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A DISSERTATION FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

**Phenology and Yield Responses of Soybean
to Elevated Air Temperatures in a Temperate Region**

BY

DOUG-HWAN CHOI

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MAJOR IN CROP SCIENCE AND BIOTECHNOLOGY

DEPARTMENT OF PLANT SCIENCE

THE GRADUATE SCHOOL OF SEOUL NATIONAL UNIVERSITY

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UNDER THE DIRECTION OF DR. BYUN-WOO LEE
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF SEOUL NATIONAL UNIVERSITY

BY
DOUG-HWAN CHOI

MAJOR IN CROP SCIENCE AND BIOTECHNOLOGY
DEPARTMENT OF PLANT SCIENCE
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BY THE COMMITTEE MEMBERS
DECEMBER, 2016

CHAIRMAN

Suk-Ha Lee, Ph. D.

VICE-CHAIRMAN

Byun-Woo Lee, Ph. D.

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MEMBER

Junhwan Kim, Ph. D.

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Doug-Hwan Choi

Major in Crop Science and Biotechnology

Department of Plant Science

The Graduate School of Seoul National University

GENERAL ABSTRACT

Increased temperature means and fluctuations associated with climate change are predicted to exert profound effects on the development, growth, and yield of soybean. Experiments were conducted to evaluate the impacts of global warming on the phenology, yield-related traits, and yield of two determinate soybean cultivars in a temperate region (37.27°N, 126.99°E; Suwon, South Korea). These two soybean cultivars, Sinpaldalkong [maturity group (MG) IV] and Daewonkong (MG VI), were cultured on various sowing dates within a four-year period, under no water-stress conditions. Soybeans were kept in greenhouses controlled at the current ambient temperature (AT),

AT+1.5°C, AT+3.0°C, and AT+5.0°C throughout the growth periods.

Growth periods (VE–R7) were significantly prolonged by the elevated temperatures, especially the R1–R5 period. Cultivars exhibited no significant differences in seed yield at the AT+1.5°C and AT+3.0°C treatments, compared to AT, while a significant yield reduction was observed at the AT+5.0°C treatment. Yield reductions resulted from limited seed number, which was due to an overall low numbers of pods and seeds per pod. Heat stress conditions induced a decrease in pod number to a greater degree than in seed number per pod. Individual seed weight exhibited no significant variation among temperature elevation treatments; thus, seed weight likely had negligible impacts on overall seed yield.

The number of pods, the main yield determinant, was determined by flower number and pod set ratio. Regardless of cultivars or temperature treatments, the temporal distribution of flowering showed a bimodal temporal distribution. The latter peak was delayed and increased with temperature elevation above ambient in both cultivars, indicating that elevated temperatures increased the flowering duration and the number of flowers differentiated lately. The relative frequency of early flower abscission and the proportion of flower abscission to pod abscission increased with temperature rise, indicating that the increase of pod set failure would be attributed to non-viable pollen or a reduction in photosynthate supply under high temperature

stress. Temperature elevation significantly decreased the pod set in hot summer (the period of flowering and pod setting) years, 2013 and 2015, but not in cool summer year, 2014 without a temperature \times cultivar interaction. Regardless of cultivars, pod number variations were more closely associated with pod set percentage variations rather than with flower number variations in hot summer years (2013 and 2015), whereas the opposite associations were observed in cool summer year (2014).

Using the boundary line analysis with quadratic and beta function, cardinal temperatures (T_{opt} , T_{max}) for pod set were estimated at 34.8, and 42.9°C for the Sinpaldalkong cultivar and 34.5, and 41.6°C for the Daewonkong cultivar, respectively. The temperature response of pod set was shown to be similar to the reported temperature response of pollen germination or pollen tube growth; suggesting that pod set would be strongly related to pollen viability. Although the temperature rise could lead to the increase of flower production, the temperature above 35°C would sharply decrease the pod set ratio in soybean. A boundary line analysis (using quantile regression) estimated optimum temperatures for seed number at 26.4 to 26.8°C (VE–R5) for both cultivars; the optimum temperatures (R5–R7) for single seed weight were estimated at 25.2°C for the Sinpaldalkong smaller-seeded cultivar, and at 22.3°C for the Daewonkong larger-seeded cultivar. The optimum growing season (VE–R7) temperatures for seed yield, which were estimated by

combining the two boundary lines for seed number and seed weight, were 26.4 and 25.0°C for the Sinpaldalkong and Daewonkong cultivars, respectively. Considering the current soybean growing season temperature, which ranges from 21.7 (in the north) to 24.6°C (in the south) in South Korea, and the temperature response of potential soybean yields, further warming of less than approximately 1°C would not become a critical limiting factor for soybean production in South Korea. However, further warming of more than 1°C may have adverse effects on the soybean yield from southern region in South Korea, and temperature above 35°C would cause severe damage to the formation of pod number in soybean.

Keywords: Soybean, Temperature, Phenology, Flowering, Pod setting, Yield

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GENERAL INTRODUCTON

Soybeans (*Glycine max* L. Merr.) are native to East Asia including Korea, and have been adapted and cultivated long ago (Singh, 2010). Soybean seeds have been utilized as not only a food source for human but also a feed for livestock due to their high protein and oil content (Hartman et al., 2011). Soybeans are utilized in various products including tofu, soy sauce, bean paste, soybean oil, and soy milk, etc. Soybean is one of the most important crops worldwide in terms of area harvested and production, and its demand is increasing (Masuda and Goldsmith, 2009).

Increasing air temperature is an important indicator of climate change. Korea has experienced warming approximately twice as fast as the average rate of global warming, and the country is expected to experience continued warming in the future (Korea Meteorological Administration, 2015). The average surface temperature of the Korean peninsula is projected to rise by 3.0 to 5.7°C by the end of this century, under RCP 4.5 (greenhouse gas emissions peak around 2040) and 8.5 scenarios (greenhouse gas emissions continue to rise), respectively (Vachani and Usmani, 2014); warming is predicted to increase the average global surface temperature from 2.5 to 4.6°C, under the same scenarios (Stocker et al., 2014). Furthermore, hot extremes will occur

more frequently and intensely. Temperature rise due to global warming is likely to impact on future agricultural production, including soybean (Mall et al., 2004; Hatfield et al., 2011; Van Alfen, 2014).

Temperature is an important environmental factor that affects the development, growth, and yield of soybeans (Norman, 2012; Sengar and Sengar, 2014). Development rates accelerate when temperatures increase from below the optimum or decrease from above the optimum temperature (Hatfield et al., 2011). Optimum temperatures were reported to be 30.0°C for vegetative development (Hesketh et al., 1973), 25.0-29.0°C for reproductive development (Boote et al., 1998). The maximum vegetative biomass of soybeans was achieved at temperatures ranging from 25.0 to 37.0°C (Grimm et al., 1994; Boote et al., 1997). Reproductive growth stages are more sensitive to temperature than vegetative growth in soybean. The reproductive processes are impeded by unfavorable temperature conditions, which can lead to lower seed yield (Ferris et al., 1998; Thanacharoenchanaphas and Rugchati, 2011; Siebers et al., 2015). The optimum temperatures for single seed growth (23.5°C) and seed size (23°C) of soybeans were reported by Egli and Wardlaw (1980). The soybean crop growth model CROPGRO-Soybean predicted that the highest grain yield would occur between the temperatures of 22.0 to 24.0°C, and a progressive yield decrease would result from plummeting temperatures (Boote et al., 1997; Boote et al., 1998).

Increasing temperatures associated with climate change impacts on soybean seed production. Elevated temperatures caused lower net photosynthetic carbon assimilation and biomass production, which were attributed to declines in stomatal conductance and intercellular carbon dioxide and resulted in yield reduction (Ruiz-Vera et al., 2013). Yield responses to temperature elevation (above current levels) vary according to different climate regions. In the southern United States, where growing season temperatures range from 25.0 to 27.0°C, soybean yields were predicted to decline with a temperature increase to 26.7°C. Conversely, soybean yields would increase in the upper Midwestern United States, with a growing season temperature of 22.5°C (Hatfield et al., 2008). Increasing air temperature significantly reduced pod number, seed number, seed size, and seed yield in temperature gradient chambers that maintained up to approximately 3.0°C higher than 26.4°C, which is typical of growing season air temperatures in warm parts of Japan (Takarindua et al., 2013). However, the numbers of pods and seeds, and seed yield increased at elevated temperatures in Japanese regions, with a mean growing season temperature of approximately 21.0°C (Kumagai and Sameshima, 2014). Temporary exposure to extreme temperatures can also affect yield-determining processes. Short heat stress (6°C above ambient) only for 3 days reduced photosynthesis and increased oxidative stress that can cause yield loss in soybean under field condition

(Siebers et al., 2015). Pollen viability (seed set) is decreased by exposure to instantaneous temperatures above 30.0°C in vitro (Salem et al., 2007). Understanding how yield components respond to elevated temperatures is important for predicting soybean yields.

The advantage of pot experiments in the greenhouse is that environmental factors determining yield can be more easily controlled than in the field (Sage and Kubien, 2007). Although the absolute values related to growth and yield can be limited by pot size, responses to environmental factors are similar across pot and field experimental data, regardless of soil volume (Lecoeur and Sinclair, 1996; Ray and Sinclair, 1998; Tubiello et al., 2007). In the controlled experiments, day/night temperatures are generally fixed during the crop growth period, while temperatures in the field change diurnally and seasonally. Diurnal and seasonal temperature variations in our temperature-controlled greenhouses are very close to field condition. Thus, temperature-controlled greenhouses can be useful to assess the impact of global warming on crop growth.

The mean air temperature of the soybean growing season (VE–R7) during the last ten years ranged from 21.7°C (northern region) to 24.6°C (southern region) in South Korea. According to the reported optimum temperature range of 22.0 to 24.0°C (Boote et al., 1997; Boote et al., 1998), current soybean growing season temperatures are close to the optimum. Thus, further warming

is anticipated to exceed the reported optimum temperature range and decrease soybean yields in southern regions of South Korea. However, few experimental studies have documented the impacts of global warming on soybean growth and yield in South Korea. Therefore, this study aimed (1) to examine the effects of elevated air temperatures on the phenology, flowering, pod setting, yield components, and yield, (2) to estimate the optimum temperatures for pod setting, seed number, seed weight, and seed yield, and (3) to evaluate the impacts of global warming on production of soybeans in a temperate region of South Korea.

LITERATURE REVIEW

Phenology responses of soybean to temperature

The developmental stages in soybean were established by Fehr et al. (1971). Vegetative stages are determined by counting the number of nodes on the main stem, beginning with the unifoliolate node. Reproductive stages R1 and R2 are based on flowering, R3 and R4 on pod development, R5 and R6 on seed development, and R7 and R8 on maturation. As soybean is short-day plant, the development rate is primarily affected by photoperiod and modified by growth temperature (Summerfield and Wilcox, 1978; Cregan and Hartwig, 1984; Ephrath and Hesketh, 1991; Setiyono et al., 2007). Development rates accelerate when temperatures increase from below the optimum or decrease from above the optimum temperature (Hatfield et al., 2011). Optimum temperatures were reported to be 30.0°C for vegetative development (Hesketh et al., 1973) and 25.0-29.0°C for reproductive development, without significant differences between cultivars of differing maturity. (Grimm et al., 1994; Boote et al., 1998). The optimum temperatures for early and late reproductive stages are 26.0-30.0°C and 26.0-34.0°C in CROPGRO-Soybean (Jones et al., 2010), whereas 25.0 and 21.5°C in SOYDEV, respectively (Setiyono et al., 2007).

Flowering and pod setting responses of soybean to temperature

There are three racemes at each leaf axil in soybean, and it takes 4 to 10 days for all flowers to open on a single raceme, thus flowers continue to open for two or more weeks (Wiebold, 2012). High night temperatures increased the number of flowers on the secondary and tertiary racemes (Zheng et al., 2002). However, reproductive growth stages are more sensitive to temperature than vegetative growth in soybean. Temperatures above 33/28°C (day/night) during the flowering and pod set period reduce seed yield, regardless of the temperature during the seed filling period (Egli and Wardlaw, 1980). High temperature stress during the early reproductive phases of soybean causes pod and seed set failure resulted from abortion and abscission of reproductive organs (Djanaguiraman et al., 2011). The number of fertile pods is reported to be associated with the numbers of aborted and abscised flowers and pods, which occur due to heat stress during the R1–R5 period (Puteh et al., 2013). Abortion and abscission of flowers, pods, and seeds can occur due to a reduction in photosynthate supply during the flowering and pod set growth periods (Egli and Bruening, 2006; Ruiz-Vera et al., 2013; Siebers et al., 2015). Pod and seed set failure under high temperature stress can be a result of decreased pollen viability or stigma receptivity (Prasad et al., 2002; Prasad et al., 2006; Snider et al., 2009). Lower pod and seed set are related to non-viable pollen, unsuccessful anther dehiscence, and a reduction in the penetration of

the pollen tube into the stigma (Schoper et al., 1987; Gross and Kigel, 1994; Sato et al., 2002; Hall, 2004). Salem et al. (2007) reported that cardinal temperatures (T_{min} , T_{opt} , and T_{max}) for pollen germination and pollen tube growth of soybeans were 13.2, 30.2, and 47.2°C and 12.1, 36.1, and 47.0°C, respectively. Reproductive organs are vulnerable to short events of high temperatures during the flowering phase (Reddy and Kakani, 2007). Soybean pollen viability is decreased by exposure to instantaneous temperatures above 30.0°C in vitro (Salem et al., 2007). Exposure to high temperatures of 30–35°C for few days can cause abscission and abortion of flower, pod, and seed, resulting in severe yield loss (Gross and Kigel, 1994; Prasad et al., 1999; Siddique et al., 1999).

Yield responses of soybean to temperature

The number of seeds and seed size are two main yield components of soybeans; the number of seeds is determined by the number of pods and number of seeds per pod (Woodworth, 2013). Soybean yield components are negatively correlated and temperature-dependent (Pandey and Torrie, 1973; Swank et al., 1987). For example, maximum seed size is determined genetically, whereas the actual seed size is affected by seed number and environmental conditions during seed filling (Sadras and Egli, 2008). Single seed weight decreased from its maximum value to compensate for the increase

in seed number per pot (Baker et al., 1989; Acquah, 2012). Soybean ovaries contain one to four ovules, and the number of seeds averages between two and three per pod (Whigam, 1983). The number of seeds per pod is reduced by seed set failure, due to unfertilized ovules and the abortion of fertilized ovules from environmental stress, such as high temperatures during flowering and early seed developmental stages (Whigam, 1983; Tischner et al., 2003; Puteh et al., 2013).

The optimum temperatures for soybean growth and yield differed from the optimum temperatures for plant development. The maximum vegetative biomass of soybeans was achieved at temperatures ranging from 25.0 to 37.0°C (Boote et al., 1997). Compared with the optimum temperature for vegetative growth, the optimum temperatures for single seed growth (23.5°C) and seed size (23°C) of soybeans were lower as reported by Egli and Wardlaw (1980). The daily mean temperature of approximately 25.0°C during the early reproductive stages favored a higher pod set than temperatures below 25.0°C (Lawn and Hume, 1985); temperatures exceeding a day temperature of 30.0°C resulted in decreased pod numbers (Gibson and Mullen, 1996).

Several studies have examined the impacts of increasing temperatures associated with climate change on soybean seed production. Elevated temperatures caused lower net photosynthetic carbon assimilation and biomass production, which were attributed to declines in stomatal conductance

and intercellular carbon dioxide and resulted in yield reduction (Ruiz-Vera et al., 2013). Yield responses to temperature elevation (above current levels) vary according to different climate regions. In the southern United States, where growing season temperatures range from 25.0 to 27.0°C, soybean yields were predicted to decline with a temperature increase to 26.7°C. Conversely, soybean yields would increase in the upper Midwestern United States, with a growing season temperature of 22.5°C (Hatfield et al., 2008). Increasing air temperature significantly reduced pod number, seed number, seed size, and seed yield in temperature gradient chambers that maintained up to approximately 3.0°C higher than 26.4°C, which is typical of growing season air temperatures in warm parts of Japan (Takarindua et al., 2013). However, the numbers of pods and seeds, and seed yield increased at elevated temperatures in Japanese regions, with a mean growing season temperature of approximately 21.0°C (Kumagai and Sameshima, 2014). The soybean crop growth model CROPGRO-Soybean predicted that the highest grain yield would occur between the temperatures of 22.0 to 24.0°C, and a progressive yield decrease would result from plummeting temperatures (Boote et al., 1997; Boote et al., 1998).

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CHAPTER I. Phenology and Seed Yield Performance of Soybean Grown at Elevated Temperatures in a Temperate Region

Abstract

Increased temperature means and fluctuations associated with climate change are predicted to exert profound effects on the seed yield of soybean. We conducted an experiment to evaluate the impacts of global warming on the phenology and yield of two determinate soybean cultivars in a temperate region (37.27°N, 126.99°E; Suwon, South Korea). These two soybean cultivars, Sinpaldakong [maturity group (MG) IV] and Daewonkong (MG VI), were cultured on various sowing dates within a four-year period, under no water-stress conditions. Soybeans were kept in greenhouses controlled at the current ambient temperature (AT), AT+1.5°C, AT+3.0°C, and AT+5.0°C throughout the growth periods. Growth periods (VE–R7) were significantly prolonged by the elevated temperatures, especially the R1–R5 period. Cultivars exhibited no significant differences in seed yield at the AT+1.5°C and AT+3.0°C treatments, compared to AT, while a significant yield reduction was observed at the AT+5.0°C treatment. Yield reductions resulted from

limited seed number, which was due to an overall low numbers of pods and seeds per pod. Heat stress conditions induced a decrease in pod number to a greater degree than in seed number per pod. Individual seed weight exhibited no significant variation among temperature elevation treatments; thus, seed weight likely had negligible impacts on overall seed yield. A boundary line analysis (using quantile regression) estimated optimum temperatures for seed number at 26.4 to 26.8°C (VE–R5) for both cultivars; the optimum temperatures (R5–R7) for single seed weight were estimated at 25.2°C for the Sinpaldalkong smaller-seeded cultivar, and at 22.3°C for the Daewonkong larger-seeded cultivar. The optimum growing season (VE–R7) temperatures for seed yield, which were estimated by combining the two boundary lines for seed number and seed weight, were 26.4 and 25.0°C for the Sinpaldalkong and Daewonkong cultivars, respectively. Considering the current soybean growing season temperature, which ranges from 21.7 (in the north) to 24.6°C (in the south) in South Korea, and the temperature response of potential soybean yields, further warming of less than approximately 1°C would not become a critical limiting factor for soybean production in South Korea.

Keywords: Soybean, Temperature, Phenology, Yield, Yield components

Introduction

Soybeans (*Glycine max* L. Merr.) are intensely cultivated worldwide due to the seeds containing high levels of oil and protein (Brek, 1992; Hartman et al., 2011). Soybeans are native to Northeast Asia, including Korea (Qiu and Chang, 2010), and are utilized in various products including tofu, soy sauce, bean paste, soybean oil, and soy milk.

Korea has experienced warming approximately twice as fast as the average rate of global warming, and the country is expected to experience continued warming in the future (Korea Meteorological Administration, 2015). The average surface temperature of the Korean peninsula is projected to rise by 3.0 to 5.7°C by the end of this century, under RCP 4.5 and 8.5 scenarios, respectively (Vachani and Usmani, 2014); warming is predicted to increase the average global surface temperature from 2.5 to 4.6°C, under the same scenarios (Stocker et al., 2014). The rise in temperature is expected to have substantial effects on the development and growth of crops, including soybeans (Hatfield and Walthall, 2014).

Temperature is an important environmental factor that affects the development, growth, and yield of soybeans. Development rates accelerate when temperatures increase from below the optimum or decrease from above

the optimum temperature (Hatfield et al., 2011). Optimum temperatures were reported to be 30.0°C for vegetative development (Hesketh et al., 1973) and 26.0°C for anthesis (Boote et al., 1998). In addition, the optimum temperature for reproductive development was reported to vary between 25.0 and 29.0°C, without significant differences between cultivars of differing maturity. However, a slight increasing trend was observed from V1 to R7 (Grimm et al., 1994). The optimum temperatures for soybean growth and total yield differed from the optimum temperatures for plant development. The maximum vegetative biomass of soybeans was achieved at temperatures ranging from 25.0 to 37.0°C (Boote et al., 1997). The number of seeds and seed size are two main yield components of soybeans; the number of seeds is determined by the number of pods and number of seeds per pod (Woodworth, 2013). Soybean yield components are negatively correlated and temperature-dependent (Pandey and Torrie, 1973; Swank et al., 1987). Compared with the optimum temperature for vegetative growth, the optimum temperatures for single seed growth (23.5°C) and seed size (23°C) of soybeans were lower as reported by Egli and Wardlaw (1980). Temporary exposure to extreme temperatures can also affect yield-determining processes. Short heat stress (6°C above ambient) only for 3 days reduced photosynthesis and increased oxidative stress that can cause yield loss in soybean under field condition (Siebers et al., 2015). Pollen viability (seed set) is decreased by exposure to instantaneous temperatures

above 30.0°C in vitro (Salem et al., 2007). Understanding how yield components respond to elevated temperatures is important for predicting soybean yields.

Several studies have examined the impacts of increasing temperatures associated with climate change on soybean seed production. Elevated temperatures caused lower net photosynthetic carbon assimilation and biomass production, which were attributed to declines in stomatal conductance and intercellular carbon dioxide and resulted in yield reduction (Ruiz-Vera et al., 2013). Yield responses to temperature elevation (above current levels) vary according to different climate regions. In the southern United States, where growing season temperatures range from 25.0 to 27.0°C, soybean yields were predicted to decline with a temperature increase to 26.7°C. Conversely, soybean yields would increase in the upper Midwestern United States, with a growing season temperature of 22.5°C (Hatfield et al., 2008). Increasing air temperature significantly reduced pod number, seed number, seed size, and seed yield in temperature gradient chambers that maintained up to approximately 3.0°C higher than 26.4°C, which is typical of growing season air temperatures in warm parts of Japan (Tacarindua et al., 2013). In addition, temperature stress was induced by a daily maximum temperature and a minimal night temperature of 38.0 and 28.0°C, respectively. These temperature regimes resulted in the abscission of flowers and pods, and a low

pod set percentage (Djanaguiraman et al., 2011). However, the numbers of pods and seeds, and seed yield increased at elevated temperatures in Japanese regions, with a mean growing season temperature of approximately 21.0°C (Kumagai and Sameshima, 2014). The soybean crop growth model CROPGRO-Soybean predicted that the highest grain yield would occur between the temperatures of 22.0 to 24.0°C, and a progressive yield decrease would result from plummeting temperatures (Boote et al., 1997; Boote et al., 1998).

The mean air temperature of the soybean growing season (VE–R7) during the last ten years ranged from 21.7°C (northern region) to 24.6°C (southern region) in South Korea. According to the reported optimum temperature range of 22.0 to 24.0°C (Boote et al., 1997; Boote et al., 1998), current soybean growing season temperatures are close to the optimum. Thus, further warming is anticipated to exceed the reported optimum temperature range and decrease soybean yields in southern regions of South Korea. However, few experimental studies have documented the impacts of climate change on soybean growth and yield in South Korea. Therefore, this study aimed to examine the effects of elevated air temperatures on the phenology, yield components, and yield of two determinate soybean cultivars in a temperate region of South Korea.

Materials and Methods

Plant materials and growth conditions

Two determinate soybean cultivars, Sinpaldalkong (MG IV) and Daewonkong (MG VI) (Ha et al., 2009), were pot-cultured (15 cm in diameter, 40 cm in height) in four sunlit temperature-controlled greenhouses ($W \times D \times H$; $5.0 \times 14.0 \times 3.5$ m) at the Experimental Farm of Seoul National University, Suwon, South Korea ($37^{\circ}16'N$, $126^{\circ}59'E$). To establish a soybean canopy similar to field conditions, the pots were arranged in four rows, where plants and rows were spaced 15 and 45 cm apart, respectively. Only the inner two rows were used for observing phenology, seed yield, and yield-related traits. A pot experiment was conducted, rather than a field experiment, to control soil water more precisely (Sage and Kubien, 2007). Although the absolute growth and yield performances tend to differ between field and pot experiments, the responses to environmental variables, such as temperature and soil water, are reported to exhibit similar trends (Lecoeur and Sinclair, 1996; Tubiello et al., 2007). Greenhouses were controlled to targets of current ambient air temperature (AT), AT+1.5°C, AT+3.0°C, and AT+5.0°C using heating and ventilation systems linked to a CR1000 Measurement and Control Datalogger (Campbell Scientific Inc., Logan, UT, USA). In addition, the greenhouses

were covered by polyethylene film with solar transmittance of approximately 60% (2009, 2013, and 2014) or 85% (2015). Sidewalls were removed from the AT treatment greenhouse to maintain outdoor ambient temperatures. Loam soil with a pH of 6.6, soil organic matter of 1.9%, and CEC of 15.4 cmol(+)/kg was utilized in the experiments, and chemical fertilizers were applied to each pot, which contained 0.08, 0.08, and 0.09 g of N, P₂O₅, and K₂O, respectively. The Sinpaldalkong cultivar was sown on: May 31, 2009; June 15, 2009; June 15, 2013; June 30, 2013; May 30, 2014; June 20, 2014; and June 15, 2015. The Daewonkong cultivar was sown on: May 31, 2009; June 15, 2009; June 20, 2014; July 11, 2014; and June 20, 2015. After emergence from the soil, the plants were thinned to one (2013, 2014, and 2015) or two (2009) plants per pot, and then exposed to no water-stress conditions by sub-irrigation. Weeding and pesticide applications were carried out when necessary.

Measurements of phenology, yield, and weather

The developmental stages, as described by Fehr et al., were surveyed every two to three days, and then the following was recorded: date of emergence (VE), beginning of flowering (R1), beginning of seed filling (R5), and physiological maturity (R7). The number of newly opened flowers was recorded every day during the flowering period from four pots only in 2015. Plant components observed above ground were harvested at maturity (R8)

from five pots in 2013, and from eight pots in 2009, 2014, and 2015. The numbers of fertile pods and seeds, total fertile seed weight, and seed moisture content of each pot were measured to calculate the yield and components per pot. The single seed weight and seed yield per pot were adjusted to a moisture content of 15%. Air temperature and solar radiation values in each greenhouse were recorded (per minute) using a CR1000 data logger equipped with a platinum resistor thermoprobe housed in a naturally ventilated, six-plate radiation shield (Campbell Scientific), and a pyranometer (Kipp & Zonen, Delft, Netherlands), respectively. Outdoor air temperature and solar radiation values were obtained from the Suwon Meteorological Station, which is located approximately 0.5 km from the experimental greenhouses.

Data analysis

Outliers identified by median quantile regression (with a cut-off value of 3.0) in scatter plots of seed yield and yield components versus mean air temperature, during the specific growth period of each cultivar, were eliminated. Development rates were calculated as the inverse of the number of days between two developmental stages. Pod set ratio of each pot was determined by dividing the number of fertile pods at maturity by the total number of opened flowers. To evaluate the effects of elevated temperature on phenology, seed yield, and yield components, analysis of variance (ANOVA)

and Duncan's multiple range test for significant differences between the treatment means were performed. A correlation and path analysis (Covariance Analysis of Linear Structural Equations: CALIS) was conducted to identify relationships between seed yield and its components, and to determine the direct contribution of yield components and yield-related components to yield and yield components, respectively. A boundary line analysis (Webb, 1972), which can exclude experimental errors and the effects of limiting factors (Elliott and de Jong, 1993), was employed to delineate the responses of seed yield components to mean air temperatures measured during: the VE–R5 period to calculate seed number per pot, the R5–R7 period to calculate single seed weight, and the VE–R7 period to calculate seed yield. The boundary line parameters of seed number and single seed weight were estimated by a quadratic quantile regression (95th percentile). The boundary line response of potential yield to whole growing season temperature was obtained by combining those two boundary lines for yield components. Furthermore, mean growing season temperatures were calculated as the average of the mean temperature of VE–R5 and R5–R7 weighted by the durations of the two periods. Statistical analyses were performed using the statistical analysis software SAS Version 9.4 (SAS Institute Inc., Cary, NC, USA).

Results

Meteorological conditions

The four-month mean air temperature in the AT ranged from 23.5 to 25.1°C during the experiments; the four-month mean temperatures of AT+1.5°C, AT+3.0°C, and AT+5.0°C were 1.5–1.8°C, 2.7–3.0°C, and 4–4.6°C higher than the AT, respectively (Table I-1). The monthly mean air temperatures in the ATs throughout the experimental periods were similar to outdoor air temperatures, with any observed differences ranging within $\pm 1.0^\circ\text{C}$. Figure I-1 presents the daily changes in mean air temperatures within the temperature-controlled greenhouses during the 2013 growing season. Differences between the temperature treatments were consistently maintained during the growing seasons.

Table I-1. Monthly mean air temperature and solar radiation values in the experimental greenhouses that were controlled to target temperatures of AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C during the growing seasons over the four-year period.

		June	July	August	September	Four-month mean
Air temperature (°C)						
2009	Outside	22.1	24.2	25.7	21.6	23.4
	AT	22.1	24.2	25.8	21.6	23.5
	AT+1.5°C	23.9	26.0	27.5	23.3	25.2
	AT+3.0°C	25.0	27.0	28.6	24.6	26.3
	AT+5.0°C	26.4	28.7	30.6	26.4	28.1
2013	Outside	23.5	25.5	27.4	21.7	24.6
	AT	23.9	25.8	27.7	21.9	24.8
	AT+1.5°C	25.6	27.5	29.5	23.5	26.6
	AT+3.0°C	26.8	28.7	30.7	24.8	27.8
	AT+5.0°C	28.8	30.3	31.9	26.3	29.2
2014	Outside	22.9	25.6	24.7	21.8	23.8
	AT	22.9	25.6	24.7	21.8	23.8
	AT+1.5°C	24.6	27.2	26.1	23.3	25.3
	AT+3.0°C	25.6	28.4	27.3	24.5	26.5
	AT+5.0°C	27.2	29.9	28.2	25.8	27.8
2015	Outside	23.1	25.5	26.2	22.1	24.2
	AT	24.0	26.3	27.1	22.8	25.1
	AT+1.5°C	25.4	27.7	28.5	24.2	26.5
	AT+3.0°C	26.9	29.2	29.0	25.5	27.7
	AT+5.0°C	28.8	31.0	31.6	27.3	29.7
Solar radiation (MJ/m ² ·day)						
2009	Inside the greenhouse	11.7	9.8	10.4	10.1	10.5
2013		11.5	6.0	9.4	8.4	8.8
2014		11.0	9.4	7.7	8.1	9.0
2015		14.5	11.5	11.4	11.3	12.2

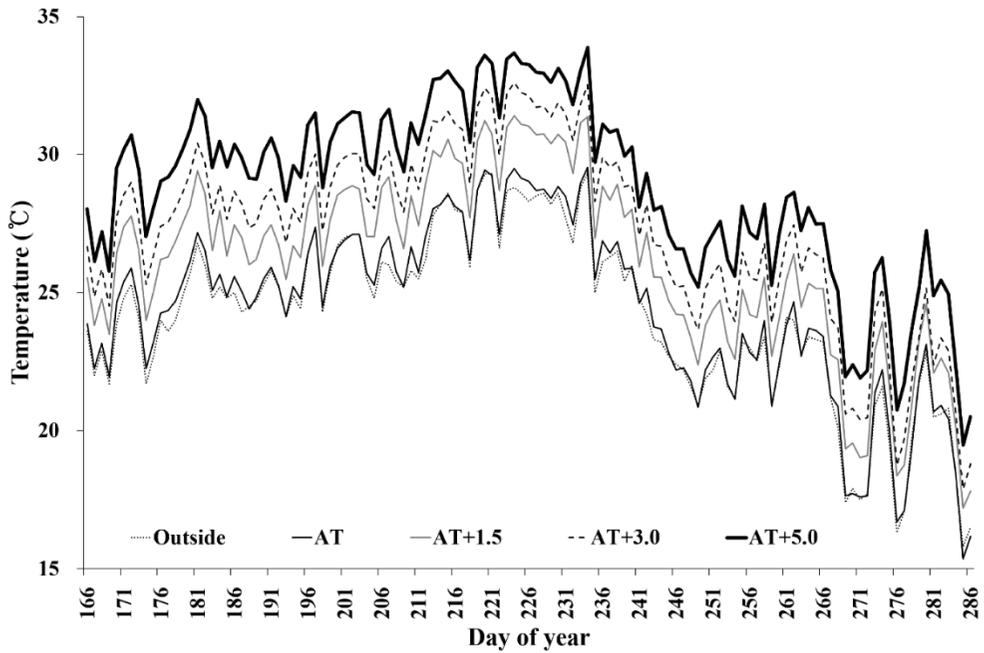


Figure I-1. Daily mean air temperatures in the experimental greenhouses that were controlled to target temperatures of AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C during the growing seasons. Only data collected in 2013 are presented as an example of seasonal temperature variation. Dotted gray, continuous black, continuous gray, dashed black, and bold black lines indicate the temperatures of outside, AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C, respectively.

Phenology responses to elevated temperature

Phenophase durations of the soybean cultivars planted during the typical sowing season (mid-June) under different temperature treatments are shown in Table I-2. The Sinpaldalkong mid-maturing cultivar had a significantly shorter growing period than the Daewonkong late-maturing cultivar. According to ANOVA, above ambient temperatures had no significant effects on the duration of emergence (VE) to flowering (R1). Although the R1–R5 and R5–R7 periods did not differ significantly among the temperature treatments, the post-anthesis period (R1–R7) was significantly prolonged by temperature elevation, without the temperature \times cultivar interaction. Compared with the AT, the R1–R7 period of the AT+5.0°C treatment was 4 and 7 days longer for the Sinpaldalkong and Daewonkong cultivars, respectively. Regardless of cultivar type, the rate of development to flowering exhibited a quadratic response to temperature, with an optimum temperature of approximately 26.7°C (Figure I-2). The development rate during the R1–R5 period decreased linearly with a rise in temperature from 25.2 to 32.3°C. The slopes of the regression lines between the mean temperature and the development rate during the R5–R7 period were not significant in both cultivars, indicating that the development rate during seed filling was not affected by a temperature increase from 22.8 to 27.9°C in both cultivars.

Table I-2. Phenology responses of two determinate soybean cultivars with different maturity groups planted during the typical sowing season (mid-June) to temperature treatments that were controlled to target temperatures of AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C.

Cultivar and temperature treatment	Days between phenophases				
	VE–R1	R1–R5	R5–R7	R1–R7	VE–R7
Sinpaldalkong (MG IV)					
AT	30.5	25.3	38.8	64.0b	94.5b
AT+1.5°C	29.8	26.3	38.8	65.0b	94.8b
AT+3.0°C	30.8	27.0	39.0	66.0b	96.8b
AT+5.0°C	31.5	28.8	39.5	68.3a	99.8a
Cultivar mean	30.6	26.8	39.0	65.8	96.4
Daewonkong (MG VI)					
AT	33.7	22.7	42.3	65.0b	98.7b
AT+1.5°C	33.0	23.7	45.0	68.7ab	101.7ab
AT+3.0°C	34.3	24.3	45.0	69.3ab	103.7ab
AT+5.0°C	34.7	26.0	46.0	71.7a	106.3a
Cultivar mean	33.9	24.2	44.6	68.7	102.6
Temp. treatment mean					
AT	31.9	24.1	40.3	64.4c	96.3c
AT+1.5°C	31.4	25.1	41.4	66.6bc	97.7bc
AT+3.0°C	32.3	25.9	41.6	67.4b	99.7b
AT+5.0°C	32.9	27.6	42.3	69.7a	102.6a
ANOVA results					
Temperature (T)	ns	ns	ns	***	***
Cultivar (C)	***	**	**	**	***
T × C	ns	ns	ns	ns	ns

Values followed by the same letters within a column for each cultivar and temperature treatment mean were not significantly different at the confidence level of 5%, as determined by Duncan's multiple range tests. ***, **, and ns denote significance at $p < 0.001$, $p < 0.01$, and not significant ($p > 0.05$), respectively.

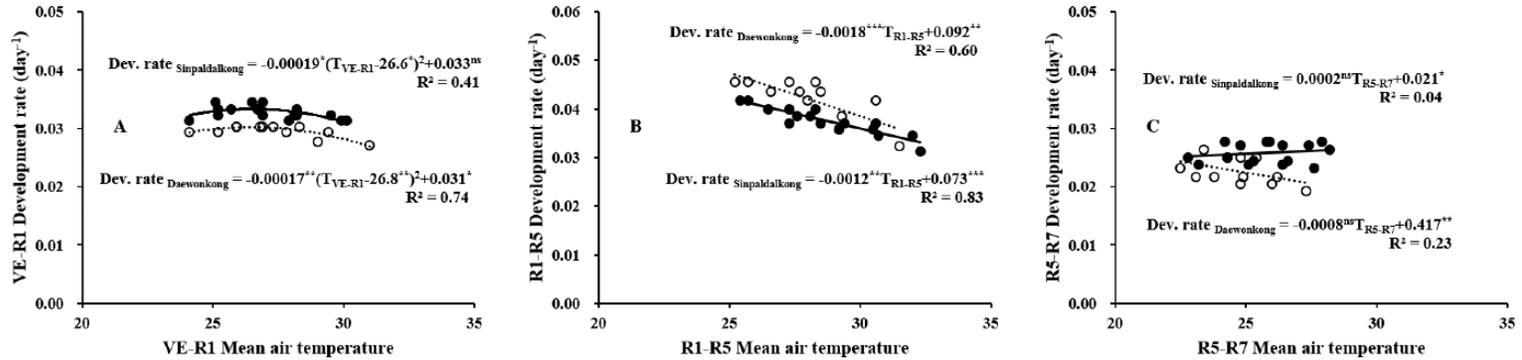


Figure I-2. Temperature responses of development rates during the VE–R1 (A), R1–R5 (B), and R5–R7 (C) periods of the Sinpaldalkong (filled circles and continuous lines) and Daewonkong (open circles and dashed lines) cultivars planted during the typical sowing season (mid-June). Plotted points represent the mean values of the temperature treatments during each growing season. ***, **, *, and ns denote significance of the regression coefficients at $p < 0.001$, $p < 0.01$, $p < 0.05$, and not significant ($p > 0.05$), respectively.

Yield and yield component responses to elevated temperatures

Seed yield and yield components of the Sinpaldalkong and Daewonkong cultivars affected by the temperature elevation treatments (planted during the typical sowing season) are shown in Table I-3. The Sinpaldalkong cultivar had a smaller seed size and a higher seed number than the Daewonkong cultivar. There were no significant temperature \times cultivar interactions for seed yield and yield components. The cultivars exhibited no significant differences in seed yield from the AT+1.5°C and AT+3.0°C treatments, compared with the AT, but a significant yield reduction was observed for the AT+5.0°C treatment. Pod number, number of seeds per pod, and number of seeds per pot increased with temperature increases of 3.0°C, 1.5°C, and 3.0°C above ambient temperature, respectively; all numbers decreased with further temperature elevation. Single seed weight tended to decrease slightly with increases in temperature; however, no significant differences were detected between the different temperature treatments.

Table I-3. Responses of seed yield and yield components to temperature treatments that were controlled to target temperatures of AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C in two determinate soybean cultivars with different maturity group planted during the typical sowing season (mid-June).

Cultivar and temperature treatment	Pod number (pot ⁻¹)	Seed number (pod ⁻¹)	Seed number (pot ⁻¹)	Single seed weight (mg)	Seed yield (g pot ⁻¹)
Sinpaldalkong (MG IV)					
AT	84.1a	2.07ab	174a	196	33.4a
AT+1.5°C	85.3a	2.11a	180a	187	33.0a
AT+3.0°C	95.3a	1.97b	186a	184	33.8a
AT+5.0°C	67.2b	1.84c	130b	194	24.7b
Cultivar mean	81.0	1.99	163	191	30.5
Daewonkong (MG VI)					
AT	71.5b	1.87a	134b	267	34.7ab
AT+1.5°C	81.4a	1.89a	155a	255	38.0a
AT+3.0°C	84.1a	1.85ab	155a	249	37.2a
AT+5.0°C	68.9b	1.79b	127b	249	32.0b
Cultivar mean	75.6	1.85	141	255	35.1
Temp. treatment mean					
AT	78.3ab	1.98ab	156a	228	34.0a
AT+1.5°C	83.5a	2.01a	168a	218	35.3a
AT+3.0°C	90.1a	1.91b	172a	214	35.4a
AT+5.0°C	68.0b	1.81c	129b	219	28.0b
ANOVA results					
Temperature (T)	**	***	***	ns	**
Cultivar (C)	ns	***	**	***	**
T × C	ns	ns	ns	ns	ns

Values followed by the same letters within a column for each cultivar and temperature treatment mean were not significantly different at a confidence level of 5%, as determined by Duncan's multiple range tests. ***, **, and ns denote significance at $p < 0.001$, $p < 0.01$, and not significant ($p > 0.05$), respectively.

Correlations between seed yield and yield components in two determinate soybean cultivars, Sinpaldalkong and Daewonkong, are presented in Figure I-3. Seed yield showed highly significant positive correlations ($r = 0.92^{***}$) with seed numbers per pot in both cultivars; no significant correlations with single seed weight were observed. Seed number per pot showed highly significant positive correlations ($r = 0.86^{***}$ and 0.94^{***}) with pod numbers per pot in the Sinpaldalkong and Daewonkong cultivars, respectively; a significantly positive correlation with the number of seeds per pod was observed only for the Sinpaldalkong cultivar ($r = 0.36^{***}$). Single seed weight showed significantly negative correlations ($r = -0.21^{***}$ and -0.54^{***}) with seed number per pot for the Sinpaldalkong and Daewonkong cultivars, respectively.

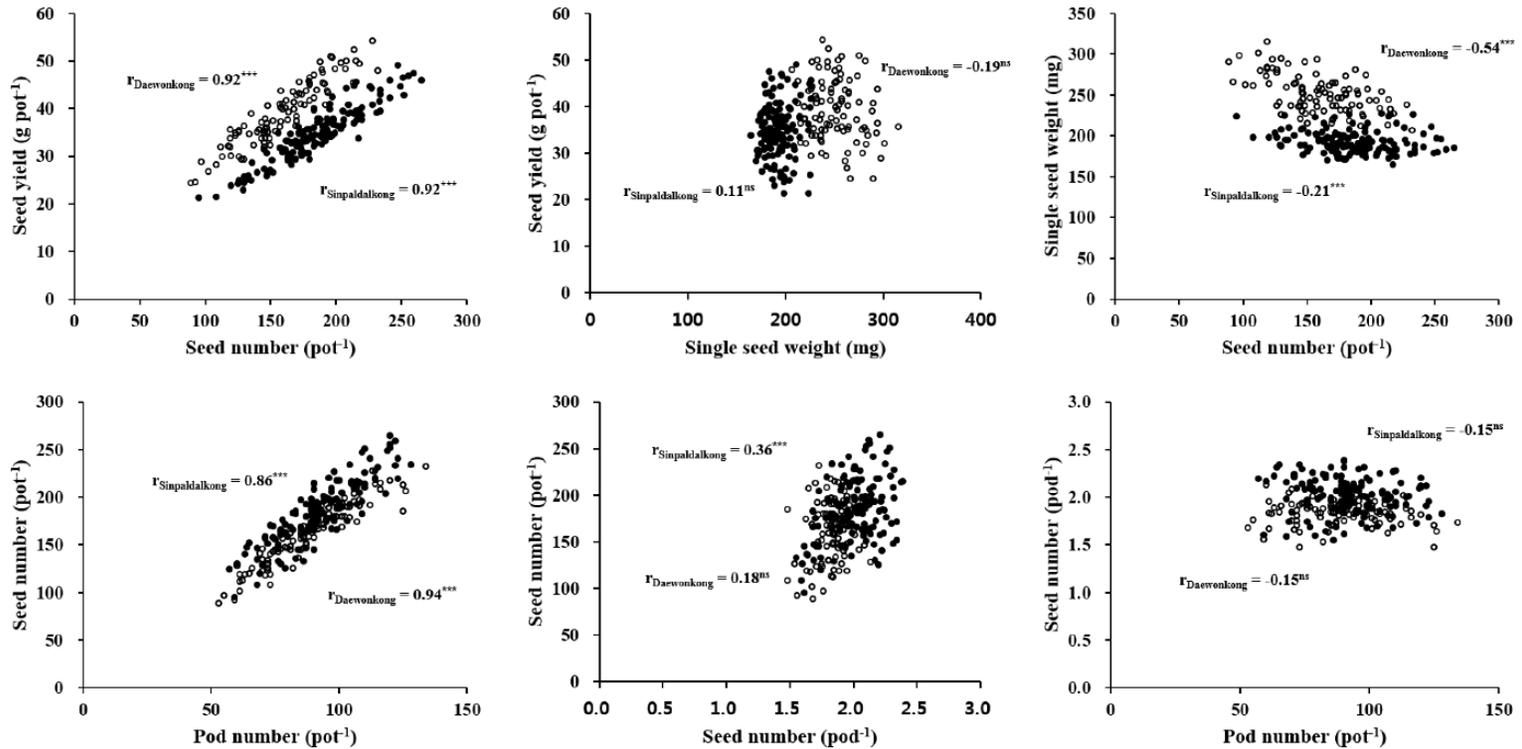


Figure I-3. Correlations between seed yield and yield components of the Sinpaldalkong (filled circles) and Daewonkong (open circles) cultivars grown under elevated temperature conditions with different sowing dates over a four-year period.

*** and ns denote significance at $p < 0.001$ and not significant ($p > 0.05$), respectively.

Path analyses were conducted according to the predetermined causal relationships between seed yield and yield components (Figure I-4). Regardless of cultivar type, the seed yield variation was more closely associated with seed number per pot, rather than with the single seed weight. Pod number per pot showed significant association with the variation in seed number per pot, rather than with the seed number per pod. Pod number exerted negligible effects on the seed number per pod. Furthermore, the seed number per pot negatively affected single seed weight.

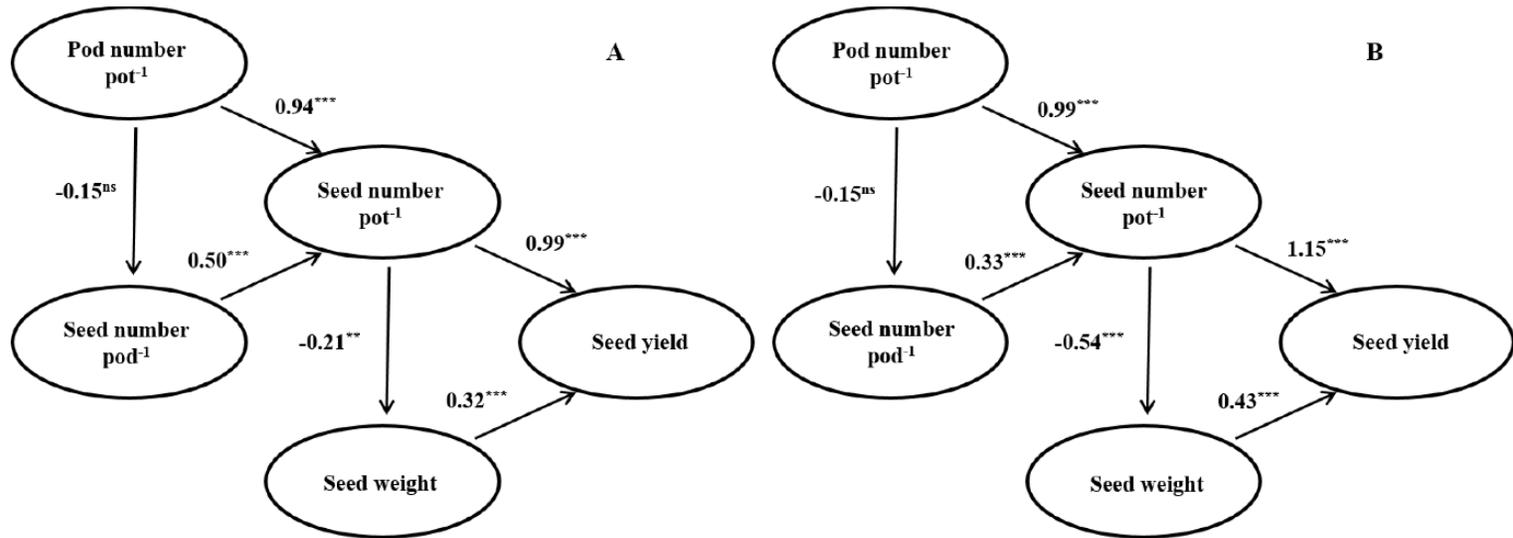


Figure I-4. Path diagram: the direct contribution of yield components to yield, pod number per pot and seed number per pod to seed number per pot, and seed number per pot to single seed weight in two soybean cultivars, Sinpaldalkong (A) and Daewonkong (B), grown under elevated temperature conditions with different sowing dates over a four-year period. ^{***}, ^{**}, and ns denote significance at $p < 0.001$, $p < 0.01$, and not significant ($p > 0.05$), respectively.

Boundary line response of the yield and yield components to temperature

Temperature responses of plant growth and development are characterized by cardinal temperatures: minimum, optimum, and maximum temperatures. Cardinal temperatures vary among genotypes and growth stages, even within the same genotype. The boundary lines of seed number and single seed weight in relation to mean air temperature (during specific growth periods when those traits are determined) were well fitted to the quadratic equations, revealing an optimum temperature (Figure I-5). Seed number and single seed weight were well fitted to the mean a during the VE–R5 and R5–R7 periods, respectively. Optimum temperature ranges were estimated to be 26.8 and 26.4°C for seed number, and 25.2 and 22.3°C for single seed weight for the Sinpaldalkong and Daewonkong cultivars, respectively. Optimum temperatures for seed number were similar for both cultivars, whereas the optimum temperature for single seed weight was lower for the Daewonkong large-seeded cultivar than for the Sinpaldalkong cultivar. According to the boundary line response of potential seed yields to growing seasons (VE–R7), the optimum mean growing season temperature (which was established by combining the boundary responses of the two yield components) for the potential seed yield were estimated to be 26.2 and 25.0°C for the Sinpaldalkong and Daewonkong cultivars, respectively. The optimum temperature for seed yield was lower for the Daewonkong cultivar, due to the lower optimum temperature for single seed weight.

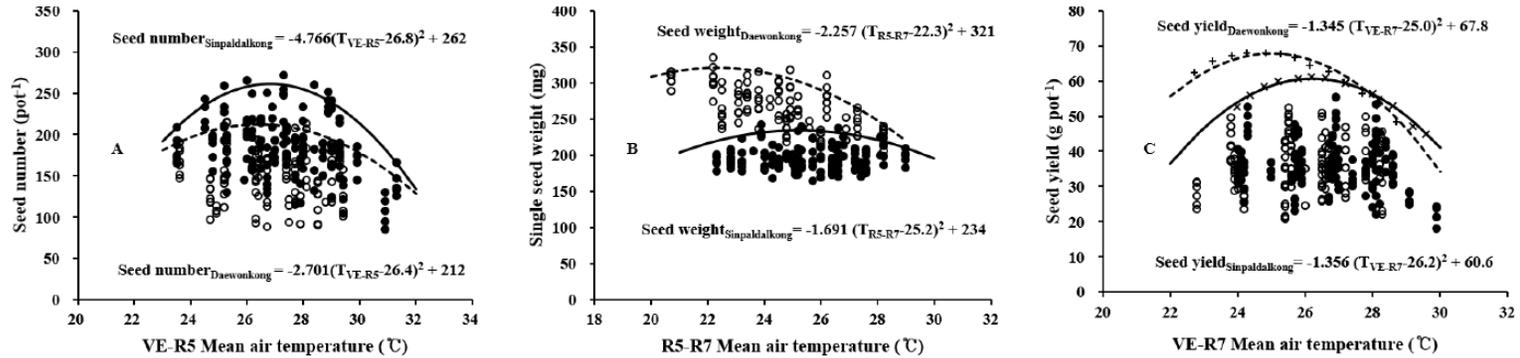


Figure I-5. Boundary line analysis of seed number (A), single seed weight (B), and seed yield (C) responses to mean air temperatures during specific growth periods for two determinate soybean cultivars, Sinpaldalkong and Daewonkong. Filled and open circles represent the data for the Sinpaldalkong and Daewonkong cultivars, respectively. In A and B, each continuous and dashed line indicates the 95% quantile regression lines for the Sinpaldalkong and Daewonkong cultivars, respectively. In C, the cross and plus symbols indicate potential yields, which were calculated by multiplying the boundary points of the seed number by the single seed weight for the Sinpaldalkong and Daewonkong cultivars, respectively. Continuous and dashed lines represent the quadratic regression lines of potential yield points for the Sinpaldalkong and Daewonkong cultivars, respectively.

Discussion

Phenology responses to elevated temperatures

Owing to the short-day nature of soybean plants, the onset of flowering (R1) is primarily affected by the photoperiod and temperature prior to flowering (Summerfield and Wien, 1980; Cregan and Hartwing, 1984; Ephrath and Hesketh, 1991; Setiyono et al., 2007). No significant effects on flowering time (VE–R1) were observed for the two cultivars, which were grown under similar photoperiod conditions and various temperature treatments (Table I-2). This indicates that temperature (VE–R1) variation within the range from 24.1 to 31.0°C, which is very close to the reported optimum temperature range of 25.0 to 29.0°C for flower induction in soybeans (Grimm et al., 1994; Boote et al., 1998), exerted negligible effects on the development rate during the growth period (Figure I-2). The developmental rate during this period exhibited a small quadratic response to mean growth temperatures, with a maximum rate occurring at approximately 27.0°C. The post-flowering duration (R1–R7) was lengthened with elevated temperatures, mainly due to the increased duration of R1–R5. Growth temperatures during the R1–R5 period increased with the temperature elevation treatments within the range of 25.2 to 32.3°C (Figure I-2); this surpassed the optimum

temperature (21.5°C) for the post-flowering (R1–R7) development rate (Setiyono et al., 2007). These supra-optimum temperatures should have slowed the post-flowering development increasingly with temperature elevation above ambient, which would have subsequently lengthened the post-flowering period (Figure I-2). Tacarindua et al. reported similar results, where increasing air temperatures had no effect on the flowering time (R1), but the pod set period (R1–R5) was significantly increased by the increasing air temperatures above 26.4°C (average temperature for the entire growing season) for MG IV cultivars.

Yield and yield component responses to elevated air temperatures

Pod number and seed number per pot increased with temperatures elevation up to 3.0°C above AT treatment, and then decreased with further temperature elevation (Table I-3). Seed number is determined by the number of pods and the number of seeds per pod (Woodworth, 2013). Increased flowering and pod set (R1–R5) periods (due to temperature increases) may lead to higher pod numbers in the AT+1.5°C and AT+3.0°C treatments. Increases in pod numbers are likely attributable to increased flower numbers, rather than the pod set ratio, as the flower number increased and the pod set ratio decreased with temperature elevation treatments above the outside ambient temperature in 2015 (Figure I-6). Temperatures were abnormally high

during the 2015 flowering period. The number of fertile pods is reported to be associated with the numbers of aborted and abscised flowers and pods, which occur due to heat stress during the R1–R5 period (Puteh et al., 2013). The daily mean temperature of approximately 25.0°C during the early reproductive stages favored a higher pod set than temperatures below 25.0°C (Lawn and Hume, 1985); temperatures exceeding a day temperature of 30.0°C resulted in decreased pod numbers (Gibson and Mullen, 1996). Considering the temperature conditions during the R1–R5 period, which ranged between 25.2 and 32.3°C in our study (Figure I-2), the high temperatures likely imposed adverse effects on pod sets at the AT+3.0°C and AT+5°C treatments. Seed number per pot and pod number per pot showed similar responses to temperature, as the variation in seed number per pot was predominantly determined by the pod number (Figure I-4).

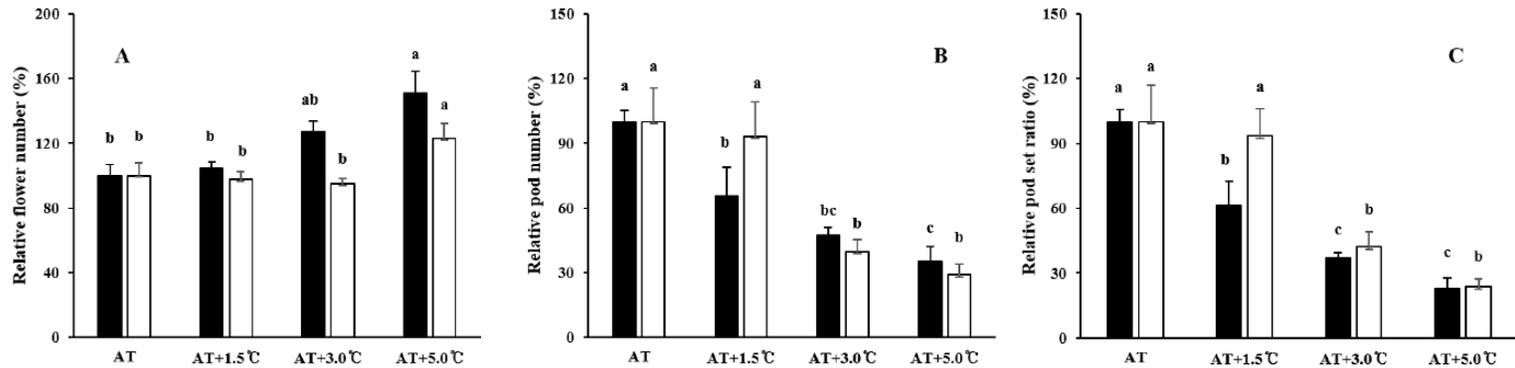


Figure I-6. The numbers of flowers (A), pods (B), and the pod set ratio (C) presented as relative values to the AT for the Sinpaldalkong (filled rectangles) and Daewonkong (open rectangles) cultivars, grown under four different temperature conditions in 2015. The error bars represent the standard error of the mean. The same letters above the bars within each cultivar indicate no significant differences between the temperature treatments, as determined by Duncan's multiple range test at a confidence level of 5%.

The number of seeds per pod significantly decreased with increases in temperatures above AT+1.5°C in our study. However, the number of seeds per pod was reported to be the yield component least affected by environmental conditions, including temperature (Baker et al., 1989); this number is regarded as a fixed value of the genotype coefficient in the CROPGRO-Soybean model (Boote et al., 2010). The number of seeds per pod is a function of the number of ovules per pod and the success of a seed set. Soybean ovaries contain one to four ovules, and the number of seeds averages between two and three per pod (Whigam, 1983). The number of seeds per pod is reduced by seed set failure, due to unfertilized ovules and the abortion of fertilized ovules from environmental stress, such as high temperatures during flowering and early seed developmental stages (Whigam, 1983; Tischner et al., 2003; Puteh et al., 2013).

Maximum seed size is determined genetically, whereas the actual seed size is affected by seed number and environmental conditions during seed filling (Sadras and Egli, 2008). The optimum temperature for single seed growth and size is reported to be approximately 23.0°C (Egli and Wardlaw, 1980). An increase in temperature above the reported optimum from 22.5 to 28.2°C during the R5–R7 period (Figure I-2) had no significant effects on single seed weight (Table I-3). This result would be ascribed to the compensation effect of seed number on single seed weight. As in Table I-3,

seed number per pot increased with temperatures elevation up to 3.0°C above AT treatment, and then decreased with further temperature elevation. For both cultivars, single seed weight showed significant negative correlations with seed number per pot (Figure I-3), indicating that single seed weight decreased from its maximum value to compensate for the increase in seed number per pot (Baker et al., 1989; Acquah, 2012).

Our results demonstrate that seed yield variations due to different temperature treatments, sowing dates, and experimental years were more closely associated with seed number variations, rather than with seed weight variations (Figures I-3 and I-4). Seed number had a strong association with the variation in pod number. The reproductive processes were impeded by high temperatures during early pod developmental stages, which led in lower seed yield despite a rapid physiological recovery from the heat stress (Siebres et al., 2015). Excluding the temperature elevation treatment of AT+5.0°C, our results revealed that a temperature increase within the range of 22.8 to 28.6°C (data not shown) during the whole growth period (VE–R7) had no significant effects on seed yield.

Boundary line responses of yield and yield components to temperature

Seed number and individual seed weight are two main yield components of soybeans (Woodworth, 2013). Optimum temperatures for seed number and seed weight were estimated using the boundary line analysis method first suggested by Webb, where it was frequently utilized for analyzing agronomic data obtained from field experiments where all factors could not be strictly controlled (Kim et al., 2001, Shatar and Mcbratney, 2004). The boundary line method involves fitting a line through the boundary points that appear in the uppermost section of the data scatter plot, as opposed to fitting regression lines through scattered data points. For a large data set, the boundary line is assumed to represent the maximum potential expression of a trait in response to a predictor variable, and in the absence of other limiting factors (Elliott and de Jong, 1993). That is, the boundary lines in Figure I-5 represent the potential maximum responses of yield components and yield to the mean temperatures during the phenophases (when those traits are determined). The estimated optimum temperatures are also the temperatures at which maximum expression is expected, in the absence of other limiting factors.

Seed number is affected by flower differentiation, pod setting, pod abortion, ovule differentiation, and ovule abortion. The number of differentiated flowers is affected by the degree of vegetative growth prior to flowering, as flowers can be produced on a plant's main stem and on branch

nodes (Wiebold, 2012). Flowering ends and plants reach their maximum vegetative weight at the beginning of the R5 period (Purcell et al., 2014). Abscission and abortion of flowers, pods, and fertilized ovules occur due to heat stress experienced during the R1–R5 period (Puteh et al., 2013). Accordingly, the seed number is affected by temperature conditions from emergence (VE) to the R5 stage. The optimum temperature for seed number estimated at approximately 26.5°C during the VE–R5 period for both cultivars (Figure I-5) is an appropriate value upon consideration of the reported temperature responses for seed number components (as previously discussed). Moreover, in temperature gradient chamber experiments featuring the MG IV cultivar, the seed number was found to increase with growth temperature increases ranging from 20.0 (current) to 27.0°C in a cool region (Kumagai and Sameshima, 2014), and decrease with temperatures above the current growth temperature of 26.4°C in a warm region (Tacarindua et al., 2013).

Although single seed weight did not significantly differ among the temperature treatments, the optimum temperatures for single seed weight were found using a boundary line analysis. Seed weight was primarily affected by the temperature during the seed filling period (Dornbos and Mullen, 1991). Optimum temperatures for soybean seed size and seed growth rate were reported to be 23.0°C (Egli and Wardlaw, 1980; Baker et al., 1989) and 23.5°C (Egli and Wardlaw, 1980), respectively. These reported optimum temperatures

differed slightly from our results; the optimum temperatures during the seed filling duration (R5–R7) for single seed weight were estimated at 25.2°C for the Sinpaldalkong (medium seed size) cultivar, and at 22.3°C for the Daewonkong (large seed size) cultivar (Figure I-5). Evidence demonstrating that the optimum temperature for seed weight should differ according to the cultivar seed size has not yet been documented. However, plausible indirect evidence is available. A small-seeded soybean variety was reported to be less sensitive to yield components (including seed weight), resulting in deterioration due to high-temperature stress, compared with large-seeded genotypes (Puteh et al., 2013). Sexton et al. also reported similar results, where small-seeded cultivars were found to be more advantageous than large-seeded ones, with regard to seed growth rate. In another leguminous crop, the chickpea, cultivars with small seed sizes were also found to have a higher heat tolerance than large-seeded cultivars (Wang et al., 2006). These findings provide indirect evidence for crops other than soybeans, and thus further studies should document genotypic differences in the temperature responses of seed weight and seed yield.

According to the boundary line responses of seed yield to the mean growing season (VE–R7), the optimum temperature for potential yield was estimated to be 26.2°C and 25.0°C for Sinpaldalkong and Daewonkong cultivars, respectively (Figure I-5). The lower optimum temperature for

potential seed yield in the Daewonkong large-seeded cultivar may be attributable to its lower optimum temperature for single seed weight. To evaluate the validity of these estimates, seed yields for the same experimental sets in this study were simulated using the CROPGRO-Soybean (Boote et al., 2010; Jones et al., 2010) model; the simulated seed yields were subjected to boundary line analyses in response to growing season (VE–R7) temperatures (Figure I-7). The optimum temperature ranges during the VE–R7 period for seed yield were estimated to be 26.3°C and 25.8°C for the Sinpaldalkong and Daewonkong cultivars, respectively. The simulated yield response to temperature coincided very closely with the experimental results for the Sinpaldalkong cultivar (Figures I-5C and I-6), whereas the simulated yield responses to temperature differed slightly from the experimentally estimated responses, where an optimum temperature of 0.8°C higher was reported for the simulated Daewonkong cultivar response. This difference may be a result of employing the same seed growth rate response to the growth temperature during the grain filling period set in the CROPGRO-Soybean model, regardless of genotype. Further studies should be conducted to explain this discrepancy.

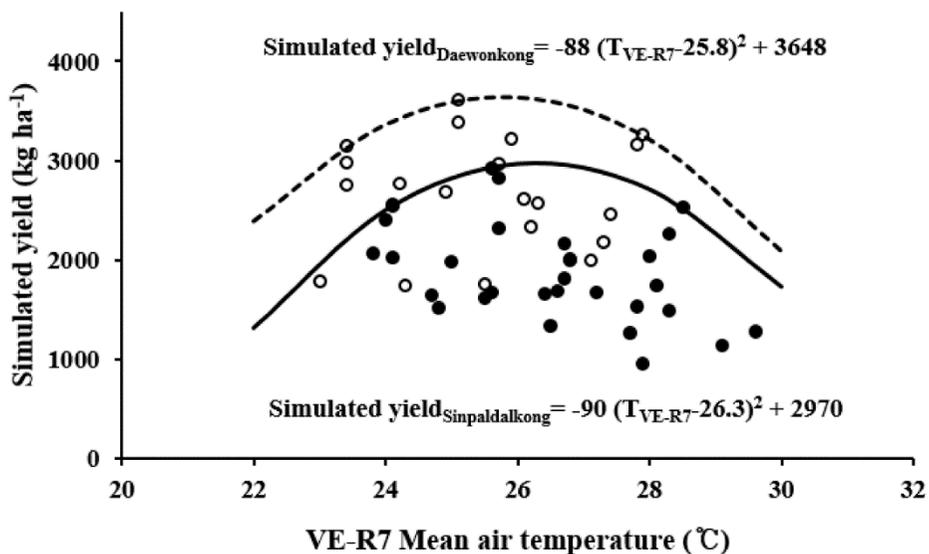


Figure I-7. Boundary line analysis of temperature responses in simulated soybean yields using the CROPGRO-Soybean model for Sinpaldalkong (filled circles) and Daewonkong (open circles) cultivars, grown under elevated temperatures with different sowing dates over a four- year period. Genetic coefficients were calibrated with field experiment data independent from this experiment; soil characteristic data from the pot experiments were used; weather data were obtained inside the experimental greenhouses, and cultivation methods were used for the simulations. Continuous and dashed lines indicate the 95% quantile regression lines for the Sinpaldalkong and Daewonkong cultivars, respectively.

Considering previous studies and the boundary line analysis of our four-year experiment under elevated air temperatures, it is concluded that the current air temperatures in South Korea remain below the optimum level for potential soybean yields. As the current mean air temperatures during the soybean growing season (VE–R7) ranges from 21.7 (in the north) to 24.6°C (in the south) in South Korea, further warming of only 1°C may have adverse effects on the potential yield of Daewonkong cultivar in the southern regions. However, on the whole, temperature rise of less than approximately 1°C would not become a critical limiting factor for soybean production in South Korea.

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CHAPTER II. Effects of Elevated Air Temperatures on Flowering and Pod Setting of Soybean in a Temperate Region

Abstract

Future climate change characterized by the increased mean and variability of temperature is expected to exert substantial impacts on yield determining factors of soybean including the number of flowers and pods. To evaluate the effects of elevated air temperature on flowering and pod setting in soybean, we conducted experiments from 2013 to 2015 using determinate soybean cultivars Sinpaldalkong [maturity group (MG) IV] and Daewonkong (MG VI), which were grown in pots (15cm in diameter and 40cm in height) at four temperature-controlled greenhouses under no water stress conditions. Greenhouses were located in a temperate region (37.27°N, 126.99°E; Suwon, South Korea) and controlled at the current ambient temperature (AT), AT+1.5°C, AT+3.0°C, and AT+5.0°C throughout the entire growing seasons. The number of newly opened flowers and abscised flowers and pods were recorded every day during the reproductive growth period. Regardless of cultivars or temperature treatments, the temporal distribution of flowering

showed a bimodal temporal distribution. The latter peak was delayed and increased with temperature elevation above ambient in both cultivars, indicating that elevated temperatures increased the flowering duration and the number of flowers differentiated lately. The relative frequency of early flower abscission and the proportion of flower abscission to pod abscission increased with temperature rise, indicating that the increase of pod set failure would be attributed to non-viable pollen or a reduction in photosynthate supply under high temperature stress. Temperature elevation significantly decreased the pod set in hot summer (the period of flowering and pod setting) years, 2013 and 2015, but not in cool summer year, 2014 without a temperature \times cultivar interaction. Regardless of cultivars, pod number variations were more closely associated with pod set percentage variations rather than with flower number variations in hot summer years (2013 and 2015), whereas the opposite associations were observed in cool summer year (2014). Using the boundary line analysis with quadratic and beta function, cardinal temperatures (T_{opt} , T_{max}) for pod set were estimated at 34.8, and 42.9°C for the Sinpaldalkong cultivar and 34.5, and 41.6°C for the Daewonkong cultivar, respectively. The temperature response of pod set was shown to be similar to the reported temperature response of pollen germination or pollen tube growth; suggesting that pod set would be strongly related to pollen viability. Although the temperature rise could lead to the increase of flower production, the

temperature above 35°C would sharply decrease the pod set ratio and cause severe damage to the formation of pod number in soybean.

Keywords: Soybean, Temperature, Flowering, Pod setting

Introduction

Soybean (*Glycine max* L. Merr.) is native to East Asia including Korea, and have been adapted and cultivated long ago (Singh, 2010). Soybean seeds have been utilized as not only a food source for human but also a feed for livestock due to their high protein and oil content (Hartman et al., 2011). Soybean is one of the most important crops worldwide in terms of area harvested and production, and its demand is increasing (Masuda and Goldsmith, 2009).

The number of seeds and seed size are two main yield components of soybeans; the number of seeds is more important yield component and is determined by the number of flowers opened, the percentage of pod set, and number of seeds per pod (Wiebold, 2012; Woodworth, 2013). Soybean plants bear two to three times more flowers than the number of pods retained at harvest. Soybean plants produce flowers on racemes which have multiple flowers. It takes 4 to 10 days for all flowers to open on a single raceme. There are three racemes at each leaf axil, thus flowers may continue to open at a node for more than two weeks.

In the IPCC's fifth assessment report, the global-mean surface temperature is projected to rise 2.6-4.8°C by the end of this century, in

comparison with 1986-2005, under RCP 8.5 (greenhouse gas emissions continue to rise) scenarios (Stocker et al., 2014). Furthermore, hot extremes will occur more frequently and intensely. Temperature rise due to global warming is likely to impact on future agricultural production, including soybean (Mall et al., 2004; Hatfield et al., 2011; Van Alfen, 2014).

Temperature is an important environmental factor affecting development and growth of soybean (Norman, 2012; Sengar and Sengar, 2014). Optimum temperature for vegetative growth and development was reported to be around 30°C (Hesketh et al., 1973; Raper and Kramer, 1987; Boote et al., 1997). Reproductive growth stages are more sensitive to temperature than vegetative growth in soybean. The reproductive processes are impeded by unfavorable temperature conditions, which can lead to lower seed yield (Ferris et al., 1998; Thanacharoenchanaphas and Rugchati, 2011; Siebers et al., 2015). Temperatures above 33/28°C (day/night) during the flowering and pod set period reduce seed yield, regardless of the temperature during the seed filling period (Egli and Wardlaw, 1980). High temperature stress during the early reproductive phases of soybean causes pod and seed set failure resulted from abortion and abscission of reproductive organs (Djanaguiraman et al., 2011). Abortion and abscission of flowers, pods, and seeds can occur due to a reduction in photosynthate supply during the flowering and pod set growth periods (Egli and Bruening, 2006; Ruiz-Vera et al., 2013; Siebers et al., 2015).

Pod and seed set failure under high temperature stress would be related to non-viable pollen, unsuccessful anther dehiscence, a reduction in the penetration of the pollen tube into the stigma, or stigma receptivity (Schoper et al., 1987; Gross and Kigel, 1994; Prasad et al., 2002; Sato et al., 2002; Hall, 2004; Prasad et al., 2006; Snider et al., 2009). Salem et al. (2007) reported that cardinal temperatures (T_{min} , T_{opt} , and T_{max}) for pollen germination and pollen tube growth of soybeans were 13.2, 30.2, and 47.2°C and 12.1, 36.1, and 47.0°C, respectively.

Temporary exposure to high temperatures can also affect yield-determining processes. Heat stress (6°C above ambient) only for 3 days had a direct effect on photosynthesis and transpiration, consequently, affecting soybean yield under field condition (Siebers et al., 2015). Reproductive organs are vulnerable to short events of high temperatures during the flowering phase (Reddy and Kakani, 2007). Soybean pollen viability is decreased by exposure to instantaneous temperatures above 30.0°C *in vitro* (Salem et al., 2007). Exposure to high temperatures of 30–35°C for few days can cause abscission and abortion of flower, pod, and seed, resulting in severe yield loss (Gross and Kigel, 1994; Prasad et al., 1999; Siddique et al., 1999).

Further warming is anticipated to disturb the reproductive process and decrease soybean yield. However, few experimental studies have been performed to investigate the impacts of increasing temperature on the number

of flowers and pod set for determinate soybean. Thereby, this study was conducted to examine the effects of elevated air temperatures on flowering and pod setting characteristics of two determinate soybean cultivars in a temperate region of South Korea.

Materials and Methods

Plant materials and growth conditions

The experiments were conducted from 2013 to 2015 with two Korean determinate soybean cultivars, Sinpaldalkong and Daewonkong, of maturity group IV and VI, respectively (Ha et al., 2009), in four sunlit temperature-controlled greenhouses ($W \times D \times H$; $5.0 \times 14.0 \times 3.5$ m) at the Experimental Farm of Seoul National University, Suwon, South Korea ($37^{\circ}16'N$, $126^{\circ}59'E$). Five seeds were sown at 3cm depth in 7L PVC pot (15 cm in diameter, 40 cm in height) containing loam soil with a pH of 6.6 and CEC of $15.4\text{cmol}(+)/\text{kg}$ in 2013 and 2014 and loamy sand soil with a pH of 4.9 and CEC of $6.6\text{cmol}(+)/\text{kg}$ in 2015 (Table 1). The Sinpaldalkong cultivar was sown on: June 15, 2013; June 30, 2013; May 30, 2014; June 20, 2014; and June 15, 2015. The Daewonkong cultivar was sown on: June 20, 2014; July 11, 2014; and June 20, 2015. Chemical fertilizers were applied to each pot before sowing, which contained 0.08, 0.08, and 0.09 g of N, P_2O_5 , and K_2O , respectively. To set up a soybean canopy similar to field conditions, the pots were arranged in four rows, where plants were spaced 15cm apart in rows 45 cm apart. After emergence from the soil, the plants were thinned to one plants per pot, and then exposed to no water-stress conditions by sub-irrigation. Weeding was

carried out by hand weekly and pesticide was applied when necessary. Greenhouses were controlled to targets of current ambient air temperature (AT), AT+1.5°C, AT+3.0°C, and AT+5.0°C using heating and ventilation systems linked to a CR1000 Measurement and Control Datalogger (Campbell Scientific Inc., Logan, UT, USA). Sidewalls of the AT treatment greenhouse were removed to be close to outdoor ambient temperatures. The greenhouses were covered by polyethylene film, which was changed before the experiment in 2015.

The advantage of pot experiments in the greenhouse is that environmental factors determining yield can be more easily controlled than in the field (Sage and Kubien, 2007). Although the absolute values related to growth and yield can be limited by pot size, responses to environmental factors are similar across pot and field experimental data, regardless of soil volume (Lecoeur and Sinclair, 1996; Ray and Sinclair, 1998; Tubiello et al., 2007). In the controlled experiments, day/night temperatures are generally fixed during the crop growth period, while temperatures in the field change diurnally and seasonally. Diurnal and seasonal temperature variations in our temperature-controlled greenhouses are very close to field condition. Thus, temperature-controlled greenhouses can be useful to assess the impact of global warming on crop growth.

Table II-1. Chemical and physical characteristics of the soil at the beginning of the experiment in 2013, 2014, and 2015.

Soil attribute	2013 and 2014	2015
pH	6.55	4.90
Soil organic matter (%)	1.925	0.495
TOC (%)	1.115	0.290
T-N (%)	0.123	0.026
NH ⁴⁺ (mg/kg)	6.35	3.36
CEC (cmol/kg)	15.4	6.6
P ₂ O ₅ (mg/kg)	3.75	1.33
Soil texture	Loam	Loamy sand

Measurements of air temperatures, flowers, and pods

Air temperatures in each greenhouse were recorded (per minute) using a CR1000 data logger equipped with a platinum resistor thermoprobe housed in a naturally ventilated shelter. Outdoor air temperature values were obtained from the Suwon Meteorological Station, which is located approximately 0.5 km from the experimental greenhouses. A newly opened flower was tagged with flowering date (figure II-1) and opened flowers were recorded every day during the flowering period from five pots in 2013, from two to four pots in 2014, and from four pots in 2015. By comparing with the number of flowers in a day ago, abscised flowers and pods number were recorded every day with their flowering dates during the reproductive growth period only for the Sinpaldalkong cultivar in 2015. The number of fertile pods were observed at maturity (R8).



Figure II-1. Soybean flowers tagged with flowering date.

Data analysis

Multiple linear regression analysis was used to relate the flowering duration to sowing date and mean daily maximum temperature during the flowering as follows:

$$D(s, t_m) = \alpha \times s + \beta \times t_m + i \quad (1)$$

where $D(s, t_m)$ is the predicted flowering duration for the sowing date s (day of year) and mean daily maximum temperature during the flowering t_m ($^{\circ}\text{C}$); α and β slopes associated with s and t_m , respectively; i intercept. The temporal distribution of flowering (the number of opened flowers per day) was fitted to a bimodal distribution function as follows:

$$f(t) = f_1 \frac{1}{\sqrt{2\pi}\sigma_1} \exp \left[-\frac{(t-t_1)^2}{2\sigma_1^2} \right] + f_2 \frac{1}{\sqrt{2\pi}\sigma_2} \exp \left[-\frac{(t-t_2)^2}{2\sigma_2^2} \right] \quad (2)$$

where $f(t)$ denotes the number of flowers at t days after first flower; f_1 and f_2 amplitude parameters of the first and second peaks respectively; t_1 and t_2 the numbers of days after first flower when the flowering reaches first and second peaks (means) of left and right distributions, respectively; and σ_1 and σ_2 shape parameters (standard deviations) of first and second distributions, respectively. Pod set percentage of each pot was determined as the ratio of total number of opened flowers produced to the number of fertile pods at maturity multiplied by 100. Analysis of variance (ANOVA) and

Duncan's multiple range test for significant differences between the treatment means were performed to evaluate differences between temperature treatments on flowering duration, flower number, pod set percentage, and pod number. Correlation and path analysis (Covariance Analysis of Linear Structural Equations: CALIS) were conducted to identify relationships among flower number, pod set percentage, and pod number, and to determine the direct contribution of flower number and pod set percentage to pod number. A boundary line analysis (Webb, 1972), which can exclude experimental errors and the effects of limiting factors (Elliott and De Jong, 1993), was employed to delineate the responses of pod set percentage to the mean daily maximum temperature weighted by frequency distribution of flowering. The boundary line parameters of pod set were estimated by two methods: a quadratic quantile regression (95th percentile) and a regression for boundary points with beta function (Yan and Hunt, 1999) as follows:

$$p(T) = a(T - T_{opt})^2 + p_{max} \quad (3)$$

$$p(T) = p_{max} \left(\frac{T_{max}-T}{T_{max}-T_{opt}} \right) \left(\frac{T}{T_{opt}} \right)^{\frac{T_{opt}}{T_{max}-T_{opt}}} \quad (4)$$

where $p(T)$ represents the percentage of pod set at the mean daily maximum temperature weighted by frequency distribution of flowering of T (°C); a the leading coefficient of quadratic function; p_{max} the maximum

pod set percentage; T_{opt} (°C) the optimum temperature; T_{max} (°C) the high temperature limit at which the pod set percentage becomes 0. All statistical analyses were conducted using the statistical analysis software SAS Version 9.4 (SAS Institute Inc., Cary, NC, USA).

Results

Meteorological conditions

The mean air temperature of the growing season (from VE to R7) in the AT ranged from 22.8 to 26.6°C during the experimental years; the growing season mean temperatures of AT+1.5°C, AT+3.0°C, and AT+5.0°C were 1.1–1.8°C, 1.9–3.0°C, and 3.6–4.4°C higher than the AT, respectively (Table 2). Figure II-2 presents, as an example, the daily and diurnal changes in air temperatures within the temperature-controlled greenhouses during the 2013 growing season. The air temperatures in the AT were similar to outdoor air temperatures throughout the growth periods, and differences between the temperature treatments were consistently maintained during the growing seasons. The solar transmittance of polyethylene film in greenhouses were approximately 60% (2013 and 2014) or 85% (2015).

Table II-2. Mean air temperature and solar radiation values from emergence (VE) to physiological maturity (R7) in the experimental greenhouses that were controlled to target temperatures of AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C.

Cultivar	Year	Sowing date	Air temperature (°C)				Solar radiation (MJ m ⁻² day ⁻¹)
			AT	AT+1.5	AT+3.0	AT+5.0	
Sinpaldalkong (MG IV)	2013	Jun 15	25.6	27.4	28.6	29.9	8.3
		Jun 30	25.0	26.7	27.8	29.1	7.9
	2014	May 30	24.3	25.8	26.9	28.1	9.4
		Jun 15	24.2	25.7	26.7	28.0	8.8
2015	Jun 15	25.6	27.1	28.1	30.0	11.8	
Daewonkong (MG VI)	2014	Jun 20	24.0	25.4	26.5	27.8	8.6
		Jul 11	22.8	24.2	25.4	26.5	7.9
	2015	Jun 20	25.5	26.6	27.4	29.1	11.4

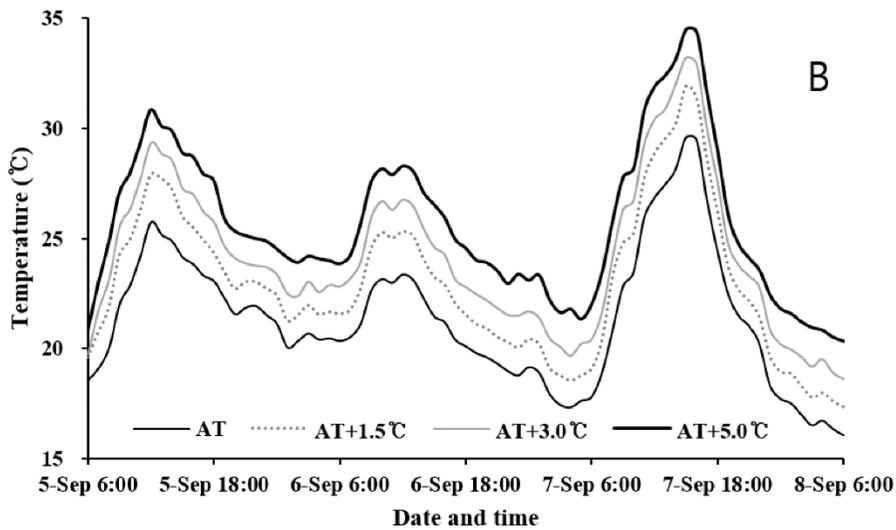
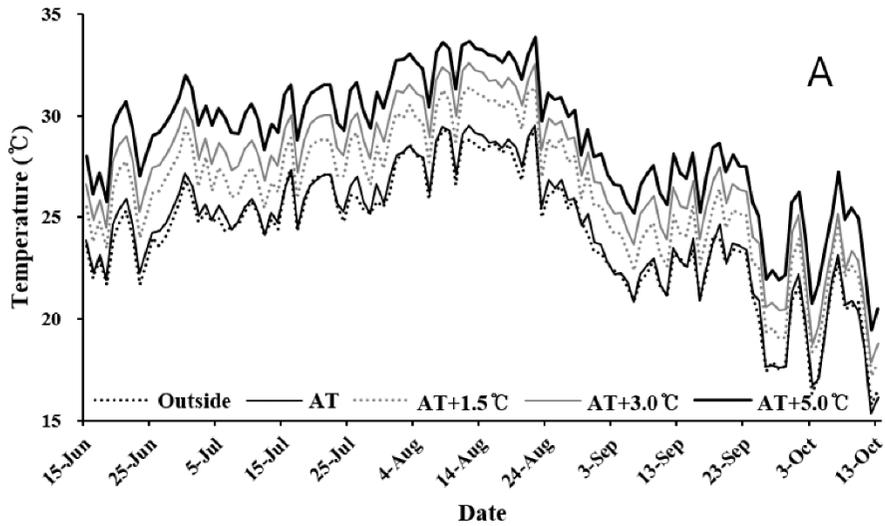


Figure II-2. Daily mean air temperatures (A) and diurnal changes of temperature (B) in the experimental greenhouses that were controlled to target temperatures of ambient (AT), AT+1.5°C, AT+3.0°C, and AT+5.0°C during the growing seasons. Only data collected in 2013 are presented as an example of temperature variation. Dotted black, continuous black, dotted gray, continuous gray, and bold black lines indicate the temperatures of outside, AT, AT+1.5°C, AT+3.0°C, and AT+5.0°C, respectively.

Flowering period and flower number

The initial flowering was shortened in earlier sowing and not much affected by temperature elevation treatments, whereas the end of flowering was delayed by the elevated temperatures (Table 3). The end flowering date of AT+5.0°C treatment was, on average, delayed by 10 and 9 days as compared with AT for the Sinpaldalkong and Daewonkong cultivars, respectively. According to multiple regression analysis for the flowering duration as shown in Figure II-3, the flowering duration was shortened by 0.38 and 0.34 days with the delayed sowing of 1 day and by 1.79 and 1.94 days prolonged with temperature elevation of 1°C for the Sinpaldalkong and Daewonkong cultivars, respectively. Elevated temperatures induced the greater number of flowers in both cultivars. Compared with the AT, the number of flowers of the AT+5.0°C treatment was increased by 56 and 23% for the Sinpaldalkong and Daewonkong cultivars, respectively.

Table II-3. Flowering phenology and the estimated parameters of bimodal flowering distribution equation (2) for the Sinpaldalkong and Daewonkong cultivars sown at different dates and years under four different temperature conditions.

Cultivar	Sowing date	Temperature treatment	Initial flowering date	End flowering date	Flowering duration (days)	Flower number (pot ⁻¹)	Parameter estimates from equation (2)					
							f_1	t_1	σ_1	f_2	t_2	σ_2
Sinpaldalkong (MG IV)	Jun 15, 2013	AT	Jul 18	Aug 24	38	141	96	9.1	4.6	48	28.6	6.6
		AT+1.5°C	Jul 18	Aug 27	41	175	89	9.4	5.0	86	28.3	5.9
		AT+3.0°C	Jul 19	Aug 28	41	215	131	10.1	6.6	90	30.8	4.8
		AT+5.0°C	Jul 21	Sep 2	43	189	123	13.3	6.2	66	34.7	5.2
	Jun 30, 2013	AT	Jul 31	Aug 29	30	124	126	11.6	5.8	17	24.7	1.8
		AT+1.5°C	Jul 31	Aug 31	32	150	100	11.7	5.0	50	26.4	3.6
		AT+3.0°C	Aug 1	Sep 1	33	192	84	9.1	3.3	113	22.7	6.7
		AT+5.0°C	Aug 3	Sep 9	38	240	111	10.0	2.6	127	20.8	7.2
	May 30, 2014	AT	Jul 5	Aug 12	39	186	149	14.2	5.4	37	33.2	3.2
		AT+1.5°C	Jul 1	Aug 12	43	197	123	12.7	5.6	73	33.0	4.6
		AT+3.0°C	Jul 1	Aug 13	44	210	118	13.5	5.9	90	34.1	4.1
		AT+5.0°C	Jul 2	Aug 18	48	301	133	12.8	6.3	167	35.1	4.9
	Jun 20, 2014	AT	Jul 26	Aug 23	29	111	106	13.9	6.3	5	23.1	8.3
		AT+1.5°C	Jul 24	Aug 21	29	126	111	11.7	6.1	8	28.0	3.4
		AT+3.0°C	Jul 25	Aug 26	33	169	123	11.6	4.3	36	24.1	2.8
		AT+5.0°C	Jul 25	Aug 26	33	161	126	12.1	4.8	34	25.8	3.6
Jun 15, 2015	AT	Jul 21	Aug 22	33	97	85	10.4	6.6	13	28.0	2.6	
	AT+1.5°C	Jul 18	Aug 22	36	104	85	12.4	6.4	17	28.5	4.3	

		AT+3.0°C	Jul 21	Aug 28	40	123	118	11.6	6.9	5	33.4	1.8
		AT+5.0°C	Jul 22	Sep 13	54	163	105	11.7	8.7	60	37.5	6.8
	Temperature treatment mean across sowing date and year	AT	Jul 20	Aug 22	34	135	111	11.9	6.1	27	28.9	6.4
		AT+1.5°C	Jul 18	Aug 23	36	150	99	11.4	5.6	49	28.9	5.7
		AT+3.0°C	Jul 19	Aug 25	38	182	114	11.0	5.5	70	28.9	6.9
		AT+5.0°C	Jul 21	Sep 1	43	211	130	12.1	5.7	89	33.3	7.1
Daewonkong (MG VI)	Jun 20, 2014	AT	Jul 29	Aug 22	25	213	134	4.2	1.5	83	14.8	6.3
		AT+1.5°C	Jul 27	Aug 25	30	207	72	4.3	1.5	148	13.7	8.9
		AT+3.0°C	Jul 28	Aug 27	31	242	136	4.5	2.1	108	18.4	5.4
		AT+5.0°C	Jul 29	Aug 27	30	243	127	5.2	2.2	116	19.2	5.0
	Jul 11, 2014	AT	Aug 21	Sep 11	22	116	62	4.0	1.8	61	13.1	7.7
		AT+1.5°C	Aug 19	Sep 14	27	108	55	3.7	1.2	56	11.1	7.2
		AT+3.0°C	Aug 19	Sep 11	24	128	54	2.5	1.3	79	9.6	7.3
		AT+5.0°C	Aug 20	Sep 15	27	164	72	2.9	1.4	84	13.7	4.6
	Jun 20, 2015	AT	Jul 29	Aug 31	34	147	67	4.1	1.9	85	19.5	9.7
		AT+1.5°C	Jul 28	Sep 7	42	163	70	4.7	2.3	98	25.1	9.8
		AT+3.0°C	Jul 31	Sep 8	40	140	56	6.4	2.1	87	20.7	10.9
		AT+5.0°C	Aug 3	Sep 19	48	181	61	5.6	2.0	126	28.1	13.5
	Temperature treatment mean across sowing date and year	AT	Aug 6	Sep 1	27	159	87	4.1	1.7	74	15.0	7.8
		AT+1.5°C	Aug 4	Sep 5	33	159	61	4.2	1.6	105	14.9	10.6
		AT+3.0°C	Aug 5	Sep 5	32	170	83	4.2	2.4	86	16.3	7.7
		AT+5.0°C	Aug 7	Sep 10	35	196	81	4.4	2.2	107	17.6	8.1

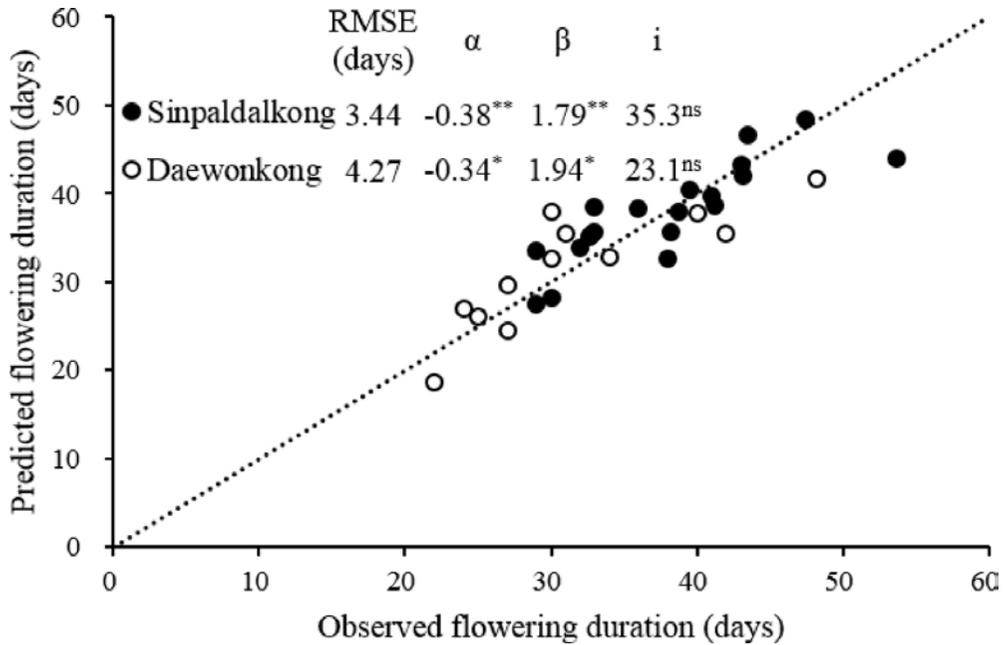


Figure II-3. Flowering duration observed and predicted by equation (1) for the Sinpaldalkong and Daewonkong cultivars sown at different dates and years under four different temperature conditions. Filled and open circles represent the data for the Sinpaldalkong and Daewonkong cultivars, respectively. Root mean square error (RMSE) and the regression coefficients (α , β , and i) of equation (1) are shown in the legend. **, *, and ns denote significance of the regression coefficients at $p < 0.001$, $p < 0.01$, and not significant ($p > 0.05$), respectively.

The temporal distribution of flowering had two peaks in all the treatments in both cultivars and was well fitted to a bimodal frequency distribution of function (2) (Figure II-4). The estimated values from equation (2) in each treatment and temperature treatment mean of the Sinpaldalkong and Daewonkong cultivars are shown in Table 3. Sinpaldalkong cultivar had smaller and later peaks of flowering than Daewonkong cultivar. Flowering reached its first and second peaks at 11.6 and 30.0 days after initial flowering in the Sinpaldalkong cultivar, respectively, and at 4.2 and 16.0 days in the Daewonkong cultivar, respectively. Regardless of cultivars, the first peak was higher than the second one, and the second peak was delayed and higher with temperature elevation treatments above ambient.

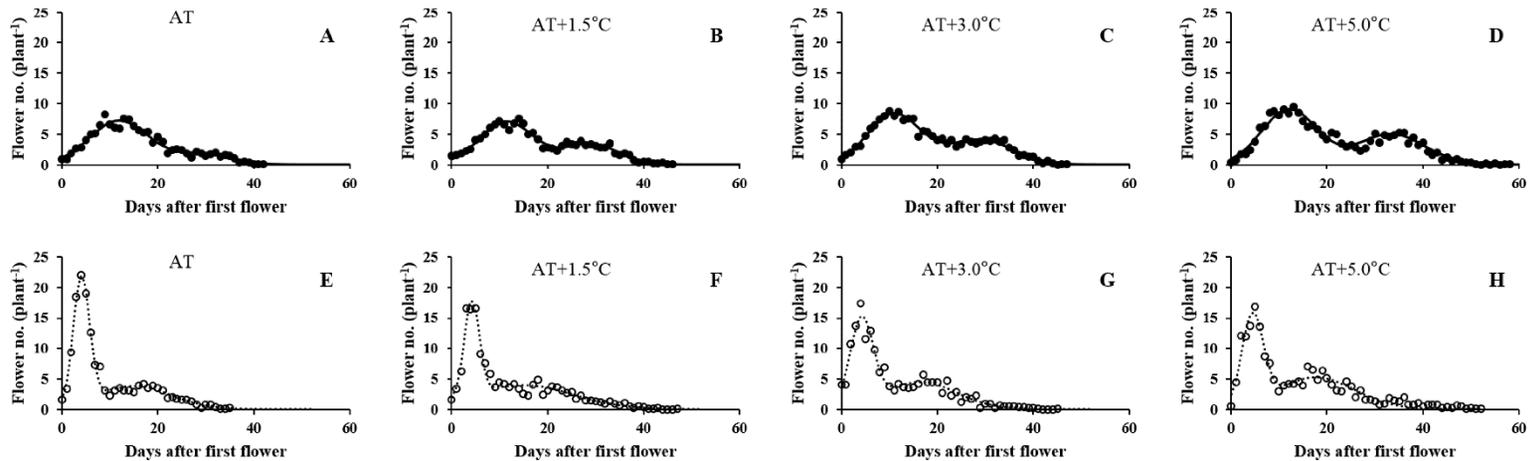


Figure II-4. The temporal frequency distribution of flowering under different temperature treatments in Sinpaldalkong (A, B, C, and D) and Daewonkong (E, F, G, and H) cultivars. In A, B, C, D, E, F, G, and H, filled and open circles represent the data averaged over sowing dates and years for each temperature elevation treatment in Sinpaldalkong and Daewonkong cultivars, respectively. Continuous and dashed lines indicate regression lines for the Sinpaldalkong and Daewonkong cultivars, respectively.

Flower and pod abscission

After flower opening, flower abscission began to happen and mainly occurred at from 2 to 5 days after their opening (Figure II-5). Since then, the flower abscission decreased and continued to happen until about a month after their opening (data not shown). More than 50% of fallen flowers abscised within 7 days after their opening. The relative frequency of early flower abscission (abscission within 7 days from flower opening) increased with temperature increase above ambient temperature. Increasing air temperature increased the number of abscised flowers, but not abscised pods (Figure II-6A). The proportion of flower abscission to pod abscission increased with elevated temperatures; the proportion of flower abscission to total (flower plus pod) abscission increased from 62.3 to 92.5% as temperature increases from ambient temperature (AT) to AT+5.0°C treatment (Figure II-6B).

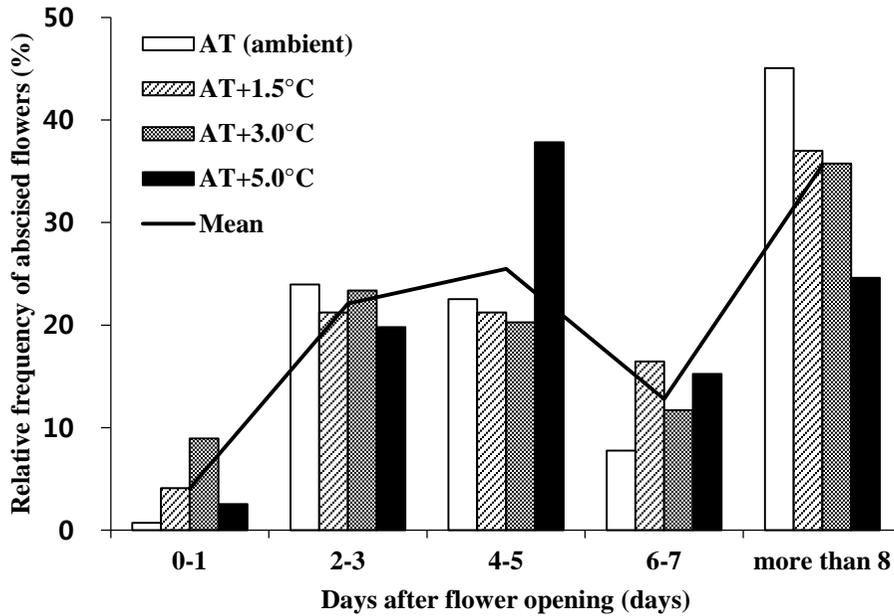


Figure II-5. The relative frequency of abscised flowers along with number of days after flower opening for Sinpaldalkong cultivar grown under four different temperature conditions in 2015.

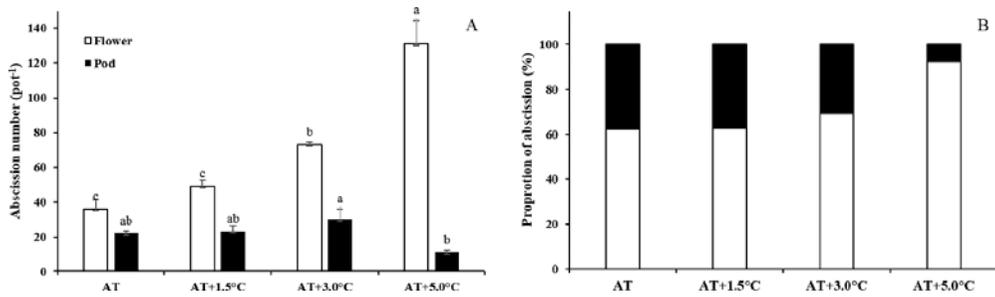


Figure II-6. The number (A) and proportion (B) of abscised flowers and pods for Sinpaldalkong cultivar grown under four different temperature conditions in 2015. Open and filled bars indicate abscission of flowers and pods, respectively. The same letters above the bars within each organ indicate no significant differences between the temperature treatments, as determined by Duncan's multiple range test at a confidence level of 5%.

Pod set and pod number

Flowering and pod setting characteristics of the Sinpaldalkong and Daewonkong cultivars as affected by the temperature elevation treatments are shown in Tables II-4 and II-5. ANOVA and Duncan's multiple range test were performed separately for warm and cool summer years, because the air temperature during the flowering period in 2014 was much lower than the other two experimental years (2013 and 2015). There were no significant temperature \times cultivar interactions for flowering and pod setting characteristics. Regardless of growing season, elevated temperatures significantly prolonged the flowering duration and significantly increased the total number of opened flowers. The effects of temperature for pod set percentage and the number of pods were different between growing seasons. The percentage of pod set decreased with temperature elevation from 30.0 (AT) to 33.9°C (AT+5.0°C) of day temperature in hot summer years (2013 and 2015), whereas no significant differences were detected between the different temperature elevation which were recorded day time temperature of 26.5 (AT) to 30.4°C (AT+5.0°C) in cool summer year (2014). Pod number increased with temperature rise from ambient in cool summer year, whereas in hot summer year it was increased until AT+1.5°C treatment and then decreased with further temperature elevation.

Table II-4. Responses of flowering and pod setting to elevated temperature treatments in two determinate soybean cultivars with different maturity group (MG) in hot summer year (2013 and 2015).

Cultivar and temp. treatment	Air temperature for the flowering period (°C)			Flowering duration (days)	Flower number (pot ⁻¹)	Pod set (%)	Pod number (pot ⁻¹)
	Mean	Day	Night				
Sinpaldalkong (MG IV)							
AT	27.7	30.0	25.4	34b	129c	53a	70a
AT+1.5°C	29.3	32.1	26.5	36b	149c	50a	76a
AT+3.0°C	30.2	33.0	27.4	37b	178b	36b	69a
AT+5.0°C	31.2	34.1	28.3	44a	202a	29c	61b
Cultivar mean	29.6	32.3	26.9	38	164	42	69
Daewonkong (MG VI)							
AT	27.2	30.0	24.4	34c	147b	16a	23a
AT+1.5°C	28.2	31.1	25.3	42b	144b	15a	22a
AT+3.0°C	28.7	32.0	25.4	40b	140b	7b	9b
AT+5.0°C	29.9	33.3	26.5	48a	181a	4b	7b
Cultivar mean	28.5	31.6	25.4	41	154	10	15
Temp. treatment mean							
AT	27.6	30.0	25.2	34c	133c	45a	59b
AT+1.5°C	29.0	31.9	26.2	38b	148c	44a	66a
AT+3.0°C	29.8	32.8	26.9	38b	169b	29b	55b
AT+5.0°C	30.9	33.9	27.9	45a	197a	23c	48c
ANOVA results							
Temperature (T)				**	**	**	**
Cultivar (C)				*	ns	**	**
T × C				ns	ns	ns	ns

Values followed by the same letters within a column for each cultivar and temperature treatment mean were not significantly different at a confidence level of 5%, as determined by Duncan's multiple range tests. **, *, and ns denote significance at $p < 0.01$, $p < 0.05$, and not significant ($p > 0.05$), respectively.

Table II-5. Responses of flowering and pod setting to elevated temperature treatments in two determinate soybean cultivars with different maturity group (MG) in cool summer year (2014).

Cultivar and temp. treatment	Air temperature for the flowering period (°C)			Flowering duration (days)	Flower number (pot ⁻¹)	Pod set (%)	Pod number (pot ⁻¹)
	Mean	Day	Night				
Sinpaldalkong (MG IV)							
AT	25.5	26.8	24.2	35c	154c	50	77c
AT+1.5°C	26.9	28.6	25.2	38b	173bc	48	82bc
AT+3.0°C	28.0	29.7	26.3	39b	193b	49	93ab
AT+5.0°C	28.9	30.7	27.1	41a	241a	45	104a
Cultivar mean	27.3	29.0	25.7	38	191	48	89
Daewonkong (MG VI)							
AT	24.4	26.1	22.7	24b	164b	35	56ab
AT+1.5°C	25.8	27.8	23.8	29a	157b	35	51b
AT+3.0°C	27.0	29.0	25.0	28ab	185ab	34	61ab
AT+5.0°C	28.0	30.1	25.9	29a	203a	35	69a
Cultivar mean	26.3	28.3	24.4	27	177	35	59
Temp. treatment mean							
AT	25.0	26.5	23.5	31c	158c	45	69c
AT+1.5°C	26.4	28.2	24.5	34b	167c	43	70c
AT+3.0°C	27.5	29.4	25.7	35ab	190b	43	81b
AT+5.0°C	28.5	30.4	26.5	37a	227a	41	91a
ANOVA results							
Temperature (T)				**	**	ns	**
Cultivar (C)				**	ns	**	**
T × C				ns	ns	ns	ns

Values followed by the same letters within a column for each cultivar and temperature treatment mean were not significantly different at a confidence level of 5%, as determined by Duncan's multiple range tests. **, *, and ns denote significance at $p < 0.01$, $p < 0.05$, and not significant ($p > 0.05$), respectively.

Pod number showed highly significant positive correlations ($r=0.77^{***}$ and 0.98^{***}) with pod set percentage for the Sinpaldalkong and Daewonkong cultivars, respectively, in hot summer years (2013 and 2015); whereas highly significant positive correlations ($r=0.93^{***}$ and 0.91^{***}) with the number of flowers were observed for the Sinpaldalkong and Daewonkong cultivars, respectively, in cool summer year (2014). Path analyses were conducted according to the predetermined causal relationships between the number of pod and pod number-related traits (Figure II-7). Regardless of cultivar type, pod number variation was more closely associated with pod set percentage, rather than with flower number in hot summer year. In cool summer year, however, flower number per pot showed stronger association with the variation in the number of pods per pot, rather than with the percentage of pod set. The flower number per pot negatively affected pod set percentage in cool summer year, whereas flower number exerted negligible effects on the pod set percentage in hot summer year.

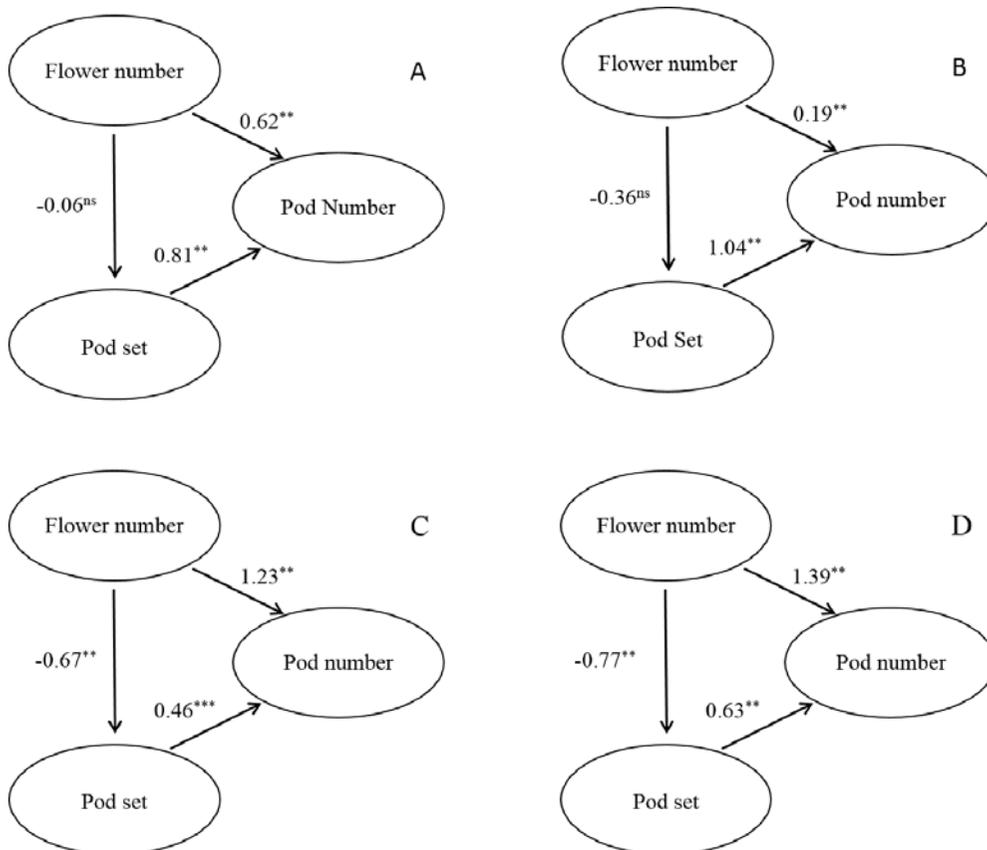


Figure II-7. Path analysis showing the direct contribution of flower number to pod number, pod set percentage to pod number, and flower number to pod set percentage in two soybean cultivars, Sinpaldalkong (left, A and C) and Daewonkong (right, B and D), grown under elevated temperature conditions during the warm (2013 and 2015, top, A and B) and cool (2014, bottom, C and D) growing season. **, *, and ^{ns} denote significance at $p < 0.001$, $p < 0.01$, $p < 0.05$, and not significant ($p > 0.05$), respectively.

Boundary line response of pod set to temperature

The boundary lines of pod set percentage to mean daily maximum temperature weighted by frequency distribution of flowering were well fitted to the quadratic and beta functions, revealing the maximum pod set percentage and cardinal temperatures (Figure II-8 and Table II-6). The percentage of maximum pod set was higher for the Sinpaldalkong cultivar (65%) than for the Daewonkong cultivar (45%). Optimum and maximum temperatures for pod set were not different between the function types. Cardinal temperatures for pod set were estimated to be 34.8 and 34.5°C for the optimum, and 42.9 and 41.6°C for the maximum (the high temperature limit) for the Sinpaldalkong and Daewonkong cultivars, respectively. Optimum temperatures for pod set were similar for both cultivars, whereas the maximum temperature for pod set was a little bit lower for the Daewonkong cultivar than for the Sinpaldalkong cultivar.

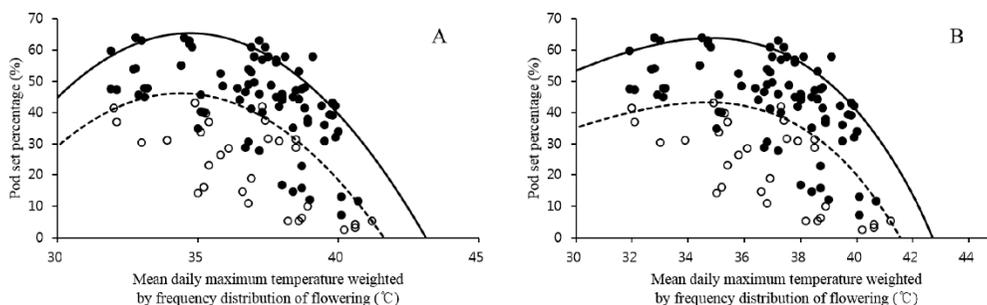


Figure II-8. Boundary line analysis of pod set responses to mean daily maximum temperature weighted by frequency distribution of flowering for two determinate soybean cultivars, Sinpaldalkong and Daewonkong. The boundary line parameters of pod set were estimated by a quadratic quantile regression (A) and a regression for boundary points with beta function (B). Filled and open circles represent the data for the Sinpaldalkong and Daewonkong cultivars, respectively. In A and B, each continuous and dashed line indicates the boundary lines for the Sinpaldalkong and Daewonkong cultivars, respectively.

Table II-6. The maximum pod set percentage (p_{max}) and cardinal temperatures (optimum temperature, T_{opt} ; maximum temperature, T_{max}) of pod set responses to mean daily maximum temperature weighted by frequency distribution of flowering for the Sinpaldalkong and Daewonkong cultivars.

Cultivar	Function type	a	p_{max}	Cardinal temperatures (°C)	
				T_{opt}	T_{max}
Sinpaldalkong (MG IV)	Quadratic function	-0.93	65.4	34.7	43.1
	Beta function		63.9	34.8	42.7
	Cultivar mean		64.7	34.8	42.9
Daewonkong (MG VI)	Quadratic function	-0.88	46.1	34.4	41.6
	Beta function		43.2	34.6	41.5
	Cultivar mean		44.7	34.5	41.6

Discussion

Flowering responses to elevated temperatures

Floral induction is mainly affected by the photoperiod in soybean (Cregan and Hartwig, 1984; Setiyono et al., 2007). Initial flowering in soybean plants which were grown under the same photoperiod conditions showed a little variation according to temperature treatment; normally, initial flowering was hastened with temperature increase up to 1.5°C above ambient temperature, and then delayed with further temperature elevation (Table II-3). This indicated that the developmental rate for flowering was generally maximized at AT+1.5°C treatment in the experimental site, but the temperature effect on flowering was negligible. After the first flower (R1), the number of opened flowers increased rapidly and reached its first peak, although the peak time was different between the cultivars (10.6 days for Sinpaldakong and 4.2 days for Daewonkong). About 30 and 16 days after R1, the second peaks of flowering were observed in the Sinpaldakong and Daewonkong cultivars, respectively. There are three racemes at each leaf axil in soybean, and it takes 4 to 10 days for all flowers to open on a single raceme, thus flowers continue to open for two or more weeks (Wiebold, 2012). Second peaks were related to flower opening on tertiary raceme, and high night

temperatures increased the number of flowers on the secondary and tertiary racemes (Zheng et al., 2002). Increasing air temperature shifted later and increased the second peak of flower opening (Figure II-4), resulting in the lengthened flowering period and the greater number of flowers. Flowering duration and the number of flowers significantly increased with temperature increase within the range of 25.0 to 30.9°C during the flowering period (Tables II-4 and II-5). Kumagai and Sameshima (2014) reported similar results, where elevated temperatures increased the flowering period and the number of opened flowers in temperature gradient chamber experiments employing MG IV soybean cultivars. Further studies are needed to establish the physiological mechanisms of the increase in the flowering period and flower number under high temperature condition.

Pod set and pod number responses to elevated temperatures

Even though the flower abscission continued to happen until about a month from their opening, a large number of flowers abscised within 7 days after their opening, and this early flower abscission increased under elevated temperature conditions (Figure II-5). Under high temperatures, abscission and abortion of flowers and pods can occur due to decreased pollen viability or stigma receptivity (Prasad et al., 2001; Hall, 2004). The number of abscised flowers increased with temperature rise above ambient (Figure II-6A).

Increasing temperature reduces net photosynthetic carbon assimilation, which is attributed to declines in stomatal conductance and intercellular carbon dioxide concentration (Ruiz-Vera et al., 2013; Siebers et al., 2015). Increase in abscission and abortion of flowers and pods under elevated temperatures can be due to a reduction in photosynthate supply during the flowering and pod setting periods. High temperature increased rate of ethylene production in flowers and pods, which also causes flower and pod abscission (Djanaguiraman et al., 2011). The proportion of flower abscission to pod abscission increased with elevated temperatures (Figure II-6B), indicating that proportion of fertilized flowers were reduced by high temperatures. Increasing abortion and abscission of flowers can result in decreased pod set ratio and reduced pod number. Elevated temperature effects on flower number were the same throughout the study period, but on pod set and pod number were different between the years. The percentage of pod set decreased with the temperature elevation treatments within the range from 30.0 to 33.9°C of average day temperature during the flowering period, whereas pod set was not affected by temperature increase within the range of 26.5 to 30.4 °C of average day temperature during the flowering period (Tables II-4 and II-5). In cool summer year, the number of pods significantly increased with increases in temperatures above AT treatment resulted from the increase in the number of flowers. However, pod number decreased with temperature rise above

AT+1.5°C in hot summer year because of decreased pod set ratio. Therefore, the percentage of pod set can be a limiting factor of pod number in hot growing season.

Boundary line response of pod set to temperature

Increasing temperature significantly decreased the percentage of pod set in hot summer year, but not in cool summer year without a temperature × cultivar interaction, indicating that the optimum temperature for pod set existed in experimental temperature conditions. The percentage of pod set was not affected by increasing night temperature (Gibson and Mullen, 1996; Zheng et al., 2002). Soybean pod set decreased by exposure to instantaneous high temperatures (Prasad et al., 1999; Salem et al., 2007). Consequently, pod set is related to daily maximum temperature. Optimum temperatures for pod set were estimated using the boundary line analysis method first suggested by Webb (1972). The boundary line is assumed to represent the potential expression of a trait in response to a predictor and in the absence of other limiting factors (Elliott and De Jong, 1993). Although the percentage of maximum pod set was different between the cultivars, cardinal temperatures for pod set were similar regardless of cultivars; the optimum and maximum temperatures were estimated to be about 35 and 42°C, respectively. The

cardinal temperatures for pod set were shown to be similar that for pollen germination and pollen tube growth of soybeans (Salem et al., 2007), suggesting that pod set would be strongly related to pollen viability. Although the temperature rise could lead to the increased flower production, the temperature above 35°C would sharply decrease the percentage of pod set and cause severe damage to the formation of pod number in soybean.

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OVERALL CONCLUSION

This study was conducted at the Experimental Farm of Seoul National University, Suwon, South Korea (37°16'N, 126°59'E) during the four years (1) to examine the effects of elevated air temperatures on the phenology, flowering, pod setting, yield components, and yield of soybean in a temperate region, (2) to estimate the optimum temperatures for pod setting, seed number, seed weight, and seed yield of soybean, and (3) to evaluate the impacts on global warming on soybean production in South Korea.

Growth periods (VE–R7) were significantly prolonged by the elevated temperatures, especially the R1–R5 period. Compared to the AT treatment, a significant yield reduction was observed at the AT+5.0°C treatment. Yield reductions resulted from limited seed number, which was mainly due to low the number of pods. Individual seed weight exhibited no significant variation among temperature elevation treatments; thus, seed weight likely had negligible impacts on seed yield. Regardless of cultivars or temperature treatments, the temporal distribution of flowering showed a bimodal temporal distribution. Elevated temperatures increased the flowering duration and the number of flowers differentiated, while decreased pod set in soybean. Pod number variations were more closely associated with pod set percentage variations rather than with flower number variations in hot summer years

(2013 and 2015), whereas the opposite associations were observed in cool summer year (2014).

Cardinal temperatures (T_{opt} , T_{max}) for pod set in soybean were estimated at about 35 and 42°C, indicating that pod set was strongly related to pollen viability. The optimum temperatures for seed number was estimated at about 26.5°C (VE–R5); the optimum temperatures (R5–R7) for single seed weight were estimated at 25.2°C for the Sinpaldalkong smaller-seeded cultivar, and at 22.3°C for the Daewonkong larger-seeded cultivar. The optimum growing season (VE–R7) temperatures for seed yield were estimated 26.4 and 25.0°C for the Sinpaldalkong and Daewonkong cultivars, respectively.

Considering the current soybean growing season temperature, which ranges from 21.7 (in the north) to 24.6°C (in the south) in South Korea, and the temperature response of potential soybean yields, temperature rise of less than approximately 1°C would not become a critical limiting factor for soybean production in South Korea. However, further warming of more than 1°C may have adverse effects on the soybean yield from southern region in South Korea, and temperature above 35°C would sharply decrease the pod set ratio and cause severe damage to the formation of pod number in soybean.

This study revealed that the number of pods was a major determinant in soybean yield variation under elevated temperature conditions. Heat stress could impair pollen viability resulted in a lower pod number. Under global

warming conditions, therefore, it will be required to avoid heat stress during the flowering and pod setting for stable production of soybean.

This study could not find the clear evidence that: (1) elevated temperatures increased the flowering duration and the number of flowers in soybean; (2) cultivars with small seed sizes had a higher optimum temperature for single seed weight than large-seeded cultivars in soybean. Further studies are needed to investigate the mechanism for these issues.

초 록 (ABSTRACT IN KOREAN)

온대지역의 콩 발육 및 수량 고온 반응

서울대학교 농업생명과학대학 식물생산과학부

최 덕 환

기후변화에 따른 온도 상승 및 그 변동성의 증대는 콩의 생육 및 수량에 크게 영향을 것으로 전망된다. 본 연구는 지구온난화가 콩의 발육, 수량 및 수량관련형질에 미치는 영향을 평가하고자, 유한신육형 품종인 신팔달콩 (성숙군 IV)과 대원콩 (성숙군 VI)을 공시품종으로 하여, 서울대학교 부속농장 (북위 37.27도, 동경 126.99도)에서 4년 (2009년, 2013년, 2014년, 2015년) 동안 수행되었다. 두 품종은 5월 30일부터 7월 11일에 이르기까지 다양한 시기에 걸쳐 플라스틱 포트 (직경 15cm, 높이 40cm)에 파종되었으며, 온도처리를 위해 파종 이후 수확기까지 대기온 및 대기온보다 1.5°C, 3.0°C, 5.0°C 높게 조절되는 온실에서 수분 스트레스가 없는 조건으로 재배되었다.

고온에서 두 품종 모두 전체 생육기간 (VE-R7)이 유의하게

늘어났는데, 특히 R1-R5기간이 증가하였다. 대기온 조건과 비교하였을 때, 1.5°C 및 3.0°C 높은 처리에서는 유의한 수량 차가 나타나지 않았지만, 5.0°C 상승에서는 유의한 수량 감소를 보였다. 5.0°C상승 하에서의 수량 감소는 협수 및 협당립수 감소에 기인한 입수 감소가 원인이었고, 고온 스트레스는 협당립수보다는 협수의 감소를 크게 유발하였다. 한편, 입중은 온도처리에 따른 유의한 차이를 보이지 않았고, 입중이 수량에 미치는 영향은 미미하였다.

수량의 결정요인인 협수는 화수와 결협률에 의해 결정된다. 품종 및 온도처리에 관계없이 개화의 시계열 분포는 이봉분포 (bimodal distribution)를 보였다. 고온 조건일수록 후기 피크 (peak)가 늦춰지고 커졌는데, 온도 상승이 개화기간과 화수를 증가시켰음을 나타낸다. 온도가 높아질수록 초기 화기 탈락률이 높아지고 꼬투리 대비 꽃이 떨어지는 비중이 높아졌으며 이는 고온에서 꼬투리 형성이 저해됨을 의미하고, 고온 스트레스로 인한 화분 활력 감소 또는 생식기관으로의 광합성 산물 공급 감소가 그 원인일 것으로 생각된다. 꽃이 피고 꼬투리가 형성되는 여름 기온이 고온이었던 2013년과 2015년에는 온도가 높아질수록 결협률이 유의하게 감소하였으나, 저온이었던 2014년에는 온도처리에 따른 결협률 차이가 없었으며, 온도와 품종의 상호작용효과는 없었다. 협수는 품종에 관계없이 고온이었던 해 (2013년과 2015년)에는 화수 차이보다는 결협률 차이와 깊게 연관되어 있었고, 저온이었던 해 (2014년)에는 그 반대 경향을 보였다.

결협률의 온도반응에 대하여 이차함수와 베타함수를 이용한

최대경계선 분석을 실시한 결과, 결협률을 위한 최적온도와 한계온도는 신팔달콩 34.8℃와 42.9℃, 대원콩 34.5℃와 41.6℃로 각각 추정되었다. 결협률의 온도반응이 화분발아 및 화분관 신장의 온도반응과 유사한 것으로 보아, 결협률은 화분 활력과 크게 관련 있는 것으로 여겨진다. 온도가 높아질수록 개화 수는 증가되지만, 35℃ 이상의 온도는 결협률을 급격하게 떨어뜨린다. 한편, 콩의 수량구성요소에 대한 온도 영향을 최대경계선 분석 (95% 분위회귀분석)을 통해 살펴보았을 때, 입수에 대한 적온 (VE-R5기간 기온)이 26.4에서 26.8℃로 추정되어 두 품종 간 차이가 미미하였고, 입중 적온 (R5-R7기간 기온)은 중립종인 신팔달콩이 25.2℃, 대립종인 대원콩이 22.3℃로 추정되어 대립종이 더 낮았다. 입수와 입중의 두 온도반응을 이용하여 수량을 위한 적온 (VE-R7기간 기온)을 계산한 결과, 신팔달콩과 대원콩이 각각 26.4℃와 25.0℃로 나타났다. 대한민국의 현재 콩 생육기간 (VE-R7) 평균기온은 21.7 (북부)에서 24.6℃ (남부)로 적온보다 낮은 수준이며, 앞으로 1℃ 이내의 온도상승은 대한민국 콩 생산의 제한요인으로 작용하지는 않을 것이다. 하지만, 그 이상의 온도상승은 남부지역부터 콩 수량에 부정적인 영향을 초래할 것으로 보이며, 35℃ 이상의 고온은 콩의 꼬투리 형성에 심각한 피해를 줄 것으로 보인다.

핵심어: 콩, 온도, 발육, 개화, 결협률, 수량