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Modelling predicts that heat stress and not drought will limit wheat yield in Europe

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Global warming is characterised by shifts in weather patterns and increases in extreme weather events. New crop cultivars with specific physiological traits will therefore be required if climate change is not to result in losses of yield and food shortages. However, the intrinsic uncertainty of climate change predictions poses a challenge to plant breeders and crop scientists who have limited time and resources and must select the most appropriate traits for improvement. Modelling is, therefore, a powerful tool to identify future threats to crop production and hence targets for improvement. Wheat is the most important crop in temperate zones, including Europe, and is the staple food crop for many millions of humans and their livestock. However, its production is highly sensitive to environmental conditions, with increased temperature and incidence of drought associated with global warming posing potential threats to yield in Europe. We have therefore predicted the future impacts of these environmental changes on wheat yields using a wheat simulation model combined with climate scenarios based on fifteen global climate models from the IPCC AR4 multi-model ensemble. Despite the lower summer precipitation predicted for Europe, the impact of drought on wheat yields is likely to be smaller than at present, because the warmer conditions will result in earlier maturation before drought becomes severe later in the summer. By contrast, the probability of heat stress around flowering is predicted to increase significantly which is likely to result in considerable yield losses for heat sensitive wheat cultivars commonly grown in north Europe. Breeding strategies should therefore focus on the development of wheat varieties which are tolerant to high temperature around flowering, rather than on developing varieties resistant to drought which may be required for other parts of the world.

Most Global Climate Models used in the latest IPCC 4th Assessment Report (AR4) predict decrease of precipitation in summer in Europe (SI.Fig. 2) ¹. They also predict a substantial increase in temperature and in the frequency and magnitude of extreme weather events. Using climate projections for the UK, it has been shown that heat waves will increase substantially in frequency (by an order of magnitude), length and severity (peak temperature) by the end of the century ². Even isolated incidents of extreme high temperature around flowering, a sensitive stage of crop development, could reduce grain yield significantly, while a continuous period of extreme high temperature could result in almost total loss.

We used a wheat simulation model, Sirius ³⁻⁵, combined with climate scenarios to predict the impact of climate change on wheat across Europe. Local-scale climate scenarios were generated by the LARS-WG weather generator ⁶ and were based on the projections from the AR4 multi-model ensemble of fifteen global climate models ¹. The probability of heat stress around flowering, which can considerably reduce grain yield, and the yield losses from drought were computed for the current and future climate scenarios.

The yield of wheat is determined by the number and size of the grains and these parameters are established to a large extent at the period around flowering, a stage in development known to be sensitive to high temperature stress. If the crop is unstressed, it establishes the number and potential size of the grains at sufficiently large values to accommodate all new biomass produced during grain filling, which is usually a source-limited process ^{7,8}. The grain number and potential grain size can be substantially reduced if a cultivar sensitive to heat stress is exposed to a high temperature around flowering, limiting the capacity of grains to store newly produced biomass. In this case grain filling becomes a sink-limited process. In an experiment on the effects of CO₂ and temperature on the grain yield Mitchell et al. (1993) ⁹ observed that a temperature of 27°C or higher applied mid-way through anthesis could result in a high number of sterile grains. Although the effect of reduced grain numbers on the final yield may be compensated for during grain filling by the production of larger grains, the yield losses could be still considerable. Wheeler et al (1996) ¹⁰ used a temperature gradient tunnel system to demonstrate that a temperature of 31°C or higher prior to anthesis considerably reduced the

number of grains of cv. Hereward 10,11 . In other experiments plants were transferred into controlled rooms with high temperatures at 7 days after the first anthers appeared 12,13 , showing that a temperature of 27° C and above could reduce the maximum grain size in several Australian wheat cultivars.

We estimated the probability of the maximum temperature exceeding temperature threshold of 27°C and 30°C at two developmental stages, at anthesis and at 5 days after anthesis, which can substantially reduce grain number and size. To assess the impact of drought on grain yield, we computed a drought stress index (DSI) defined as a proportion of the yield lost due to water stress: $DSI = 1 - Y_{WL}/Y_P$, where Y_{WL} and Y_P are water-limited and potential yields.

The simulation was run for nine European sites (SI.Table 1 and SI.Fig. 1). For each site and each GCM projections from the multi-model AR4 ensemble we generated 300 years of daily weather representing the baseline scenario corresponding to 1960-1990, and the future climate scenario corresponding to 2045-2065 for the A1B emission scenario, named as 2055(A1B) ⁶. For each site we selected one of the winter wheat cultivars calibrated previously using field experiments (SI.Table 1) ^{5,14-16}. The sowing dates were set to typical dates used locally for wheat and the same sowing dates were used for future climate scenarios. To make a comparison between sites, we used one soil for all sites, medium loamy drift with siliceous stones, with available water capacity of 131 mm. Future values of probability of heat stress around flowering and DSI were calculated for each of fifteen GCMs individually and then presented as box plots to emphasise the uncertainty in predictions.

To predict the impact of water limitation on wheat yields we plotted the 95-percentile of the DSI distribution, DSI⁹⁵, the level of yield losses due to drought expected on average once every 20 years (Fig. 1B). For all site except one (WA) the medians of predicted DSI⁹⁵ for individual GCMs are lower that the value of DSI⁹⁵ for the baseline scenario. This means that despite a decrease in precipitation during summer time in north Europe and during the whole growing season in south Europe, yield losses from drought are likely to be smaller in the future than at present even for currently grown wheat cultivars. This can be explained by the acceleration of wheat phenology due to

a warmer climate. Wheat development is controlled by thermal time ¹⁷. In a warmer climate thermal time will be accumulated quicker and, as a result, wheat will mature earlier. Maturity dates are predicted to be between 2 (in south Europe) and 3 (in north Europe) weeks earlier for the 2055(A1B) climate scenarios compared with 1960-1990. Because soil water deficit increases towards the end of crop growth, wheat will avoid the most severe drought stress by maturing early. It is interesting to note (Fig. 1A) that the soil water deficit (SWD) at anthesis does not vary greatly between sites in south and north Europe and the median of SWD at anthesis is predicted to stay at about the same level in the future with one exception, CF, where it increase from 50 to 67 mm.

Predicted medians of increases in monthly mean maximum temperature for the 2050(A1B) scenario are between 1.5 and 3.5°C depending on the month of the year and the site (SI.Fig. 2). Figure 2 shows the probability of two events: first, when the maximum daily temperature at anthesis exceeded temperature threshold of 27°C or 30°C (Fig. 2A and 2C), and second, when the maximum temperature exceeded thresholds both at anthesis and five days after anthesis (Fig. 2B and 2D). Exceeding a temperature threshold at anthesis will reduce the grain number for heat sensitive cultivars while exceeding a temperature threshold five days after anthesis will reduce the potential grain size. Each of these events alone will reduce the grain yield for heat sensitive wheat cultivars. If these events happen concurrently the yield losses will be significant.

Our results demonstrate that the impacts of changing climate on wheat can be counter-intuitive and that the severity of the impact will depend on cultivar characteristics and on the spatial and temporal patterns of climate change. Drought is the most significant environmental stress in agriculture worldwide and improving yields in water-limited environments is a major goal of plant breeding ¹⁸. Some researchers suggest that the impact of drought will increase with climate change ¹⁹, emphasising the importance of breeding for drought tolerant crops, and this will certainly be true for many crops and environments. However, our results demonstrate that the impact of drought stress on wheat across Europe is likely to decrease with climate change. Consequently, the drier and warmer summers, predicted for the most of Europe, will not necessary result in yield losses due to water stress. In fact, our analysis showed that a more serious impact of climate change on wheat production

in Europe is likely to result from an increase in frequency of heat stress around flowering, and that the development of heat-tolerant varieties should therefore be the major priority.

3 METHODS SUMMARY

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In this study, we used multi-model ensemble of climate predictions used in the IPCC 4th Assessment Report. The ensemble was constructed by running several global climate models (GCM) for a common set of experiments, which emphasize the uncertainty in climate predictions resulting from structural differences in climate models as well as uncertainty due to variations in initial conditions or model parameterisations. The direct use of climate predictions from the AR4 ensemble in conjunction with a crop simulation model is not possible due to coarse resolutions of GCMs. We used the LARS-WG weather generator to downscale GCM projections to a local scale ⁶. By altering the parameters of the WG distributions using changes in climate predicted by GCMs, we generated local-scale daily scenarios for the future consistent with GCM projections. The Sirius crop simulation model, used in this study, has been calibrated for several wheat cultivars and is able to simulate accurately crop growth in a wide range of conditions ^{15,16,20,21}. In Sirius, radiation use efficiency (RUE) is proportional to [CO2] and increases by 30% for a doubling in [CO2]. Similar values are used by other wheat simulation models, e.g. CERES ¹⁵ and EPIC ²². Long et al (2006) ²³ argued that the results from FACE experiments showed much lower effect of elevated [CO2] on wheat yield, about 50% of the values used in the models ^{24,25}. To account for this uncertainty, we used two values for RUE, low 15% and high 30%, for a doubling in [CO2]. Although winter wheat cultivars from north Europe are known to be sensitive to heat stress around anthesis ^{9,10}, the lack of sufficient experimental data did not allow us to calibrate cultivar parameters for heat sensitivity. Therefore, simulated yields were not affected by the heat stress around anthesis (SI.Fig. 3).

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LARS-WG weather generator and Sirius wheat simulation model are available online at www.rothamsted.bbsrc.ac.uk/mas-models.

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Figure captions.

Figure 1. Soil water deficit at anthesis and 95-percentiles of DSI. For the baseline (black rectangles) and for the 2055(A1B) climate scenarios (box plots) at nine European sites: Tylstrup, Denmark (TR), Warsaw, Poland (WS), Wageningen, the Netherlands (WA), Rothamsted, UK (RR), Mannheim, Germany (MA), Debrecen, Hungary (CF), Clermont-Ferrand, France (CF), Montagnano, Italy(MO), Seville, Spain (SL) (See SI.Table 1). Box plots represent uncertainty in predictions resulting from fifteen global climate models used in the IPCC AR4 multi-model ensemble. Box boundaries indicate the 25 and 75-percentiles, the line within the box marks the median, whiskers below and above the box indicate the 10 and 90-percentiles.

Figure 2. Probability of maximum temperature exceeding thresholds. Thresholds of 27°C (A,B) or 30°C (C,D) within 3 days of anthesis (A,C) or consecutively with 3 days of anthesis and within 3 days of five days after anthesis (B,D) for the baseline (black rectangles) and for the climate scenarios corresponding 2055 (A1B) (box plots, see explanation in Fig. 1).

Figure 1.

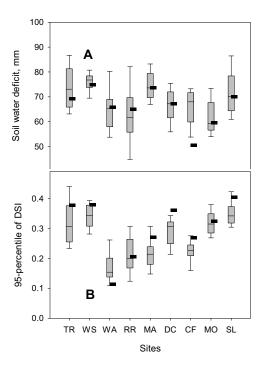
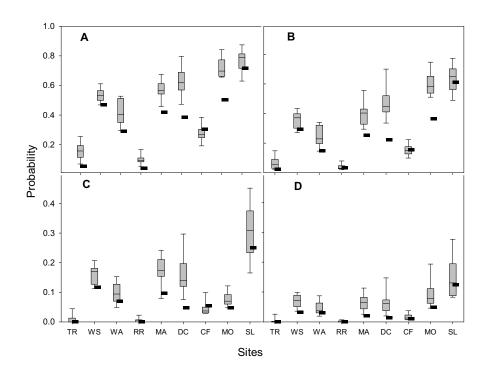


Figure 2.

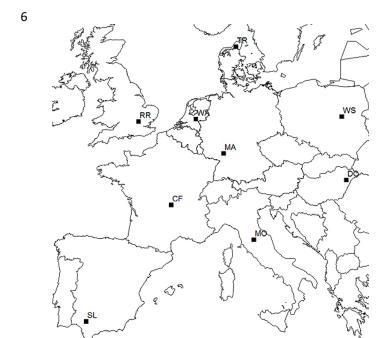


SUPPLEMENTARY INFORMATION (SI)

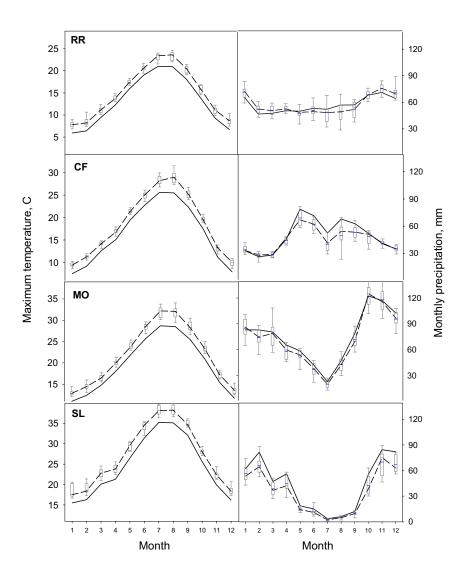
SI.Table 1. Characteristics of nine sites in Europe used in the study.

Site	Acronym	Lon	Lat	Annual	Monthly mean temperature, °C			Day of flowering,
				precipitation, mm	January, minimum	July, maximum	Cultivar	1960-1990
Tylstrup, Denmark	₹R %	9.9	57.2	668	-2.9	19.8	Avalon	23 June
Warsaw, Poland	P. S.	21.1	52.15	458	-3.6	24.4	Avalon	11 June
Wageningen, the Netherlands	:题:101窗/npre-2810.4385.1 V	5.67	51.97	765	-0.8	21.5	Claire	23 June
Rothamsted, UK	Pre- 15 15 15 15 15 15 15 15 15 15 15 15 15	-0.35	51.8	693	0.3	20.8	Mercia	19 June
Mannheim, Germany	1 90 1 90 1 90	8.6	49.5	641	-1.4	24.6	Claire	6 June
Debrecen, Hungary		21.6	47.6	563	-5.5	26.3	Thesee	26 May
Clermont-Ferrand, France	. ece . ece	3.1	45.8	600	-0.7	25.5	Thesee	23 May
Montagnano, Italy	Nature Precedings	11.8	43.3	752	-0.6	28.8	Creso	22 May
Seville, Spain	MO	-5.88	37.42	524	4.3	35.2	Cartaya	27 April

SI.Figure 1. Locations of sites. (For acronyms see SI.Table 1).



SI.Figure 2. Monthly weather statistics. Monthly mean maximum temperature (red) and mean monthly total precipitation (blue) for 1960-90 (solid) and 2055 (the A1B emission scenario) (dashed) at 4 European sites: Rothamsted, UK (RR); Clermont-Ferrand, France (CF); Seville, Spain (SL); and Montagnano, Italy (MO). Box plots represent uncertainty in predictions from fifteen global climate models used in the IPCC AR4. Box boundaries indicate the 25 and 75-percentiles, the line within the box marks the median, whiskers below and above the box indicate the 10 and 90-percentiles. Note that the scales for temperature are different, but all of them have the range of 30°C.



SI.Figure 3. Grain yield predictions. Mean simulated grain yield for the baseline (black rectangles) and for the climate scenarios corresponding 2055 (A1B) for RUE increase by 15% (open box plots) and 30% (gray box plots) for a doubling in [CO₂]. We assume that all wheat cultivars have no sensitivity to heat stress around anthesis, because of the lack of experimental data to calibrate cultivar parameters.

