



The effects of increased temperature on crop growth and yield of soybean grown in a temperature gradient chamber

Custodio R.P. Tacarindua^{a,*}, Tatsuhiko Shiraiwa^a, Koki Homma^a, Etsushi Kumagai^b, Ryoji Sameshima^{b,1}

^a Laboratory of Crop Science, Graduate School of Agriculture, Kyoto University, Japan

^b NARO Tohoku Agricultural Research Center, 4 Akahira, Shimokuriyagawa, Morioka, Iwate 020-0198, Japan

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ABSTRACT

The global surface temperature is projected to rise and will affect crop performances. This study investigated the effects of increased temperature on yield and dry matter production in a controlled environment that mimicked field conditions using a temperature gradient chamber (TGC). Experiments were conducted from 2009 to 2012 using the soybean cultivar Enrei, which was grown in soil culture beds. Plants were grown in two TGCs as replicates for temperature treatment. Three temperature treatments, near ambient temperature (T_a), ambient temperature + 1 °C ($T_a + 1$), and ambient temperature + 3 °C, in 2009 and 2010, and ambient temperature + 2 °C, in 2011 and 2012 ($T_a + 2/T_a + 3$), were established by dividing the rows along which the temperature gradient was created. The aboveground dry matter was significantly reduced by increased temperature from 11% in 2012 to 27% in 2009. Decrease of dry matter accumulation was obvious particularly from flowering to early seed filling and it was associated with decline of leaf photosynthetic rate, stomatal conductance and the carbon isotope discrimination. Reduced pod number, reduced seed number, and, to some extent, smaller seeds led to a decreased harvest index (HI). These phenomena might be associated with the delayed pod set and lower seed growth rate under warmer treatment. Seed yield was the most responsive parameter in 2009 and 2010, and in 2011 and 2012, it was still reduced under continuously wet conditions. Combined data showed that total dry matter, seed yield, and HI were consistently reduced by increased temperature. It is suggested that the concomitant increase of vapor pressure deficit with increased temperature exacerbated the temperature effects. In addition, reduced ambient CO₂ and low light intensity as the artifacts of the facility might have accounted for the greater effect of high temperature.

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1. Introduction

Soybeans are a major oilseed crop produced and consumed throughout the world, and produce the second most important vegetable oil after rapeseed (United States Department of Agriculture, 2011). It has been recognized that there is a need to increase the yield of soybean (Board and Kahlon, 2011) along with other food crops to keep pace with the growing demand caused by growing populations and rising incomes (United Nations Environmental Programme, 2006). In addition, the global average surface

temperature will increase by between 1.4 and 5.8 °C in this century (United Nations Environmental Programme, 2006), which could potentially have negative impacts on important agronomic crops, including soybeans (Hatfield et al., 2011). Not only agronomic adaptation, such as shifting cropping seasons, but also the development of heat-tolerant genotypes through conventional breeding or the use of advanced techniques of molecular breeding and genetic engineering are promising; however, a successful strategy requires concerted efforts among different areas, including plant physiology (Wahid et al., 2007). This has led to many experiments around the globe on the effects of increased temperatures or its interactions with carbon dioxide (CO₂) on soybeans; however, considerable inconsistencies exist regarding the response of total biomass and yield to increased temperature (Tacarindua et al., 2012). Biomass production or photosynthetic activity was not significantly affected by temperatures slightly higher than 30 °C (Sato, 1976; Harley et al., 1985; Baker et al., 1989) and biomass was not considerably affected by temperatures near 40 °C (Allen and Boote, 2000). Seed yield was slightly reduced by high temperature stress induced only at the

Abbreviations: DM, dry matter; g_s , stomatal conductance; HI, harvest index; Pn, leaf photosynthetic rate; TGC, temperature gradient chamber; VPD, vapor pressure deficit.

* Corresponding author at: Laboratory of Crop Science, Graduate School of Agriculture, Kyoto University, Sakyo, Kyoto 606-6042, Japan. Fax: +81 75 753 6065.

E-mail addresses: ctacarindua@hotmail.com, ctacarindua@kais.kyoto-u.ac.jp (C.R.P. Tacarindua).

¹ Present address: Research Faculty of Agriculture, Hokkaido University Kita-ku, Sapporo, Hokkaido, 060-8589 Japan.

initial seed filling period (Ferris et al., 1999), whereas seed yield was reduced under a moderately high temperature of 27.5 °C during the entire growing season (Heinemann et al., 2006).

Temperature gradient chambers (TGCs) allow the study of temperature effects on crops under field-like conditions, where the inside temperatures tend to keep track with the ambient temperatures (Horie et al., 1995). Nevertheless, experiments conducted to evaluate the effects of temperature on soybean yield and dry matter (DM) production using TGCs are very limited and have shown varied responses to increased temperatures from moderate (Allen and Boote, 2000; Shiraiwa et al., 2006) to distinct (Ohe et al., 2007). These circumstances require further studies to better quantify the impacts as well as characterize the exact mechanisms involved in the response of biomass production and seed yield of soybeans to increased temperature. The objective of this study was therefore to investigate the effects of increased temperature on soybean growth and yield using TGCs.

2. Materials and methods

2.1. Environment description

Soybean cultivar Enrei, determinate and of maturity group IV, was grown under various temperatures in TGCs at the Experimental Farm of Kyoto University at Kyoto City, Japan (35.0° N lat., 135.5° E long., 71 m asl). The TGC, which was 2 m wide and 25 m long, created a nearly linear temperature gradient along its longitudinal axis from near ambient to a temperature that was several degrees higher, while maintaining the natural diurnal changes in air temperature (Horie et al., 1995). The chambers were covered with polyethylene terephthalate film with a light transmittance of 80%.

Soybean seedlings were transplanted on July 13 and July 21 in 2009 and 2010, respectively, and directly sown on July 12, in 2011 and 2012 into the soil culture bed in two TGCs, arranged in four rows of 0.25 m wide, 24 m long, and 0.25 m intra-row spacing. Three temperature treatments, near ambient temperature (Ta), ambient temperature + 1 °C (Ta + 1), and ambient temperature + 3 °C, in 2009 and 2010, and ambient temperature + 2 °C, in 2011 and 2012 (Ta + 2/Ta + 3), were established by dividing the rows along which the temperature gradient was created.

The TGC was equipped with an irrigation system containing a drainage pipe located 50 cm below the soil surface. Water was supplied through the pipe to raise the water table to approximately 30 cm below the soil surface, and the water was evenly distributed throughout the entire soil culture bed. The moisture content was monitored in 2010 using a moisture sensor (ECH2O EC-5 moisture sensor; DECAGON, Pullman, Washington, USA) installed at a depth of 15 cm, whereas in 2011 and 2012, soil moisture content was monitored using a time domain reflectometry (TDR) meter (SONY Tektronix Co. Ltd., Tokyo, Japan) installed at a depth of 30 cm. The volumetric water content was maintained at approximately 22.2% and 24.2% (in 2009 and 2010, respectively) and 24% (in 2011 and 2012) throughout the entire growth period by sub-soil irrigation. Considering that the range of soil water content for plant transpiration was considered to be between 33% (field capacity) and 13% (data not shown), these values appear to be approximately one-half the level of transpirable soil water. A detailed description of the irrigation system can be found in Tacarindua et al. (2012).

The soil used is classified as alluvial sandy loam (Fluvic Endoaquepts) and the plots were kept weed free by chemical control or hand weeding.

2.2. Measurements

Dates of the developmental stages (Fehr and Caviness, 1977) were recorded and the aboveground parts of six plants per

treatment were sampled at the onset of flowering (R1), the beginning of seed filling (R5) (2011 and 2012), at 5 days after R5 at Ta (in 2009), or at 10 days after R5 at Ta (in 2010) and eight plants at harvest maturity (R8) to determine the changes in aboveground DM accumulation. At harvest maturity, plant components were separated into leaves (including petioles), stems, pod shells, and seeds that were used to calculate the final single-seed size, seed number, seed yield, and total aboveground DM.

In 2011 and 2012, photosynthetic rate (Pn) and stomatal conductance (gs) were measured in the central leaflets of fully developed leaves of three plants per treatment (Ta and Ta + 2) once a week from near flowering, using LI-6400 (LI-COR, Inc., Lincoln, NE, USA). According to these measurements, which were conducted during the day, CO₂ concentration [CO₂] at Ta + 2 was 350 ± 13 μL/L compared to 372 ± 8 μL/L under Ta. The carbon isotope discrimination of milled samples (0.5 mg for seed and 2.0 mg for leaf) collected at harvest maturity from Ta and Ta + 2 plots was determined by mass spectrometry (Delta V; Thermo Fisher Scientific) at Kyoto University Ecological Center. Carbon isotopic composition of seed and leaf samples was expressed relative to the standard Pee Dee Formation of Belemnite.

2.3. Statistical analysis

The effects of increased air temperature on seed yield, yield components, DM accumulation, and carbon isotope discrimination (CID) were evaluated using an analysis of variance (ANOVA) with statistical software SAS version 9.3 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Temperature environment and vapor pressure deficit

The day, night, and mean air temperatures for the entire growing season are shown in Table 1. In the TGC, the lower temperature treatment was near the ambient temperature, and a temperature difference of approximately 2–3 °C was achieved for the day, night, and mean temperatures. Changes in the daily mean temperature during the entire growing season are shown in Fig. 1. The inside temperatures tended to track the diurnal fluctuation of the outdoor temperatures. As generally happens in soybean production in this region, the plants experienced a period of relatively high temperature from R1 to R5 in the four study years. The temperatures tended to decrease in the mid-seed filling period and then increased slightly toward physiological maturity (R7). This was followed by relatively low temperatures until harvest maturity.

Estimated day, night, and mean vapor pressure deficit (VPD) from emergence (VE) to R7 are shown in Table 2. In general, most data for daily mean VPD ranged from 0.82 to 1.37 kPa in 2009, and from 1.40 to 2.13 kPa in 2010. In 2011 and 2012, the daily mean VPD ranged from 0.9 to 1.5 kPa and the day average reached approximately 2.1 kPa before R1. The VPD tended to be higher in the warmer treatment compared to that under Ta, and if we compare the four study years, the VPD in 2010 was the highest of all years.

3.1.1. Developmental stages

Increasing air temperature by approximately 2–3 °C did not have a significant effect on R1, except in 2010, when flowering was delayed by 3 days. The number of days from R1 to R5 and the duration of seed filling (R5–R7) were significantly increased by increased temperatures (Table 1). The progress of pod setting (R1–R5) was more affected by the increase in temperature than the progress from VE to R1 and R5 to R7, particularly in 2009 and 2010. During these years, the time from R1 to R5 increased by 5

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