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Research Paper

Modelling the effects of post-heading heat stress on biomass growth of winter wheat

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ABSTRACT

Climate change scenarios project an increase in the frequency of heat stress events, making it critical to quantify adverse heat stress effects on wheat production. Biomass growth determines much of grain yield in winter wheat, but it is substantially reduced under heat stress during the reproductive phase. In this study, leaf photosynthesis, biomass production, and leaf area index (LAI) dynamics were measured under various heat stress treatments in a 4-year phytotron experiment with two winter wheat cultivars. Heat stress at anthesis and during grain filling accelerated the measured degradation of leaf chlorophyll (SPAD) and resulted in a lower leaf photosynthesis rate with decreased final biomass growth. The observed relationships between leaf photosynthesis, LAI, and high temperatures were integrated into the WheatGrow model. In this study, we introduced a new cultivar parameter into the model to simulate cultivar difference in the sensitivity of biomass growth to heat stress. The new heat stress routines in the WheatGrow model significantly improved the simulated growth dynamics and the root mean square error (RMSE) with an independent validation data set for LAI and final aboveground biomass by 40% and 57% under heat stress treatments, respectively. This improvement in the crop model WheatGrow enables more reliable studies on climate change impacts and reduces uncertainties in simulations, particularly the impacts of extreme temperature events on crop growth and yields.

1. Introduction

Increased temperature variability under climate change will lead to more heat stress events during crop production, which poses additional risks on global food security (IPCC, 2012). Extreme heat stress events will become more frequent in many main wheat-producing regions (Asseng et al., 2011; Gouache et al., 2012; Gourdji et al., 2013; Lobell et al., 2015; Lobell et al., 2012; Semenov and Shewry, 2011; Teixeira et al., 2013). For instance, in China, the largest wheat producer in the world, heat stress already had significant negative impacts on wheat yields during the last 50 years (Liu et al., 2014; Tao et al., 2015). Several studies have reported the severe negative effects of heat stress on wheat growth and yield; these negative effects occur especially during the reproductive period (Farooq et al., 2011; Pradhan et al., 2012; Prasad and Djanaguiraman, 2014; Tashiro and Wardlaw, 1990; Wardlaw et al., 1989). One of the most sensitive crop growth processes affected by heat stress is biomass accumulation (including photosynthesis and respiration), affecting grain yield (Feng et al., 2014; Prasad et al., 2011). During the reproductive period, heat stress usually accelerates the degradation of leaf chlorophyll and results in lower leaf photosynthesis rate with smaller green leaf area (Prasad et al., 2011; Zhao et al., 2007). A reduction in both photosynthesis rate and green leaf area index will reduce biomass growth and consequently grain yield. Also, higher temperatures during heat stress could increase plant respiration (Atkin and Tjoelker, 2003; Kaše and Čatský, 1984), which could decrease biomass growth. Diverse genetic differences of heat tolerance in the response of photosynthesis to heat stress has been found in wheat (Feng et al., 2014; Wang et al., 2015) and could be a key trait to adapt wheat to climate change (Semenov et al., 2014; Stratonovitch and Semenov, 2015).

Process-based crop models have been widely used to assess the impact of climate on crop production (Challinor et al., 2014; Rosenzweig et al., 2014). However, only few studies have dealt with heat stress effects in crop models. When testing 30 wheat models, Asseng et al. (2015) found a wide range of model responses to increasing temperature, especially under higher temperature conditions.

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In our previous study (Liu et al., 2016a), four wheat models (APSIM-Wheat, CERES-Wheat, Nwheat, and WheatGrow) were systematically evaluated with observed heat stress dataset from environment-controlled phytotron experiments. That study indicated that most crop models only represent parts of heat stress effects on biomass production. Grain yield simulations in most crop models depend on the simulation of biomass growth; therefore, it is critical for crop models to simulate biomass growth accurately. Some studies have implied that improving the algorithms and functions under heat stress could be helpful to enhance the performances of crop models in wheat (Liu et al., 2016a; Stratonovitch and Semenov, 2015). For example, a leaf senescence acceleration function recently incorporated into the Sirius model improved the model predictions under high post-anthesis temperature (Stratonovitch and Semenov, 2015). However, few studies have focused on improving crop models when simulating leaf photosynthesis and biomass growth under heat stress. In this study, with detailed observed data of leaf photosynthesis and biomass growth, we examined and improved the response of biomass growth to post-heading heat stress in a wheat crop model, which will enable better simulations of wheat production under climate change.

The objectives of this study were: (1) to determine the post-heading heat stress effects on leaf photosynthesis, leaf area index and biomass growth in wheat and (2) to use this knowledge to improve the predictions of biomass growth under heat stress with the WheatGrow model.

2. Materials and methods

2.1. Environment-controlled phytotron experiments

Environment-controlled phytotron experiments were conducted for four years at Nanjing (118.78°E, 32.04°N) and Rugao (120.33°E, 32.23°N) in Jiangsu Province of China. Winter wheat (Yangmai16 and Xumai30) was planted in plastic pots, with a plant density of 10 plants per pot. The height and inside diameter of pots were 30 cm and 25 cm. Sowing dates in the four growing seasons were November 1, November 6, November 4, and November 5. Wheat was grown in pots installed outside, in an ambient environment, with no environmental control, before and after the heat stress treatments. Once wheat developed into the appropriate growth stages (anthesis or grain filling), wheat was transferred into phytotrons to be exposed to different heat stress conditions. Table 1 summarizes the heat stress treatments, including two cultivars (Yangmai16 and Xumai30); five temperature levels (Tmin/Tmax): 17/27 °C (T1), 21/31 °C (T2), 25/35 °C (T3), 29/39 °C (T4), and 33/43 °C (T5); three heat stress durations (3 days, 6 days, and 9 days); and two heat stress stages (anthesis and grain filling). There were 27 pots for sampling after heat stress and measuring grain yield at harvest for each treatment. Heat stress treatments at anthesis and the grain filling stage started when wheat began flowering and 10 days after anthesis (DAA10), 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 used as a check or control treatment. The average temperature in T1 was 22 °C, which has been considered as the optimal temperature for post-heading period in wheat (Porter and Gawith, 1999). T2, T3, T4, and T5 were used as heat stress treatments.

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. Day-night temperature fluctuations shown in the supplementary material (Fig. S1) were similar to the ambient temperatures. After a heat stress period, plants were moved out of the phytotrons and maintained at normal ambient environmental conditions until harvest. The fertilization applied was 18.3 g N m^{-2}, 10.2 g P_2O_5 m^{-2}, and 18.3 g K_2O m^{-2} prior to sowing, and another 18.3 g N m^{-2} 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 ensure no water or nitrogen stress in the experiments. Meteorological records, including daily temperature, rainfall, and radiation during wheat growing season, were measured by Dynamet–1 K (Dynamet Inc., USA) near the experiment sites. More details about our experiment can be found in Liu et al. (2016a).

2.2. Sampling and measurements

2.2.1. Biomass and leaf area index

Plant samples were taken before and after heat stress treatments. On the day prior to heat stress treatments, plant samples were taken once to obtain initial growth variables before heat stress. After heat stress treatments, 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. Sample plants were separated into different plant tissues including stem 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. Green leaf area was measured with LI-3000 leaf area meter (LI-COR, Lincoln, NE, USA).

2.2.2. Leaf chlorophyll content

The significant positive relationship between SPAD and chlorophyll content has been shown in several previous studies especially during the grain filling period (Uddling et al., 2007), and leaf senescence is the main reason for the lose of leaf greenness during grain filling period. Therefore, leaf chlorophyll status were reflected with SPAD values in this study. Leaf chlorophyll SPAD content was determined using a chlorophyll meter SPAD502 (Soil Plant Analysis Development; Minolta, Japan) at the same time with plant samples were taken in the four growing seasons. Top three leaves on each stem were sampled separately, and there were five replications for each leaf position from

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

Cultivar	Growing season	Site	Starting time of treatment	Duration	Temperature regime (T_{min}/T_{max})
Yangmai16	2010–2011	Nanjing	Anthesis, DAA10	D3 (3d), D6 (6d)	T1 (17 °C/27 °C), T2 (21 °C/31 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C)
	2011–2012	Nanjing	Anthesis, DAA10	D3 (3d), D6 (6d)	T1 (17 °C/27 °C), T2 (21 °C/31 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C)
	2012–2013	Nanjing	Anthesis, DAA10	D3 (3d), D6 (6d)	T1 (17 °C/27 °C), T2 (21 °C/31 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C)
	2013–2014	Rugao	Anthesis, DAA10	D3 (3d), D6 (6d), D9 (9d)*	T1 (17 °C/27 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C), T5(33 °C/43 °C)
Xumai30	2011–2012	Nanjing	Anthesis, DAA10	D3 (3d), D6 (6d)	T1 (17 °C/27 °C), T2 (21 °C/31 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C)
	2012–2013	Nanjing	Anthesis, DAA10	D3 (3d), D6 (6d)	T1 (17 °C/27 °C), T2 (21 °C/31 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C)
	2013–2014	Rugao	Anthesis, DAA10	D3 (3d), D6 (6d), D9 (9d)*	T1 (17 °C/27 °C), T3 (25 °C/35 °C), T4 (29 °C/39 °C), T5 (33 °C/43 °C)

*DAA10: 10 days after anthesis.
*D9 (9d): only for treatments during anthesis, not for treatments starting from DAA10.
*T1: the control or check treatment.