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Response of biomass accumulation in wheat to low-temperature stress at jointing and booting stages

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ABSTRACT

Climate change has resulted in a continuous increase in the frequency, intensity, and duration of extreme low-temperature events and poses a serious threat to wheat production in China. To better understand the effects of low temperature on wheat photosynthetic production and yield formation, two-year temperature controlled experiments in phytotrons were performed with two different cold-sensitive winter wheat cultivars at five daily maximum/minimum temperature levels and three temperature durations—2, 4 and 6 days—at both jointing and booting stages. Except for its effect on mean net assimilation rate (*MNAR*) at jointing, low temperature level had significant negative effects on mean leaf area index (*MLAI*), mean net assimilation rate (*MNAR*), harvest index (*HI*), biomass per plant (BPP_M) and grain yield per plant (*GYPP*), while photosynthetic duration (*D*) (except for Yangmai16 at jointing) was significantly positively affected. Moreover, low temperature duration and its interaction with low temperature level had negative effects on *MLAI, MNAR, HI,* BPP_M and *GYPP*, but only the effects of low temperature duration on *HI,* BPP_M and *GYPP* and the interaction effect on BPP_M and *GYPP* reached a significant level. In addition, BPP_M and *GYPP* were more sensitive to low temperature at booting than at jointing stage. Furthermore, significant negative linear relationships were observed between the accumulated cold degree days (*ACDD*) and *MLAI, MNAR, HI,* BPP_M and *GYPP*, while a significant positive linear relationship was observed between *ACDD* and *D* in both cultivars. The contribution of BPP_M to the variation of *GYPP* was greater than that of *HI* in both cultivars. However, for biomass, from the first day of low-temperature treatment to maturity ($BPP_{T\text{-}M}$), the major variation was caused by *MLAI* when low temperature occurred at jointing and by *MNAR* when low temperature occurred at booting. These results could support the improvement of crop model algorithms under cold stress and assist in the wheat breeding with higher cold tolerance.

1. Introduction

Recent global warming has markedly shifted the distribution of temperature variability and extremes and precipitation patterns (Trnka et al., 2014). These shifts have resulted in more frequent cold stress events (including chilling stress and freezing stress) during the wheat-growing season (Gu et al., 2008; Lobell et al., 2015), with consequent negative effects on wheat production (Fuller et al., 2007; Venzhik et al., 2011). Moreover, global warming has accelerated the process of wheat growth and development, resulting in significant advancement of the low-temperature-sensitive stage of wheat, thereby increasing the probability of cold or frost injury in wheat (Ji et al., 2017). A recent study showed that during the last several decades, low temperature has seriously affected wheat production in China (Zhong et al., 2008), the United States of America (Gu et al., 2008), Europe (Peings et al., 2013; Trnka et al., 2014) and Australia (Barlow et al., 2015; Crimp et al., 2016). However, due to the increasing global mean temperature during the last several decades, most studies have been concerned with the effects of heat stress on crop production (Gourdji et al., 2013; Liu et al., 2014; Rahmstorf and Coumou, 2011). Low-temperature injury to crops, which includes both cold and freezing injury, has usually been ignored (Ding et al., 2010; Rigby and Porporato, 2008).

Leaf photosynthesis and biomass accumulation, which are the primary sources of grain yield, are the two most sensitive crop growth processes affected by cold stress (Marcellos, 1977; Sassenrath and Ort, 1990). During the vegetative period, cold stress usually exacerbates the

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balance between the source of energy and the metabolic sink, which inhibits the photosynthesis rate and results in reduced green leaf area (Allen and Ort, 2001; Paul and Foyer, 2001). A reduction in both photosynthesis rate and green leaf area index will reduce the biomass accumulation and, consequently, grain yield (Subedi et al., 1998). Leonardos et al. (2003) investigated the effects of cold stress (day/night, 5/5 °C) at the seedling stage on photosynthesis in winter wheat and found that the photosynthesis rate of the primary leaf in the cold condition was 45% lower than that of the control (day/night, 20/16 °C). Compared with the control, they also found that the plants in the cold condition had a lower relative growth rate and smaller leaf area and biomass but greater specific leaf weight. Fuller et al. (2007) reported that the flag leaves of two wheat cultivars were damaged under the treatment at −3 °C for 2 h, with damage increasing as the low temperature declined to −5 °C and −7 °C, resulted in 10%–100% grain yield loss. Venzhik et al. (2011) exposed wheat at the seeding stage to a low temperature at 4 °C for 7 days in a chamber and found that photosynthesis rate of the first leaf decreased by 18% after 5 h of low-temperature treatment, and the maximum quantum efficiency of photosystem II (*PSII*) decreased by 8% after 24 h of treatment. Li et al. (2015) reported that spring freeze (8 °C lower than ambient temperature for 5 days) at jointing significantly decreased gas exchange rates and the maximum quantum efficiency of *PSII* in wheat leaves, causing a 5%–14% reduction in grain yield. Previous studies have primarily focused on the effects of low temperature on wheat photosynthesis and yield (Fuller et al., 2007; Subedi et al., 2010; Venzhik et al., 2011), with less focus on wheat biomass production and the relative importance of biomass production to grain yield. Additionally, previous studies have primarily investigated the effect of either low temperature level or low temperature duration alone on wheat production (Al-Issawi et al., 2013; Whaley et al., 2004), whereas the combined effects of low temperature level and duration have rarely been reported. Furthermore, the temperature regimes in most previous studies were based on fixed day/night temperature treatments (Li, et al., 2015; Venzhik et al., 2011), which are not consistent with the natural daily temperature dynamics. In the actual environment, the impact of low temperature on crop growth and development is often affected by the combination of low temperature intensity and duration under the daily temperature variation pattern (Shimono et al., 2007).

Accumulated cold degree days (*ACDD*, °C d), which includes both duration and intensity of low temperature, has been used to quantify the effects of low temperature on the growth, development and yield formation in rice (Roel et al., 2005; Shimono et al., 2005) and wheat (Ji et al., 2017). Godwin et al. (1994) introduced *ACDD* into the CERES-Rice model to improve the simulation accuracy under low-temperature environments, suggesting that *ACDD* could effectively quantify the chilling injury effect in an extensive field experiment. Shimono (2011) employed *ACDD* to quantify the effects of low temperature on rice yield in northern Japan during the past fifty years and found that for each 1 °C·d increase in *ACDD*, rice yield was predicted to decline by 0.86%. Ji et al. (2017) used accumulated cold degree days (*ACDD*) to analyze the relationship between low-temperature stress and grain yield and yield components of wheat and observed significant negative linear relationships between *ACDD* and grain yield per plant, spike number per plant, grain number per spike and 1000-grain weight. Although several studies have quantified the effects of low temperature on the yield of rice and wheat with *ACDD*, few similar studies have been conducted on wheat biomass production.

In the present study, two years of environment-controlled phytotron experiments were conducted with different cold-sensitive winter wheat cultivars under different low temperature levels and durations at two growth stages. Our primary objectives were to (1) analyze the effects of low temperature level and duration at jointing and booting stages on leaf photosynthetic properties and biomass production, (2) investigate the relative contributions of photosynthetic properties to the variability of wheat biomass accumulation and grain yield under low-temperature conditions, and (3) quantify the interaction effects of low temperature level and duration on wheat photosynthetic properties, biomass accumulation and grain yield production with *ACDD*.

2. Materials and methods

2.1. Experimental design

The experiments were conducted in eight independent environment-controlled phytotrons during the 2013–2015 growing seasons at the experimental station of the National Engineering and Technology Center for Information Agriculture (NETCIA), which is located in Rugao City, Jiangsu Province, China (120°45′ E, 32°16′ N). Each phytotron was 3.4 m long, 3.2 m wide and 2.8 m high. The air temperature and relative humidity in the phytotrons were controlled using air conditioners and a bubbling system. Two fans in each phytotron were employed to keep CO_2 concentration consistent with the ambient environment. Temperature and humidity in the phytotrons were controlled precisely to simulate the daily changing patterns observed under field conditions. EM50 data loggers (Decagon Devices, Inc., Washington, USA) were used to record temperature and relative humidity every 5 min during the treatment periods. The daily temperature dynamics in phytotrons were shown in Fig. 1. Supplemental light was applied with a halogen lamp to ensure sufficient irradiation for wheat growth in the phytotrons. The light intensity in the phytotrons at noon was approximately $1380\ \mu mol\ m^{-1}\ s^{-1}$ with sunshine and approximately $240\ \mu mol\ m^{-1}\ s^{-1}$ with cloud cover.

Two winter wheat cultivars, Yangmai16 (cold-sensitive cultivar, bred and released from Agricultural Research Institute of Lixiahe Region, Yangzhou, China in 2004) and Xumai30 (cold-tolerant cultivar, bred and released by Xuzhou Agricultural Institute, Xuzhou, China in 2003), were planted in plastic pots (the height and inside diameter of pots were 30 cm and 25 cm, respectively), with a planting density of 10 plants per pot. To select the uniform plants to conduct the low temperature treatments, more than 400 pots for each cultivar were planted every year. Each pot was filled with sieved yellow brown soil. Both wheat cultivars were sown on November 4, 2014, and on November 3, 2015. Before sowing, 0.9 g N, 0.5 g P_2O_5 and 0.9 g K_2O per pot were applied as basal dressing, and an additional 0.9 g N per pot at jointing was applied as top-dressing. Water, weeds, insects and diseases were controlled as required to avoid yield loss. Before and after low-temperature treatments, wheat was grown in pots outside of the phytotrons

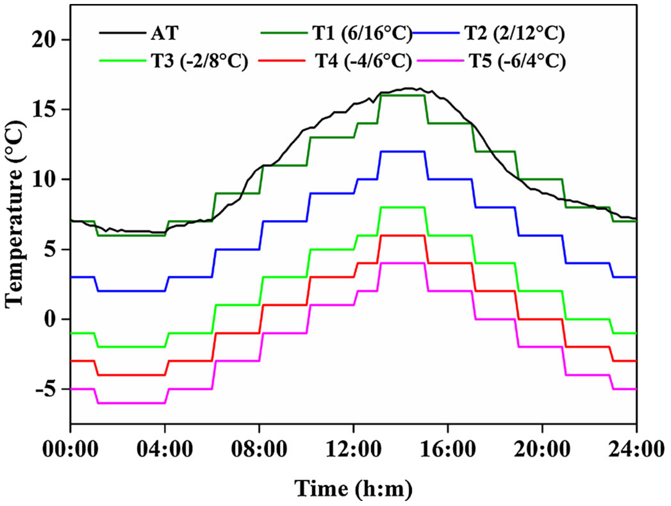

Fig. 1. Design of the daily temperature dynamics in the environment-controlled phytotrons during the low-temperature treatments (data were obtained on March 26, 2015). AT indicates the ambient temperature. T1, T2, T3, T4 and T5 indicate different temperature levels.