: Houghton, J.T., et al. (Eds.), *Climate Change. The Science of Climate Change. Contribution of Working Group 1 to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 285–358.
- Mahan, J.R., McMichael, B.L., Wanjura, D.F., 1995. Methods for reducing the adverse effects of temperature stress on plants: a review. *Environ. Exp. Bot.* 35, 251–258.
- Mearns, L.O., Rosenweig, C., Goldberg, R., 1997. Mean and variance change in climate scenarios: methods, agricultural applications, and measures of uncertainty. *Clim. Change* 35, 367–396.
- Moot, D.J., Henderson, A.L., Porter, J.R., Semenov, M.A., 1996. Temperature, CO<sub>2</sub> and the growth and development of wheat: changes in the mean and variability of growing conditions. *Clim. Change* 33, 351–368.
- Morison, J.I.L., Lawlor, D.W., 1999. Interactions between increasing CO<sub>2</sub> concentration and temperature on plant growth. *Plant Cell Environ.* 22, 659–682.



- Nicholls, N., Gruza, G.V., Jouzel, J., Karl, T.R., Ogallo, L.A., Parker, D.E., 1996. Observed climate variability and change. In: Houghton, J.T., et al. (Eds.), *Climate Change. The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp. 133–192.
- Porter, J.R., Gawith, M., 1999. Temperatures and the growth and development of wheat: a review. *Eur. J. Agron.* 10, 23–36.
- Porter, J.R., Semenov, M.A., 1999. Climatic variability and crop yields in Europe. *Nature* 400, 724.
- Porter, J.R., Kirby, E.J.M., Day, W., Adam, J.S., Appleyard, M., Ayling, S., Baker, C.K., Beale, P., Besford, R.K., Chapman, A., Fuller, M.P., Hampson, J., Hay, R.K.M., Hough, M., Matthews, S., Thompson, W.J., Weir, A.H., Willington, V.B.A., Wood, D.W., 1987. An analysis of morphological development stages in Avalon winter wheat with different sowing dates at 10 sites in England and Scotland. *J. Agric. Sci.* 109, 107–121.
- Porter, J.R., Jamieson, P.D., Wilson, D.R., 1993. Comparison of the wheat simulation models AFRCWHEAT2, CERES-Wheat and SWHEAT for non-limiting conditions of crop growth. *Field Crops Res.* 33, 131–157.
- Riha, S.J., Wilks, D.S., Simeons, P., 1996. Impact of temperature and precipitation variability on crop model predictions. *Clim. Change* 32, 293–311.
- Roberts, E.H., Summerfield, R.J., 1987. Measurement and prediction of flowering in annual crops. In: Atherton, J.G. (Ed.), *Manipulation of Flowering*. Butterworths, London, pp. 17–50.
- Roberts, E.H., Qi, A., Ellis, R.H., Summerfield, R.J., Lawn, R.J., Shanmugasundaram, S., 1996. Use of field observation to characterise genotypic flowering responses to photoperiod and temperature: a soyabean exemplar. *Theoret. Appl. Genetics* 93, 519–533.
- Semenov, M.A., Porter, J.R., 1995. Climatic variability and the modelling of crop yields. *Agric. For. Meteorol.* 73, 265–283.
- Slafer, G.A., Rawson, H.M., 1994. Sensitivity of wheat-phenic development to major environmental factors: a re-examination of assumptions made by physiologists and modellers. *Aust. J. Plant Physiol.* 21, 393–426.
- Srinivasan, A., Takeda, H., Senboku, T., 1996. Heat tolerance in food legumes as evaluated by cell membrane thermostability and chlorophyll fluorescence techniques. *Euphytica* 88, 35–45.
- Summerfield, R.J., Lawn, R.J., Qi, A., Ellis, R.H., Roberts, E.H., Chay, P.M., Brouwer, J.B., Rose, J.L., Shanmugasundaram, S., Yeates, S.J., Sandover, S., 1993. Towards the reliable prediction of time to flowering in six annual crops. II. Soyabean (*Glycine max*). *Exp. Agric.* 29, 253–289.
- Tashiro, T., Wardlaw, I.F., 1990. The response to high temperature shock and humidity changes prior to and during the early stages of grain development in wheat. *Aust. J. Plant Physiol.* 17, 551–561.
- Thorne, G.N., Wood, D.W., 1987. Effects of radiation and temperature on tiller survival, grain number and grain yield in winter wheat. *Ann. Bot.* 59, 413–426.
- Vara Prasad, P.V., Craufurd, P.Q., Summerfield, R.J., 1999. Sensitivity of peanut to timing of heat stress during reproductive development. *Crop Sci.* 39, 1352–1357.
- Vara Prasad, P.V., Craufurd, P.Q., Summerfield, R.J., Wheeler, T.R., 2000. Effect of short episodes of heat stress on flower production and fruit set of groundnut (*Arachis hypogaea* L.). *J. Exp. Bot.* 51, 777–784.
- Wardlaw, I.F., Dawson, I.A., Munibi, P., Frewster, R., 1989. The tolerance of wheat to high temperatures during reproductive growth. I. Survey procedures and general responses. *Aust. J. Agric. Res.* 40, 1–13.
- Wheeler, T.R., Batts, G.R., Ellis, R.H., Hadley, P., Morison, J.I.L., 1996a. Growth and yield of winter wheat (*Triticum aestivum*) crops in response to CO<sub>2</sub> and temperature. *J. Agric. Sci.* 127, 37–48.
- Wheeler, T.R., Hong, T.D., Ellis, R.H., Batts, G.R., Morison, J.I.L., Hadley, P., 1996b. The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO<sub>2</sub>. *J. Exp. Bot.* 47, 623–630.
- Yan, W., Wallace, D.H., 1998. Simulation and prediction of plant phenology for field crops based on photoperiod×temperature interaction. *Ann. Bot.* 81, 705–716.
- Yin, X., Kropff, M.J., McLaren, G., Visperas, R.M., 1995. A nonlinear model for crop development as a function of temperature. *Agric. For. Meteorol.* 77, 1–16.
- Yoshida, S., 1981. *Fundamentals of Rice Crop Science*. IRRI, Los Baños, The Philippines, p. 269.