Accepted Article

Running head: Testing responses of wheat crop models to heat stress

Title: Testing the responses of four wheat crop models to heat stress at anthesis and grain filling

Author: Bing Liu\(^1\), Senthold Asseng\(^2\), Leilei Liu\(^1\), Liang Tang\(^1\), Weixing Cao\(^1\), Yan Zhu\(^1\)*

Authors’ affiliation

\(^1\)National Engineering and Technology Center for Information Agriculture, Jiangsu Key Laboratory for Information Agriculture, Jiangsu Collaborative Innovation Center for Modern Crop Production, Nanjing Agricultural University, Nanjing, Jiangsu 210095, P. R. China;

\(^2\)Department of Agricultural and Biological Engineering, University of Florida, Gainesville, FL 32601, USA

*Correspondence: Yan Zhu

Tel: +86-25-84396598

Fax: +86-25-84396672

E-mail: yanzhu@njau.edu.cn

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/gcb.13212

This article is protected by copyright. All rights reserved.
Abstract:

Higher temperatures caused by future climate change will bring more frequent heat stress events and pose an increasing risk to global wheat production. Crop models have been widely used to simulate future crop productivity but are rarely tested with observed heat stress experimental datasets. Four wheat models (DSSAT-CERES-Wheat, DSSAT-Nwheat, APSIM-Wheat, and WheatGrow) were evaluated with four years of environment-controlled phytotron experimental datasets with two wheat cultivars under heat stress at anthesis and grain filling stage. Heat stress at anthesis reduced observed grain numbers per unit area and individual grain size, while heat stress during grain filling mainly decreased the size of the individual grains. The observed impact of heat stress on grain filling duration, total aboveground biomass, grain yield and grain protein concentration varied depending on cultivar and accumulated heat stress. For every unit increase of heat degree days (HDD, degree days over 30°C), grain filling duration was reduced by 0.30% to 0.60%, total aboveground biomass was reduced by 0.37% to 0.43%, and grain yield was reduced by 1.0% to 1.6%, but grain protein concentration was increased by 0.50% for cv Yangmai16 and 0.80% for cv Xumai30. The tested crop simulation models could reproduce some of the observed reductions in grain filling duration, final total aboveground biomass, and grain yield, as well as the observed increase in grain protein concentration due to heat stress. Most of the crop models tended to reproduce heat stress impacts better during grain filling than at anthesis. Some of the tested models require improvements in the response to heat stress during grain filling, but all models need improvements in simulating heat stress effects on grain set during anthesis. The observed significant genetic variability in the response of wheat
to heat stress needs to be considered through cultivar parameters in future simulation studies.

Keywords:
Heat stress; winter wheat; crop models; model evaluation; anthesis; grain filling

Introduction

More extreme climate events, including heat stress, are expected with increased climate variability (IPCC, 2012). These events are likely to produce significant negative impacts on crop production (Porter & Semenov, 2005). Wheat is sensitive to high temperature stress (Porter & Gawith, 1999). Negative impacts of heat stress have been reported, and these occur especially during the reproductive period, harming wheat development, grain yield, and grain quality (Dias & Lidon, 2009, Porter & Gawith, 1999, Tashiro & Wardlaw, 1990, Wardlaw & Moncur, 1995, Wheeler et al., 2000, Zhao et al., 2007). Global and regional impact assessments suggested that increasing heat stress already threatens wheat production and global food security, and this impact will increase with future global warming (Asseng et al., 2015, Liu et al., 2014, Lobell et al., 2012, Semenov & Shewry, 2011, Teixeira et al., 2013).

Wheat is the third largest grain crop and supplies food for 60% of the world population (FAO, 2012). Therefore, it is critical to better understand future climate change impacts, especially the effects of heat stress on wheat production and the consequences for global food security.

Crop models are powerful tools for assessing the impact of climate change on crop production (Challinor et al., 2014). Testing crop models under various temperature conditions...
environments is essential to apply models to climate impact studies. However, crop model evaluations of temperature impacts mainly focus on the impacts of mean temperature (Challinor et al., 2014). Several wheat models have been calibrated and evaluated under temperate temperature regimes (Lobell et al., 2011). For example, CERER-Wheat, which was used in several climate change impact studies, has been evaluated in many locations in Asia, Europe, and America (Timsina & Humphreys, 2006). Only a few studies have tested the response of crop models under extreme high temperature stress (Asseng et al., 2011, Moriondo et al., 2011). Recently, 30 wheat models were evaluated under a wide range of temperature conditions (mean season temperatures ranging from 15°C to 32°C) in the Agricultural Model Intercomparsion and Improvement Project (AgMIP) for Wheat (Asseng et al., 2015), and several of the wheat models were found less accurate at higher temperatures. Nevertheless, none of these studies systematically conducted detailed crop model evaluation under heat stress events. According to Rötter et al. (2011), most crop models do not incorporate the response of crop development, growth, and yield when under extreme temperatures. Several studies have raised concerns about simulating heat stress effects when using present crop models to predict the effects of global warming on crop productivity for future climates (Moriondo et al., 2011, Rezaei et al., 2015, Sanchez et al., 2014, Siebert et al., 2014). Therefore, Craufurd et al. (2013) suggested that crop science experiments designed to inform crop modeling are urgently required for evaluating and improving crop models under heat stress for future climate impact projections.

In this study, four years of detailed environment-controlled phytotron experiments were conducted to test and improve crop models under heat stress. The objectives of this study

This article is protected by copyright. All rights reserved.
were: (1) to determine the response of wheat growth, grain yield, and grain quality to simulated heat stress at anthesis and grain filling stages; (2) to evaluate the response of four widely used wheat models (DSSAT-CERES-Wheat, DSSAT-Nwheat, APSIM-Wheat, and WheatGrow) to simulated heat stress at anthesis and grain filling stages; and (3) to identify gaps for crop model improvement.

Materials and Methods

Data sources

Environment-controlled chamber experiments were conducted at Nanjing (118.78°E, 32.04°N) in growing season 2010-2013 and at Rugao (120.33°E, 32.23°N) in growing season 2013-2014 in Jiangsu Province of China. Two winter wheat cultivars (Yangmai16 and Xumai30) were planted in plastic pots. The plant density was kept at 10 plants per pot, and the diameter of a pot was 0.28m. Sowing dates in the four growing seasons were November 1, November 6, November 4, and November 5, respectively. The wheat was grown in pots in a normal ambient environment before and after the heat stress treatments. Pots for each cultivar were in ambient conditions before heat stress split these into three blocks, with 25 rows × 8 columns in each block, and were surrounded with extra pots to avoid side effects. Once the wheat developed into the appropriate growth stages (anthesis or grain filling), pots were selected randomly from three blocks and transferred into phytotrons to expose to different heat stress conditions. Table 1 summarizes the heat stress treatments, including two cultivars (Yangmai16 and Xumai30), five temperature levels ($T_{\text{min}}/T_{\text{max}}$: 17/27°C, 21/31°C, 25/35°C, 29/39°C, and 33/43°C), three heat stress durations (3 days, 6 days, and 9 days), and two heat
stress stages (anthesis and grain filling). The 33/43°C was only conducted during the growing season 2013-2014. For each treatment combination (one cultivar under one temperature level and one heat stress duration), there were 27 pots for sampling after heat stress and measuring grain yield at harvest. Heat stress treatments at anthesis and the grain filling stage started when first anthers were observed at middle of ear (Zadoks 61) and 10 days after first anthers at middle of ear (DAA10, 10 days after Zadoks 61), respectively. According to previous studies (Farooq et al., 2011, Liu et al., 2014), 30°C was selected as the temperature threshold of heat stress for winter wheat cultivars. Therefore, T1 (17/27°C) with a maximum temperature of 27°C, was designed as a check or control treatment. The average temperature in T1 (17/27°C) was 22°C, which has been considered as the optimal temperature for post-heading period in wheat. T2 (21/31°C), T3 (25/35°C), T4 (29/39°C), and T5 (33/43°C) were designed as heat stress treatments.

The phytotrons were made of transparent glass, and the size of each phytotron was 3.4 m × 3.2 m × 2.8 m (length × width × height). Temperature and humidity in the phytotrons were controlled precisely to simulate daily temperature and humidity fluctuations in the ambient environment to capture the actual response of wheat to heat stress in the field as realistically as possible. HOBO data loggers (Onset Computer Corp., Bourne, MA, USA) were used to measure the temperature and relative humidity during heat stress periods every 5 minutes.

The day-night temperature fluctuations, as shown in Figure S1, followed a similar pattern as the ambient temperature. Supplemental light was applied by halogen lamp to insure that light condition in the phytotrons did not limit wheat growth. The light intensity in the phytotron and ambient at noon was about 1380 μmol m⁻¹ s⁻¹ and 1800 μmol m⁻¹ s⁻¹ with sunshine, while

This article is protected by copyright. All rights reserved.
about 240 $\mu$mol m$^{-1}$ s$^{-1}$ and 350 $\mu$mol m$^{-1}$ s$^{-1}$ with cloud cover. As durations of heat stress treatments were relatively short, lower light intensity in the phytotron had little impact on wheat growth. Pots in the phytotrons were randomly placed and rotated frequently to minimize positional effects. After a heat stress period, the plants were moved out of the phytotrons and maintained at normal ambient environmental conditions until harvest. Pots in the ambient conditions after heat stress were also arranged with three blocks randomly and were surrounded with extra pots to avoid side effects. Pots also were rearranged to make sure pots from the same treatment combination staying together after each sampling. The fertilization rate for each pot was 0.9 g N, 0.5 g P$_2$O$_5$ and 0.9 g K$_2$O applied before sowing, and another 0.9 g N were applied during jointing stage of wheat. All other cultivation practices, such as irrigation, and pesticide application, were performed according to local standards of wheat cultivation to make sure there was no water or nitrogen stress in the experiments. The meteorological records, including daily temperature, rainfall, and radiation during wheat growing season, were measured by Dynamet-1K (Dynamet Inc., USA) near the experiment sites. The distance between weather station and experiment location was about 15 m in Nanjing and 20 m in Rugao. Wheat phenology for each treatment was recorded accurately, including the dates of heading, anthesis, and maturity. Heading, anthesis, and maturity dates were recorded when 50% ears emerged (Zadoks 55), anthers at middle of ear were observed in 50% ears (Zadoks 65), and 80% grains were too hard to be dented by thumbnail (Zadoks 92), respectively. The phenology observation was conducted according to the standard for observations of wheat phenology in the Observation Specification for Agricultural Meteorology: Crop Part (China Meteorological Administration, 1993).
Plant samples were taken every seven days during the growing seasons 2010-2011, 2011-2012, and 2012-2013, and every five days during the growing season 2013-2014 until maturity. Samples of ten plants in one pot were analyzed with three replications, which were selected randomly from three blocks. Sample plants were separated into different plant tissues including internode and sheath, green leaves, senescence leaves, grain, peduncle, and chaff. At maturity, twelve pots were harvested for each treatment to obtain grain yields, total aboveground biomass, yield components, and grain protein concentration. Anthesis and maturity dates were recorded for each treatment. Grain filling duration was calculated as the days from anthesis to maturity. Green leaf area was measured with LI-3000 leaf area meter (LI-COR, Lincoln, NE, USA) and leaf area index (LAI) was calculated from total green leaf area in a pot and pot size. Plant tissues were oven-dried at 70°C to constant weight for dry-matter biomass measurements. Grain protein concentration was calculated from the percentage of total nitrogen, which was determined with the micro-Kjeldahl method (Page, 1982).

**Wheat simulation models**

Four widely used crop simulation models were tested under different heat stress treatments. These four models were process-based models, which simulated daily dynamics of wheat growth, including phenology, leaf area, tissue biomass, grain weight, grain yields, and grain nitrogen concentration.
DSSAT-CERES-Wheat

The CERES-Wheat model (Ritchie & Otter, 1985) in the Decision Support System for Agrotechnology Transfer (DSSAT v4.6) is one of the most widely used crop models in the world. It has been tested at several sites in the USA, Europe, and Asia (Jamieson et al., 1998, Palosuo et al., 2011, Rosenzweig & Tubiello, 1996, Timsina & Humphreys, 2006). Most of the model evaluation studies for CERES-Wheat focus on mean temperature, cultivars, planting dates, planting density, water conditions, and nitrogen application rates.

DSSAT-Nwheat

The DSSAT-Nwheat model uses the APSIM-Nwheat model, which has been integrated into the DSSAT platform (v4.6). The performance of Nwheat (as APSIM-Nwheat) has been tested over various growing environments including temperature, water, nitrogen management, and CO₂ across many locations of the world (Asseng et al., 2004, Asseng et al., 1998, Asseng et al., 2003, Asseng et al., 2002, Bassu et al., 2009, O'Leary et al., 2015, Wessolek & Asseng, 2006). Asseng et al. (2011) described the modeled heat stress impacts on wheat growth and grain yield in the Nwheat model, especially on leaf senescence.

WheatGrow

The WheatGrow model consists of five submodels: apical development and phenological development (Yan et al., 2000), photosynthesis and biomass accumulation (Liu et al., 2000b), dynamic partitioning (Liu et al., 2000a), organ growth and yield formation (Cao et al., 2002), soil water balance (Hu et al., 2004) and nitrogen dynamics (Zhuang et al., 2004). Many
model evaluations have been carried out with the WheatGrow model in several ecological regions across China, and WheatGrow performed well in the simulations of wheat development and grain yield (Lv et al., 2013, Zhao et al., 2010). In the new version of WheatGrow (v3.1), a newly developed temperature function (HTE) was incorporated into the phenology submodel to improve the predictions of wheat duration between heading and maturity under heat stress (Liu et al., 2015).

APSIM-Wheat

The Agricultural Production Systems Simulator (APSIM) for wheat (v7.7) is a widely used model that consists of modules for soil, water, nitrogen, crop residues, crop growth and development, and their interactions (Keating et al., 2003). APSIM-Wheat has been tested under various conditions across the world, including temperature, nitrogen, water, sowing dates, and CO₂ concentrations (Chen et al., 2010, Lobell et al., 2012, O'Leary et al., 2015, Zhang et al., 2012, Zhao et al., 2014).

Model calibration and validation

Independent observed experimental datasets were used for model calibration and model evaluation. Models were calibrated by adjusting only cultivar parameters to fit the experimental dataset from all treatments in one growing season (2010-2011 for Yangmai16, 2011-2012 for Xumai30), and the observed dataset from all other growing seasons were used for model validation. Table S1 supplies a list of calibrated cultivar parameters for cv. Yangmai16 and cv. Xumai30 for the four models.

The simple linear regression method was employed to analyze the responses of wheat
growth parameters (grain filling duration, total aboveground biomass at maturity, grain yield, grain number, grain size, and grain nitrogen concentration) to heat stress, and the regression slopes between observed or simulated wheat growth parameters and heat stress were the observed or simulated responses of wheat growth parameters to heat stress. The significance tests for each regression were conducted with an ANOVA. In addition, the comparison between observed and simulated wheat growth parameters from four wheat models is provided in Fig. S2-S6.

Heat degree days (HDD), which consider the duration and intensity of heat stress, were used to quantify heat stress across treatments with different temperature levels and heat stress durations. HDD was the sum of daily heat degrees (HD) during heat stress treatments. No heat stress was observed outside the heat stress treatments. HD was calculated as follows:

$$HDD_i = \frac{1}{24} \sum_{i=1}^{24} HD_i$$  \hspace{1cm} (1)

$$HD_i = \begin{cases} 0 & T_i < T_h \\ T_i - T_h & T_i \geq T_h \end{cases}$$  \hspace{1cm} (2)

HDD is the hourly high temperature degree days at day i. T_h represents the temperature threshold for heat stress. 30°C was set as the temperature threshold of heat stress for the two winter wheat cultivars according to previous studies (Farooq et al., 2011, Liu et al., 2014). T_i is the hourly temperature. As temperature during heat stress treatments was recorded precisely with HOBO data loggers, HDD can be calculated by summing up the observed heat stress hours directly. However, the temperature before and after the heat stress treatments were recorded from Dynamet-1K weather station, not the hourly temperature records from HOBO data loggers. Therefore, Eq. (3) was used to calculate the hourly temperature, in which hourly temperature T_i is determined by daily maximum and minimum temperatures.
with a cosine function (Matthews & Hunt, 1994):

\[ T_t = \frac{T_{\text{max}} - T_{\text{min}}}{2} + \frac{T_{\text{max}} - T_{\text{min}}}{2} \times \cos \left( \pi \times \frac{t-14}{12} \right) \]  

(3)

Here, \( t \) is the number of hours of a day (\( t=1, 2\ldots 24 \)). \( T_{\text{max}} \) and \( T_{\text{min}} \) indicate the measured daily maximum and minimum temperatures (°C). As shown in Fig.S1, the daily dynamic of temperature in the phytotron is similar with cosine curve pattern, and the HDD calculated with observed hourly temperature (calculated from the average of 5-minute temperature measured with HOBO) was similar with HDD estimated by using Eq. (3) during heat stress treatment periods.

Both observed and simulated responses were tested separately for heat stress at anthesis and grain filling. Absolute values of wheat growth parameters (e.g., grain filling duration, total aboveground biomass at maturity, grain yield, grain number, grain size, and grain nitrogen concentration) varied among different years and cultivars, so we used the relative value of these variables to calculate relative heat stress responses. The relative values of wheat growth variables were calculated as the ratio between the absolute and the corresponding values from the control or check treatment (T1 treatment) for the same treatment stage and cultivar.

**Results**

**Response of grain filling duration to heat stress**

Heat stress at anthesis and grain filling both reduced grain filling duration significantly \((p<0.01)\) (Fig.1). With every unit increase in heat degree days (HDD), grain filling duration decreased by 0.30% to 0.58%, depending on cultivars and stages of heat stress. The slope of linear regression indicated there was a greater observed decreasing grain filling duration
under heat stress at anthesis than at grain filling stage; this revealed that wheat grain filling
duration was more sensitive to heat stress at anthesis than grain filling (Table 2). Decreased
grain filling durations under heat stress were simulated with four models, except grain filling
duration to heat stress at grain filling increased with APSIM-Wheat. The best predictions of
grain filling duration under heat stress were with WheatGrow (Fig.1 and Fig. S2). For
example, WheatGrow simulated a 0.50% and 0.36% reductions of grain filling reductions for
cv. Yangmai16 and cv. Xumai30 with every unit increase in heat degree days (HDD) at
anthesis, while observed reductions for cv. Yangmai16 and cv. Xumai30 were 0.58% and
0.37%. The comparison between observed and simulated grain filling duration suggested that
the WheatGrow model can explain about 80% and 67% of the observed variance in grain
filling durations with heat stress at anthesis and grain filling, respectively (Fig. S2). Both
CERES-Wheat and Nwheat tended to underestimate the heat stress effects on grain filling
duration (Fig. 1), as simulated reductions of grain filling durations with CERES-Wheat and
Nwheat were much less than the observed reductions (Table 2).

Response of total aboveground biomass at maturity to heat stress

Observed total aboveground biomass at maturity decreased significantly with heat stress
at anthesis and grain filling (p<0.01). With every unit increase in heat degree days (HDD),
total aboveground biomass decreased by 0.37% to 0.43%, depending on cultivars and stages
of heat stress. Heat stress at anthesis resulted in more serious reductions in total aboveground
biomass at maturity than heat stress at grain filling in both cultivars (Table 2). All four
models simulated a decreasing total aboveground biomass at maturity with increasing heat
stress (Fig. 2). The best simulations of total aboveground biomass at maturity were with

This article is protected by copyright. All rights reserved.
Nwheat. For example, Nwheat predicted a 0.40% reductions of total aboveground biomass at maturity with every unit increase in HDD at anthesis for Yangmai16, and the observed reductions for cv. Yangmai16 was 0.43%. APSIM-Wheat tended to overestimate heat stress effects on total aboveground biomass at maturity (Fig.2 and Fig. S3).

**Response of grain yield and yield components to heat stress**

Grain yields were negatively related to heat stress for both cultivars ($p<0.01$) (Fig. 3). With every unit increase in HDD, grain yields decreased approximately 1.5% to 1.6% for heat stress at anthesis and 1.0% to 1.3% for heat stress at grain filling. Both grain number and grain size were reduced significantly by heat stress at anthesis, while heat stress at grain filling decreased only grain size. Statistical analysis with an ANOVA suggested that grain number under heat stress at grain filling was reduced significantly ($p<0.01$) only with severe heat stress (HDD>40 °C d) (Fig. 5), and no significant differences were found between heat stress treatments (T2, T3, T4, and T5) and check treatments (T1) with minor heat stress (HDD<40 °C d). The best simulations of grain yields under heat stress at anthesis were with APSIM-Wheat, while Nwheat had the best simulations of grain yields with heat stress at grain filling (Table 2 and Fig. 4). Among all four models, the Nwheat model could better reproduce the reductions in grain numbers with heat stress (Fig. 5 and Fig. S4). For example, predicted reductions in grain number for Nwheat were 0.62% and 0.60% for cv. Yangmai16 and cv. Xumai30 with every unit increase in HDD at anthesis, and the observed reductions in grain number were 1.44% and 1.28% for cv.Yangmai16 and cv. Xumai30. The other models simulated little or no response of grain numbers to heat stress (Fig. 5). For grain size, both Nwheat and APSIM-Wheat simulated approximately 60% of the observed variance due to
heat stress at grain filling, but all models underestimated grain size with heat stress at anthesis (Table 2 and Fig. 6). For example, simulated reductions in grain size of cv. Xumai30 were 0.01% (CERES-Wheat), 0.68% (Nwheat), 0.01% (WheatGrow), and 0.63% (APSIM-Wheat) with every unit increase in HDD at grain filling, while the observed reduction was 0.94%.

**Response of grain protein concentration to heat stress**

Heat stress at anthesis and grain filling increased grain protein concentration (GPC) significantly for cultivar Yangmai16 and Xumai30 ($p<0.01$). Observed response of wheat to heat stress at anthesis was similar with heat stress during grain filling. GPC increased 0.79% (cv. Yangmai16) and 0.51% (cv. Xumai30) with every unit increase in HDD at anthesis, while increased 0.82% (cv. Yangmai16) and 0.78% (cv. Xumai30) for heat stress at grain filling. Nwheat simulated the response of GPC to heat stress at grain filling reasonably (Fig. 7 and Fig. S6), while the other models tended to underestimate heat stress effects on GPC.

APSIM-Wheat simulated different response trends between moderate heat stress and severe heat stress. GPC increased with the increasing HDD when HDD was less than 30°Cd, but GPC decreased as HDD increased greater than 30°Cd (Fig. 7).

**Response of leaf area index dynamics to heat stress**

Figure 8 shows the comparison between observed and simulated response of leaf area index (LAI) for four treatments of different temperature levels (17/27°C, 25/35 °C, 29/39 °C, and 33/43 °C) for each heat stress stage (anthesis and grain filling) in growing season 2013-2014. Heat stress accelerated leaf senescence at anthesis and during grain filling; the rate of leaf senescence acceleration increased with increasing heat stress. The best simulated response of LAI to heat stress at anthesis and grain filling was with Nwheat, which

This article is protected by copyright. All rights reserved.
reproduced the LAI dynamics with the heat stress treatments (Fig. 8). APSIM-Wheat tended to over-predict heat stress effects on LAI. In contrast, CERES-Wheat and WheatGrow underestimated observed leaf senescence accelerations from heat stress.

**Response of grain filling dynamics to heat stress**

Figure 9 shows the observed and simulated grain filling dynamics for heat stress treatments at anthesis and grain filling. Heat stress at anthesis and grain filling decreased the grain filling rate after heat stress, and grain filling finished earlier with treatments 25/35°C, 29/39°C, and 33/43°C, compared with 17/27°C (Fig. 9). CERES-Wheat and WheatGrow showed few or no simulated effects of heat stress on grain filling dynamics, while Nwheat and APSIM-Wheat underestimated the observed decline in grain filling rates with heat stress.

**Discussion**

Grain yield and quality in wheat are very sensitive to heat stress during the reproductive phase (Farooq *et al.*, 2011). For two winter wheat cultivars, heat stress at anthesis and grain filling reduced photosynthesis rate and accelerated leaf senescence, resulting in a decreased total aboveground biomass at maturity, grain number, grain size, and grain yield. Other studies reported similar negative impacts of heat stress on biomass, yield, and yield components (Luo, 2011, Tubiello *et al.*, 2007, Wheeler *et al.*, 2000). Haddad *et al.* (2013) reported an increase of grain protein concentration with heat stress, which is consistent with our experiment.
The greater response of grain filling duration, total aboveground biomass, grain yield, and yield components to heat stress at anthesis than heat stress during grain filling indicated that wheat is more sensitive to heat at anthesis than heat stress during grain filling; this finding is similar to reports in other studies (Jackson et al., 2013, Prasad & Djanaguiraman, 2014).

Comparing the response of yield components (grain number and grain size) to heat stress, the greatest observed yield impact of heat stress was at anthesis and was observed through the reduced grain numbers per unit area and grain sizes. Heat stress during grain filling mainly decreased the size of the individual grains, consistent with Prasad and Djanaguiraman (2014).

Four widely used processes-based wheat models were tested against detailed measurements from a range of heat stress treatments. The response of the four crop models to heat stress varied significantly in the simulation of grain filling duration, biomass production, grain yield, and grain protein concentration. The quality of simulating one variable of a crop often depends on the simulated quality of another variable. For example, the simulation of grain filling duration in our study affected the simulation of grain size. In turn, this affected the simulation of grain yield. In contrast, Asseng et al. (2015) showed that small errors in the simulation of phenology (e.g., anthesis dates) did not necessarily translate into poor grain yield simulations. If a critical functionality is missing in a crop model (e.g., heat impact on senescence), that can lead to biased simulations of final grain yields (Lobell et al., 2012).

Among the four wheat models, Nwheat has been used to explore the impact of extreme temperature variability on wheat grain yields (Asseng et al., 2011). The specific heat stress function accelerating leaf senescence with $T_{\text{max}} > 34^\circ \text{C}$ in Nwheat explains the close simulations of observed heat stress effects during grain filling on grain yield with this model.

This article is protected by copyright. All rights reserved.
Challenging this function in Nwheat with detailed leaf senescence data under a range of heat stress treatments in our experiment showed that this is a reasonable approach for dealing with heat stress during grain filling. Other crop models without such heat stress functionality affecting senescence like CERES-Wheat and WheatGrow could be improved by including this method. For APSIM-Wheat, it claimed that leaf senescence function from Asseng et al. 2011 was incorporated according to the wheat document of APSIM (APSRU, 2014). However, the functions under heat stress in APSIM-Wheat were not identical with Nwheat model, especially on how leaf senescence was calculated, which may explain the overestimation of heat stress effects on wheat senescence (Fig.8). Therefore, more model improvement under heat stress should be conducted for APSIM-Wheat.

The heat stress sensitivity of crop yields varied during the course of crop development. Heat stress at anthesis had the largest impact on observed grain yield reductions. However, none of the models was able to capture the observed heat stress impact at anthesis on yield; therefore, all models require this aspect to be improved. Both Barlow et al. (2015) and Rezaei et al. (2015) suggested that heat stress impacts on grain number set should be included in crop models when simulating response of heat stress effects on crop production. In addition, the observed (but not simulated) reduction in grain size due to heat at anthesis points to sink reductions suggested by Calderini et al. (1999), and needs to be considered in crop models to more appropriately deal with heat stress at anthesis. Stratonovitch and Semenov (2015) recently incorporated functions for heat affecting grain numbers to improve their wheat crop model Sirius2010.
Breeding heat-tolerant cultivars was suggested as one of the most promising strategies to adapt crops to future climate change (Gouache et al., 2012, Zheng et al., 2012). Studies have shown significant genetic variability in the response of wheat to heat stress (Jackson et al., 2013, Stone & Nicolas, 1994, Vignjevic et al., 2015). The two cultivars studied in our experiment confirmed genetic variability in the response to heat stress. Cultivar Xumai30 tended to be more heat tolerant than Yangmai16. Therefore, crop models need to consider cultivar-specific tolerance to heat stress to better simulate temperature effects on wheat cropping systems. This would also enable the possibility to explore the impact of different levels of heat tolerance across growing environments and future climates. Among the four models, even in models with heat stress functions (e.g. APSIM-Wheat, Nwheat), none of the models simulate heat stress effects at cultivar level. As an examples of taking genetic differences in heat stress tolerance among cultivars into account, both Shi et al. (2015) and Stratonovitch and Semenov (2015) have incorporated genetic variability in the response to heat stress as cultivar-specific parameters, similar to other cultivar parameters, into crop models.

The data presented here to test crop models were from pot experiments in phytotrons. Pot experiments have been criticized for not adequately representing field conditions, and heat stress treatments create an unrealistic microclimate that is unlike the field, by exposing root systems, which are sensitive to high temperatures (Ewert et al., 2002, van Herwaarden et al., 1998). However, the duration of heat stress was relatively short, and the daily fluctuation of temperature was mimicked to simulate heat stress close to field conditions; both of these helped to reduce biases toward pot experiments. However, more detailed model testing with
heat stress under field conditions will assist to further improve and validate crop models.

Heat stress is expected to negatively impact wheat production with global warming. Crop models are powerful tools to study the interaction between crop and climate factors; they are often used to explore the impact of climate change on agriculture. Crop models, including some of the ones tested here, have been used to study the impact of global warming on wheat production (Asseng et al., 2015, Rosenzweig et al., 2014). Among the four models, APSIM-Wheat and Nwheat model, which included some heat stress functions, tended to better reproduce the observed heat stress response than CERES-Wheat and WheatGrow. Further model application under heat stress should be focused more on models with heat stress functions. However, the detailed model comparison with experimental data identified shortcomings and needs for further model improvements to better simulate the impact of heat stress on crop development, growth, and yields.

Acknowledgements

This work was supported by the National High-Tech Research and Development Program of China (2013AA100404), the National Natural Science Foundation of China (31271616), the National Research Foundation for the Doctoral Program of Higher Education of China (20120097110042), the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD), and the China Scholarship Council.

References


This article is protected by copyright. All rights reserved.


Beijing, China Meteorological Press.


This article is protected by copyright. All rights reserved.


Stratonovitch P, Semenov MA (2015) Heat tolerance around flowering in wheat identified as a key This article is protected by copyright. All rights reserved.
trait for increased yield potential in Europe under climate change. *Journal of Experimental Botany*.


Zhao H, Dai TB, Jing Q, Jiang D, Cao WX (2007) Leaf senescence and grain filling affected by This article is protected by copyright. All rights reserved.
post-anthesis high temperatures in two different wheat cultivars. *Plant Growth Regulation*, **51**, 149-158.


Table 1. Summary of heat stress treatments in environment-controlled phytotron experiments.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Growing season</th>
<th>Site</th>
<th>Starting time of treatment</th>
<th>Duration</th>
<th>Temperature regime (T$<em>{min}$/T$</em>{max}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yangmai6</td>
<td>2010-20</td>
<td>Nanjing</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d)</td>
<td>T1 (17°C/27°C), T2 (21°C/31°C), T3 (25°C/35°C), T4 (29°C/39°C)</td>
</tr>
<tr>
<td></td>
<td>2011-20</td>
<td>Nanjing</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d)</td>
<td>T1 (17°C/27°C), T2 (21°C/31°C), T3 (25°C/35°C), T4 (29°C/39°C)</td>
</tr>
<tr>
<td></td>
<td>2012-20</td>
<td>Nanjing</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d)</td>
<td>T1 (17°C/27°C), T2 (21°C/31°C), T3 (25°C/35°C), T4 (29°C/39°C)</td>
</tr>
<tr>
<td></td>
<td>2013-20</td>
<td>Rugao</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d), D3 (9d)*</td>
<td>T1 (17°C/27°C), T3 (25°C/35°C), T4 (29°C/39°C), T5 (33°C/43°C)</td>
</tr>
<tr>
<td>Xumai30</td>
<td>2011-20</td>
<td>Nanjing</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d)</td>
<td>T1 (17°C/27°C), T2 (21°C/31°C), T3 (25°C/35°C), T4 (29°C/39°C)</td>
</tr>
<tr>
<td></td>
<td>2012-20</td>
<td>Nanjing</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d)</td>
<td>T1 (17°C/27°C), T2 (21°C/31°C), T3 (25°C/35°C), T4 (29°C/39°C)</td>
</tr>
<tr>
<td></td>
<td>2013-20</td>
<td>Rugao</td>
<td>Anthesis, DAA10</td>
<td>D1 (3d), D2 (6d), D3 (9d)*</td>
<td>T1 (17°C/27°C), T3 (25°C/35°C), T5 (33°C/43°C)</td>
</tr>
</tbody>
</table>

*Anthesis means first observed anthers at middle of ear (Zadoks61), DAA10 means 10 days after first anthers observed
*D3 (9d): only for treatments during anthesis, not for treatments starting from DAA10
*T1: the control or check treatment
<table>
<thead>
<tr>
<th>Stage</th>
<th>Cultivar</th>
<th>Parameters</th>
<th>Observed Slope</th>
<th>Observed $R^2$</th>
<th>CERES-Wheat Slope</th>
<th>CERES-Wheat $R^2$</th>
<th>Nwheat Slope</th>
<th>Nwheat $R^2$</th>
<th>WheatGrow Slope</th>
<th>WheatGrow $R^2$</th>
<th>APSIM-Wheat Slope</th>
<th>APSIM-Wheat $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthesis</td>
<td>Yangmai16</td>
<td>Grain filling duration</td>
<td>-0.0058</td>
<td>0.88**</td>
<td>-0.0006</td>
<td>0.14*</td>
<td>-0.0012</td>
<td>0.23**</td>
<td>-0.0050</td>
<td>0.87**</td>
<td>-0.0017</td>
<td>0.49**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total aboveground biomass</td>
<td>-0.0043</td>
<td>0.83**</td>
<td>-0.0025</td>
<td>0.75**</td>
<td>-0.004</td>
<td>0.82**</td>
<td>-0.0009</td>
<td>0.41**</td>
<td>-0.0066</td>
<td>0.86**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain yield</td>
<td>-0.0164</td>
<td>0.85**</td>
<td>-0.0035</td>
<td>0.65**</td>
<td>-0.0065</td>
<td>0.75**</td>
<td>-0.0013</td>
<td>0.56**</td>
<td>-0.0102</td>
<td>0.89**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain number</td>
<td>-0.0144</td>
<td>0.92**</td>
<td>-0.0035</td>
<td>0.65**</td>
<td>-0.0062</td>
<td>0.65**</td>
<td>-0.0012</td>
<td>0.54**</td>
<td>-0.0006</td>
<td>0.32**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain size</td>
<td>-0.0141</td>
<td>0.83**</td>
<td>-0.00001</td>
<td>0.26**</td>
<td>-0.0004</td>
<td>0.01</td>
<td>-0.0001</td>
<td>0.20**</td>
<td>-0.0099</td>
<td>0.89**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain protein concentration</td>
<td>0.0079</td>
<td>0.87**</td>
<td>-0.0003</td>
<td>0.12</td>
<td>0.0012</td>
<td>0.30**</td>
<td>0.0019</td>
<td>0.60**</td>
<td>0.0043</td>
<td>0.53**</td>
</tr>
<tr>
<td></td>
<td>Xumai30</td>
<td>Grain filling duration</td>
<td>-0.0037</td>
<td>0.89**</td>
<td>-0.0006</td>
<td>0.18**</td>
<td>-0.0012</td>
<td>0.32**</td>
<td>-0.0036</td>
<td>0.92**</td>
<td>-0.0005</td>
<td>0.12**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total aboveground biomass</td>
<td>-0.0040</td>
<td>0.88**</td>
<td>-0.0022</td>
<td>0.78**</td>
<td>-0.0035</td>
<td>0.84**</td>
<td>-0.0009</td>
<td>0.59**</td>
<td>-0.0060</td>
<td>0.92**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain yield</td>
<td>-0.0150</td>
<td>0.88**</td>
<td>-0.0030</td>
<td>0.70**</td>
<td>-0.0055</td>
<td>0.77**</td>
<td>-0.0010</td>
<td>0.57**</td>
<td>-0.0094</td>
<td>0.89**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain number</td>
<td>-0.0128</td>
<td>0.88**</td>
<td>-0.0030</td>
<td>0.70**</td>
<td>-0.006</td>
<td>0.68**</td>
<td>-0.0009</td>
<td>0.60**</td>
<td>-0.0002</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain size</td>
<td>-0.0114</td>
<td>0.88**</td>
<td>-0.0009</td>
<td>0.22*</td>
<td>-0.0024</td>
<td>0.50**</td>
<td>-0.0007</td>
<td>0.09</td>
<td>-0.0049</td>
<td>0.64**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain protein concentration</td>
<td>0.0051</td>
<td>0.90**</td>
<td>-0.0001</td>
<td>0.05</td>
<td>0.0003</td>
<td>0.02</td>
<td>0.0017</td>
<td>0.63**</td>
<td>0.0039</td>
<td>0.46**</td>
</tr>
<tr>
<td>Grain</td>
<td>Yangmai16</td>
<td>Grain filling duration</td>
<td>-0.0042</td>
<td>0.73**</td>
<td>-0.0016</td>
<td>0.36**</td>
<td>-0.0013</td>
<td>0.23**</td>
<td>-0.0032</td>
<td>0.84**</td>
<td>0.0039</td>
<td>0.48**</td>
</tr>
<tr>
<td>filling</td>
<td></td>
<td>Total aboveground biomass</td>
<td>-0.0038</td>
<td>0.63**</td>
<td>-0.0031</td>
<td>0.72**</td>
<td>-0.0036</td>
<td>0.80**</td>
<td>-0.0002</td>
<td>0.56**</td>
<td>-0.0052</td>
<td>0.82**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain yield</td>
<td>-0.0136</td>
<td>0.82**</td>
<td>-0.0004</td>
<td>0.10</td>
<td>-0.0091</td>
<td>0.84**</td>
<td>-0.0005</td>
<td>0.56**</td>
<td>-0.0065</td>
<td>0.82**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain number</td>
<td>-0.0048</td>
<td>0.55**</td>
<td>-0.0005</td>
<td>0.29</td>
<td>-0.0025</td>
<td>0.28**</td>
<td>-0.0004</td>
<td>0.53**</td>
<td>0.0000</td>
<td>1.00**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain size</td>
<td>-0.0112</td>
<td>0.71**</td>
<td>0.00001</td>
<td>0.12</td>
<td>-0.0073</td>
<td>0.70**</td>
<td>-0.0001</td>
<td>0.10</td>
<td>-0.0066</td>
<td>0.83**</td>
</tr>
<tr>
<td></td>
<td>Xumai30</td>
<td>Grain protein concentration</td>
<td>0.0082</td>
<td>0.66**</td>
<td>0.0002</td>
<td>0.02</td>
<td>0.0073</td>
<td>0.82**</td>
<td>0.0009</td>
<td>0.28*</td>
<td>0.0074</td>
<td>0.79**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Grain filling duration</td>
<td>-0.0030</td>
<td>0.68**</td>
<td>-0.0014</td>
<td>0.43**</td>
<td>-0.0002</td>
<td>0.37**</td>
<td>-0.0025</td>
<td>0.88**</td>
<td>0.0044</td>
<td>0.69**</td>
</tr>
<tr>
<td>duration</td>
<td>Total aboveground biomass</td>
<td>Grain yield</td>
<td>Grain number</td>
<td>Grain size</td>
<td>Grain protein concentration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------</td>
<td>---------------------------</td>
<td>-------------</td>
<td>--------------</td>
<td>------------</td>
<td>-----------------------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.0037</td>
<td>0.89**</td>
<td>-0.0030</td>
<td>0.78**</td>
<td>-0.0035</td>
<td>0.85**</td>
<td>-0.0005</td>
<td>0.68**</td>
<td>-0.0051</td>
<td>0.95**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.0101</td>
<td>0.78**</td>
<td>0.0004</td>
<td>0.05**</td>
<td>-0.0095</td>
<td>0.83**</td>
<td>-0.0006</td>
<td>0.76**</td>
<td>-0.0059</td>
<td>0.77**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.0041</td>
<td>0.47**</td>
<td>0.0001</td>
<td>0.02</td>
<td>-0.0033</td>
<td>0.58**</td>
<td>-0.0005</td>
<td>0.67**</td>
<td>0.0000</td>
<td>1.00**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.0094</td>
<td>0.75**</td>
<td>-0.0001</td>
<td>0.47**</td>
<td>-0.0068</td>
<td>0.66**</td>
<td>-0.0001</td>
<td>0.08</td>
<td>-0.0063</td>
<td>0.81**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.0078</td>
<td>0.82**</td>
<td>-0.0002</td>
<td>0.02</td>
<td>0.0096</td>
<td>0.83**</td>
<td>0.0010</td>
<td>0.34**</td>
<td>0.0046</td>
<td>0.32**</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Regression coefficients of observed and simulated wheat growth parameters with four wheat models to heat degree days (HDD) in environment-controlled phytotron experiments. Slope and $R^2$ were the slopes of fitted lines and coefficients of determination between wheat growth parameters and HDD.

** indicates significance at $p<0.01$, * indicates significance at $p<0.05$
Figure captions

Figure 1. Relative response of observed and simulated grain filling duration to heat stress at anthesis (a-e) and grain filling (f-j) from four wheat models for two winter wheat cultivars (circle and straight line indicates cv. Yangmai16; triangle and dash line indicates cv. Xumai30) in environment-controlled phytotron experiments. Observed (a and f) and simulated with CERES-Wheat (b and g), Nwheat (c and h), WheatGrow (d and i), and APSIM-Wheat (e and j).

Figure 2. Relative response of observed and simulated total aboveground biomass to heat stress at anthesis (a-e) and grain filling (f-j) from four wheat models for two winter wheat cultivars (circle and straight line indicates cv. Yangmai16; triangle and dash line indicates cv. Xumai30) in environment-controlled phytotron experiments. Observed (a and f) and simulated with CERES-Wheat (b and g), Nwheat (c and h), WheatGrow (d and i), and APSIM-Wheat (e and j).

Figure 3. Relative response of observed and simulated grain yield to heat stress at anthesis (a-e) and grain filling (f-j) from four wheat models for two winter wheat cultivars (circle and straight line indicates cv. Yangmai16; triangle and dash line indicates cv. Xumai30) in environment-controlled phytotron experiments. Observed (a and f) and simulated with CERES-Wheat (b and g), Nwheat (c and h), WheatGrow (d and i), and APSIM-Wheat (e and j).

Figure 4. Comparison of observed and simulated grain yield (kg ha\(^{-1}\)) under heat stress at anthesis (a-d) and grain filling (e-h) from four wheat models in environment-controlled phytotron experiments. CERES-Wheat (a and e), Nwheat (b and f), WheatGrow (c and g), and APSIM-Wheat (d and h).

Figure 5. Relative response of observed and simulated grain number to heat stress at anthesis (a-e) and grain filling (f-j) from four wheat models for two winter wheat cultivars (circle and straight line indicates cv. Yangmai16; triangle and dash line indicates cv. Xumai30) in environment-controlled phytotron experiments. Observed (a and f) and simulated with CERES-Wheat (b and g), Nwheat (c and h), WheatGrow (d and i), and APSIM-Wheat (e and j).

Figure 6. Relative response of observed and simulated grain size to heat stress at anthesis (a-e) and grain filling (f-j) from four wheat models for two winter wheat cultivars (circle and straight line indicates cv. Yangmai16; triangle and dash line indicates cv. Xumai30) in environment-controlled phytotron experiments. Observed (a and f) and simulated with CERES-Wheat (b and g), Nwheat (c and h), WheatGrow (d and i), and APSIM-Wheat (e and j).

Figure 7. Relative response of observed and simulated grain protein concentration to heat stress at anthesis (a-e) and grain filling (f-j) from four wheat models for two winter wheat cultivars (circle and straight line indicates cv. Yangmai16; triangle and dash...
Figure 8. Comparison between observed and simulated dynamics of leaf area index (LAI) to heat stress at anthesis (a-d) and grain filling (e-h) from four wheat models for cv. Yangmai16 in the growing season 2013-2014 in environment-controlled phytotron experiments. Four treatments (T1, T3, T4, and T5) were chosen for anthesis and grain filling separately as an example. The heat stress durations for the four treatments were 9 days and 6 days for treatments at anthesis and grain filling, respectively. Symbols and lines indicated observed and simulated values, respectively. T1 (● and ——— ), T3 (○ and ——— ), T4 (▼ and ——— ), T5 (△ and ——— ). Simulated with CERES-Wheat (a and e), Nwheat (b and f), WheatGrow (c and g), and APSIM-Wheat (d and h).

Figure 9. Comparison between observed and simulated dynamics of grain filling to heat stress at anthesis (a-d) and grain filling (e-h) from four wheat models for cv. Yangmai16 in the growing season 2013-2014 in environment-controlled phytotron experiments. Four treatments (T1, T3, T4, and T5) were chosen for anthesis and grain filling separately as an example. The heat stress durations for the four treatments were 9 days and 6 days for treatments at anthesis and grain filling, respectively. Symbols and lines indicated observed and simulated values, respectively. T1 (● and ——— ), T3 (○ and ——— ), T4 (▼ and ——— ), T5 (△ and ——— ). Simulated with CERES-Wheat (a and e), Nwheat (b and f), WheatGrow (c and g), and APSIM-Wheat (d and h).
Figure 2.

Figure 3.
Figure 4.

Figure 5.
Figure 6.

![Graph showing relative grain size vs. HDD (°C·d) for different models and observed data.](image1)

Figure 7.

![Graph showing relative grain protein concentration vs. HDD (°C·d) for different models and observed data.](image2)

This article is protected by copyright. All rights reserved.
Figure 8.

Figure 9.

This article is protected by copyright. All rights reserved.