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A modification of temperature functions in SUBSTOR-Potato model for improving crop growth and yield simulation under high temperature condition

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Abstract

Potato phenology, growth, and yield is projected to be highly affected by global warming in the future. Therefore, assessing the climate change impacts and establishing adaptation strategies are needed. The objectives of this study were to evaluate and calibrate the potato growth model (SUBSTOR-Potato) under elevated temperature condition before applying the model to climate change impact assessments.

Planting date experiments under open field condition were conducted at the experimental farm of Seoul National University (37.27°N, 126.99°E), Korea in 2014 and 2015. For the spring season, three cultivars differing in maturity group (Irish Cobbler as extremely early; Superior as early; Atlantic as mid-late maturing) were grown at three different planting dates. Superior and Atlantic were planted at two planting dates in the fall of 2014. Tuber initiation onset dates varied from 11 to 22 days after emergence, depending on cultivars and planting dates. Tuber initiation onset was hastened curve-linearly with increasing temperature, showing optimum temperature at around 22-24°C in all the cultivars tested. and also longer photoperiod and lower solar radiation delayed tuber initiation in Superior and Atlantic. Those factors exerted interactive effects on tuber initiation multiplicatively. The most important determinant of tuber yield was growth duration, which is limited by the beginning of rainy season in summer and frost in the late fall. Yield increased along with delayed tuber initiation. Within the optimum temperature range (17-22°C), larger diurnal temperature range increased the tuber yield.

Elevated temperature experiment was conducted in four plastic houses controlled to target temperatures of ambient temperature (AT), AT+1.5°C, AT+3°C, and AT+5°C. Superior was planted at April 29 and September 17 in 2015. For the latter experiments, only emergence and tuber initiation onset was observed. Tuber initiation onset was delayed in spring season relative to fall season due to photoperiod effect. As affected by high temperature, low irradiance and long daylength, plants in AT+5.0°C failed to form tubers at spring season planting. Yield and harvest index tended to decrease with elevated temperature above ambient (22°C) and drop to almost nil at AT+5.0°C. Tuber number at early stage was reduced by higher temperature, resulting in the decrease of assimilates allocated to tuber and average weight of tubers at harvest. Stem growth was enhanced by elevated temperature at the expense of tuber growth.

The simulation performance of SUBSTOR-Potato model was evaluated using the above experimental data. The model simulated tuber initiation onset later than the actual as the model determines the tuber initiation date by extrapolating the linear tuber bulking rate to the time axis, and also showed poor performance in simulating tuber initiation onset under low solar radiation, long days, and high temperature condition. We modified the original function for determining the tuber initiation onset and also added a new function of solar radiation effects on tuber initiation under high temperature and long days. The modified model performed better than the original one in predicting not only tuber initiation but also tuber yield under both field and plastic house conditions. In addition, the original model could not explain tuber bulking rate changes as caused by the reduction of tuber number under elevated temperature conditions at early growth stage. The response of rate/duration of tuber formation to temperature was added to the model, resulting in the better accuracy but similar precision for estimating the temporal changes of tuber bulking and tuber yield.

According to our data, potato yield is expected to decrease under warmer climate than the current. However, the physiology of tuber initiation and growth are still not well understood and models are too simplified for predicting the heat stress. So further detailed studies are needed to grasp the knowledge of physiological responses of potato growth to high temperature and to add it to the models. Afterwards, validating the models under various environments should be preceded before applications.

keywords : Potato, climate change, high temperature, model, tuber initiation, tuber bulking, SUBSTOR-Potato

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Introduction

Potato is a major crop ranking not only the fifth in worldwide production but also the third in human consumption. In Korea, potato is the 2nd major food crop after rice in terms of domestic production (FAOSTAT, 2015). Due to its yielding capacity and nutritious benefits (Salaman, 1985), cultivation acreage has expanded rapidly during the last few centuries. Also Potato is highly recommended crop for food security as food demands increase due to population growth (FAO, 2009). Global climate change as accompanied by warming is projected to exert adverse impact on production of potato, which is known as cool season crop.

Global mean surface temperature has increased by 0.85°C (0.65-1.06°C) during 1880-2012 period, and it is projected to increase by 0.3-4.8°C for 2081-2100 relative to 1986-2005. South Korea experienced even faster warming, mean temperature increased by 1.87°C during 1908-2009. Mean surface temperature for South Korea is projected to increase by 5.9°C by the end of 21st century (IPCC, 2013, 2014).

Even though, role of potato as a food security crop is expected to increase in the future, the climate change impacts on potato and adaptation strategies are not sufficiently established. Generally, temperature is the most important factor for potato growth and yield (Smith, 1968). Optimal temperature for net photosynthesis is less than 25°C, but due to the reduction of harvest index under higher temperature, optimal temperature of yield is even less than that of net photosynthesis (Winkeler, 1971; Ku et al., 1977; Dwelle et al., 1981). Wheeler et al. (1986) showed optimal temperature for tuber yield are 20°C and 16°C for daylength of 12 and 24hours, respectively. However, temperature responses vary among cultivars and development stages, and especially, heat tolerance varies widely (Reynolds et al., 1990).

Various environmental factors other than temperature affect potato phenology and growth. Photoperiod is one of the most important factor for potato growth and development. Lorenzen and Ewing (1990, 1992) showed higher photosynthesis efficiency in short days and Ewing (1978) showed short days hastened tuber initiation onset. Low irradiance delays duration of tuber initiation and affects the number of tuber and tuber yield. However, interaction between environmental factors are not well understood. For instance, many studies concluded irradiance effects on tuber initiation onset is negligible, but Demagante and Vander Zaag (1988) showed low irradiance delays tuber initiation onset under high temperature and the effect varied among cultivars.

To investigate the complicated impacts of climate change and adaptation strategies, crop modeling can be a suitable tool (Haverkort and Top, 2011). Crop model is an integration of mathematical expressions about crop growth as functions of environmental factors. However, only few models are validated in diverse condition (Rubi Raymundo, 2014).

The objectives of this experiment are to examine the responses of potato growth and yield to elevated temperatures and planting dates for different cultivars and to evaluate and calibrate the potato growth model functions for tuber initiation onset and tuber bulking responses to temperature and other environmental factors.

Literature review

1. Response of potato growth to temperature

1.1 Tuber initiation onset

Tuber initiation onset is an important developmental event for potato, which is the first appearance of storage organ. Tuber initiation changes not only the proportions of assimilates partitioning to each organs, but also the whole plant photosynthesis rate by feedback effects of new sink (Moorby, 1968). Generally, delayed tuber initiation improves tuber yield (Gregory, 1965). Despite the importance of tuber initiation, definite response of tuber initiation to temperature is not established. Variation among cultivars, complex interactions between temperature and other factors and laboriousness of measuring tuber initiation made the study difficult.

However, some studies about cardinal temperature reported base temperature of 4-7°C, optimum temperature of 10-17°C, and maximum temperature above 28-30°C, which varied among cultivars (Burt, 1964, 1965; Moorby and Milthorpe, 1975; Hartz and Moore, 1978; Ingram and McCloud, 1984; Nowak and Colborne, 1989). These data have usually been obtained from mostly high latitude area (45-60°) and temperate region (above 30°). In low latitude area, different environments, such as higher temperature and relatively constant photoperiod around 12hours and irradiance, would make different responses of tuber initiation to temperature. Higher temperature enhanced the delaying effect of long photoperiod on tuber initiation onset

(Van Dam, J., 1996). Demagante and Vander Zaag (1988) showed combination of high temperature and low irradiance delayed tuber initiation onset under tropical region, but only extremely low irradiance affected tuber initiation onset under low-moderate temperature (Sale, 1973, 1976; O'Brien et al, 1998b).

1.2 Completion of tuber initiation and tuber number

Tuber initiation duration is the period between tuber initiation onset and completion of tuber initiation. Tubers are formed rapidly throughout the period, and remain constantly after the period. This period would be important for tuber yield because tuber number is highly correlated with tuber sink strength and tuber yield.

Higher temperature below relatively low temperature of 15°C hastened tuber initiation cessation and shortened the duration, but not much studies are done in tropical region (O'Brien et al., 1998a). Temperature had no significant effects on final tuber number under temperature range of 10-20°C, but final tuber number decreased with elevated temperature under tropical climate (Sale, 1979; Midmore, 1983).

For some cultivars, short days had shortened the duration of tuber initiation, but not for all cultivars. There are few evidences that photoperiod affects the duration of tuber initiation, but short days may reduce tuber number (O'Brien et al., 1998a). Struik (1986) showed that low irradiance delayed the cessation of tuber initiation. According to Menzel (1985), low irradiance reduces tuber numbers, however, removal of shading material after tuber initiation reduced the difference (Gray and Holmes, 1970). Also, Menzel (1985) showed high temperature enhanced the reduction of tuber number due to low irradiance.

1.3 Photosynthesis

Optimum temperature for leaf level photosynthesis is 24°C and decrease drastically above this temperature (Ku, 1977; Leach, 1982). Optimum temperature for gross and net photosynthesis are 24-30°C and below 25°C, respectively (Ku, 1977; Dwelle, 1981). Timlin (2006) concluded temperature effect on photosynthesis is negligible during early stage, and after this stage optimum temperature appeared to be 24°C and decreased to 16-20°C during the late stage of senescence. Therefore, optimum temperature for total biomass at the harvest is about 20°C, which is relatively low. Photosynthesis rate gets higher after tuber initiation or after early stage, and temperature and photoperiod affecting tuber initiation would play prominent role in changing the photosynthesis rate at early stage (Lorenzen and Ewing, 1990).

1.4 Assimilates allocation

Temperature is a prominent factor affecting the allocation of assimilates to different organs. After tuber initiation, proportion of assimilates allocating to tuber was reduced by high temperature and the surplus assimilates were allocated to the stem and enhanced the elongation of stem (Marinus and Bodlaender, 1975; Wheeler et al. 1986). Yield and harvest index declined under temperature above 24°C (Timlin et al., 2006).

Long photoperiod enhances stem growth, but if assimilates is sufficient, tuber bulking rate is not reduced (Wheeler, 1986). Similar to long days, low irradiance promotes leaf and stem growth at the expense of tuber growth (Gawronska and Dwelle, 1989). However, effects of long days to reduction of assimilates allocating to tuber are much smaller than the clear effect by high temperature (Van Ittersum, 1992; Van Ittersum and Scholte, 1992).

2. Temperature responses in potato growth model

Structure of potato growth models can be divided into thermal time routine including phenology calculation, canopy development routine, and assimilates allocation routine. In most of the routines, temperature functions are included as a prominent factor. Despite the importance of temperature functions in the models, most of the models are not validated under elevated high temperature.

2.1 Thermal time and phenology

Potato phenology can be divided into emergence to tuber initiation phase, tuber initiation phase, and senescence phase. Variation of phase length can be mostly explained by temperature, except the first phase during which photoperiod interacts with temperature (Kooman, 1996). Several thermal time methods have been introduced: linear functions including GDD, segmented and dent-like function; non-linear functions including beta function (Jefferies and Mackerron, 1987; Sands, 1979; Streck, 2007). Streck (2007) concluded that non-linear function for phenology showed better performance than linear functions. However, cardinal temperatures vary among cultivars and development stages; base temperature of 0-7°C(Sand, 1979; Mackerron, 2008; Streck, 2007); optimum temperature of 15-21°C and ceiling temperature of

28-30°C (Streck, 2007).

2.2 canopy development

Canopy development routine consists of photosynthesis functions and leaf growth & appearance functions. Two kinds of photosynthesis functions can be used; “big leaf” model using radiation use efficiency (RUE) with light interception and single leaf level photosynthesis model (Ritchie, 1995; Fleisher, 2010). SUBSTOR-Potato, one of the most popular RUE based model, reflects temperature effect on photosynthesis as a stress factor (Ritchie, 1995). However, RUE based model do not account for elevated atmospheric CO_2 concentration, water stress and senescence (Demetriades-Shah, 1992, 1994). Leaf-level model, including gas exchange functions, could overcome such limitations (Loomis and Amthor, 1999). The leaf-level model can simulate better under diverse environments including various temperature regimes, by using respective temperature functions to simulate leaf appearance, expansion of individual leaf and gas exchange model (Fleisher, 2006, 2010).

2.3. Partitioning

Proportion of assimilates allocated to tuber can be assumed as potato yield. Some models calculate yield by multiplying harvest index to total biomass, on the other hand, models, such as SUBSTOR and Potato Calculator, estimate daily biomass accumulation for each organ by calculating daily potential growth and priority for each organ or proportion from net assimilates (Jamieson, 2009; Ritchie, 1995). Generally, the proportion is determined by just phenology and tuber initiation is the transitional event for potato. The Potato Calculator model assumed 100% of assimilates translocate to tuber after early tuber initiation phase (after maximum canopy cover). Timlin (2006) simulated yield partitioning and growth of tuber with the consideration of temperature effects on the partitioning. Author showed that under high temperature partitioning proportion to the tuber reduced even though assimilation is similar to the lower temperature condition. Lafta and Lorenzen (1995) concluded that stem weight increased by the expenses of tuber under high temperature.

2.4. Validation

Most of validations for current potato models are performed with specific cultivars and locations (Raymundo, 2014). The SUBSTOR-Potato, which is the most tested potato model, showed wide range of RRMSE ranging from 14% to 51% with several validation studies (Kabat, 1995; Travasso, 1996; St'astna, 2010). However, potato models are not tested under high temperature and drought condition and only few models are validated under elevated CO_2 with meta analysis (Vanuytrecht, 2011). Thus, prior to applying the model to climate change impact assessments, models should be calibrated and validated with modern cultivars under the conditions of elevated temperature, CO_2 and stress condition in diverse geographical regions (Raymundo, 2014).

Materials and Methods

1. Planting date experiments

1.1. experimental setup

This study was carried out at the experimental farm of Seoul National University (37.27°N, 126.99°E), Korea. Three cultivars differing in maturity groups were planted at three different planting dates during the spring season of 2014 and 2015. Two cultivars were planted at two different planting dates during the fall season of 2014 (Table 3). Plants were grown under non-water stress condition, irrigated by hose and sprinkler in 2014 and 2015, respectively. Fertilizer were applied by the rate of 100kg ha^{-1} of N, 100kg ha^{-1} of P and 150kg ha^{-1} of K at the planting dates in the spring season of both years. For the fall season experiments, nitrogen fertilization rate was 1.5 times of the spring. Seed tubers were pre-germinated for two to three weeks and planted at a row spacing of 0.7m and 0.25m within rows.

1.2. Measurements

1.2.1. Plant growth

Emergence dates were recorded when 50% of the plants emerged from the soil surface. Tuber initiation onset date was considered to the date when 50% of sampled plants formed more than one tuber with at least 1cm diameter (Sands, 1979; Manrique and Hodges, 1989). Tuber initiation onset were observed by destructive sampling of three to five plants for each treatment. Plant dry mass, tuber fresh weight and leaf area were determined by harvesting five to six plants per one to three weeks interval. Vegetative mass was divided into leaf and stem and oven-dried at 80°C. Tubers were manually washed and sliced into 2cm before drying. Leaf area was measured with Li-3000 portable leaf area meter (Li-Cor, Lincoln, Nebraska, USA) after separated from stem. Measurements were carried out by bulk and individual in the spring season of 2014 and the rest, respectively. Tuber number per plant and fresh weight of each tuber were measured in 2015. Due to the beginning of rainy season and the frost, plants were harvested prior to the physiological maturity.

1.2.2. Meteorological data

Throughout the growing season, meterological elements, such as air temperature, solar radiation and precipitation were monitored at 5 minute intervals by data-logger (CR1000, Campbell Scientific, USA) equipped with temperature sensor, pyranometer and precipitation sensor (Fig. 1). Meteorological data from Suwon weather station, located next to the experimental farm, was used for the time when data-logger power was down. Average daily maximum temperature, minimum temperature and solar radiation throughout the growing season and period between emergence and tuber initiation onset (EM-TIO) were used for ridge regression. Daylength was calculated by the following equations (Goudriaan and Van Laar, 2012);

$$daylength = 12 * (1 + (\frac{2}{\Pi}) * asin(\frac{a}{b}))$$
$$a = \sin\lambda * \sin\sigma$$
$$b = \cos\lambda * \cos\sigma \qquad [1]$$
$$\sin\sigma = -\sin(\frac{\Pi}{180} * 23.45) * \cos(2 * \Pi * \frac{day\ of\ year + 10}{365})$$
$$\cos\sigma = \sqrt{1 - \sin\sigma^2}$$

where λ and σ are the degree of latitude and the solar declination angle, respectively.

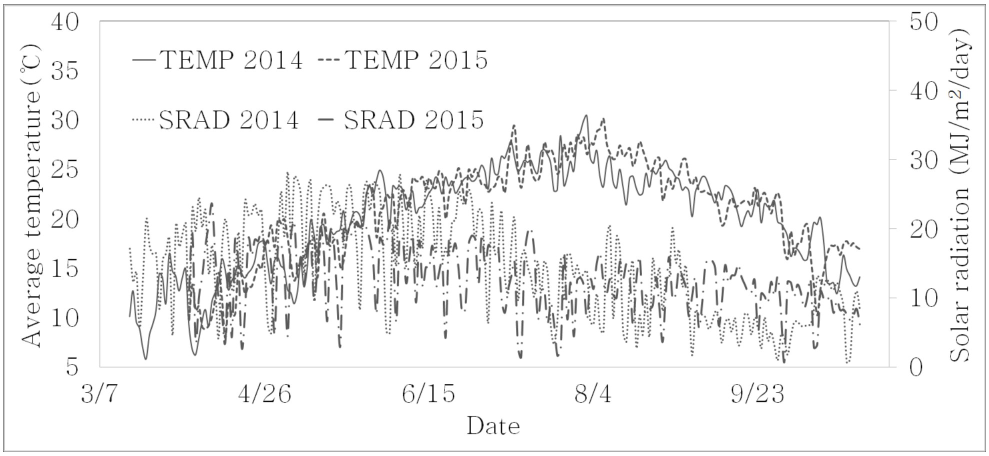

Fig. 1. Daily average air temperature and solar radiation during experimental season in 2014 and 2015.

2. Elevated temperature experiments

2.1. Experimental setup

This study was conducted under four plastic houses controlled to target temperatures of ambient temperature (AT), AT+1.5°C, AT+3.0°C, and

AT+5.0°C (Fig. 2). An early maturing cultivar, Superior was used in 2015. Pre-germinated seed tubers were planted at April 29 and September 17 with a row spacing of 0.7m and 0.2m within rows. Drip irrigation was implemented to prevent water stress. Fertilizer was applied at the rate of 1.5 times of the planting date experiments to compensate organic residues from previous cultivations.

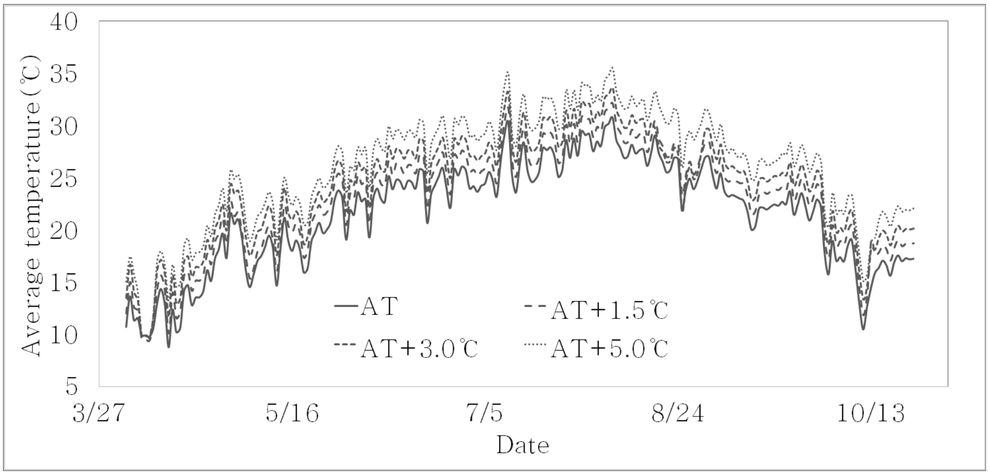

Fig. 2. Daily average air temperature inside the plastic houses which were controlled to different target temperatures in 2015.

2.2. Measurements

2.2.1. Plant growth

General methods for measuring plant growth were identical to the planting date experiments. After emergence, ten plants per treatments were sampled five times at an interval of two weeks and measurements were taken for each plant. Tuber was sorted into four groups, tuber weight of 1-49g, 50-99g, 100-149g and bigger than 150g.

2.2.2. Meteorological data

Air temperature and solar radiation were measured at 1 minute intervals with datalogger equipped with platinum resistor thermoprobe and pyranometer during the growth season. Daylength was calculated by equations [1].

2.3. Statistical analysis

Analysis of variance (ANOVA) was used to test the significance among temperature treatment means.

3. Effects of environmental factors on tuber growth

Multiplicative models [2] for tuber initiation onset using average temperature, solar radiation, daylength, and diurnal temperature range were made by a global optimization by differential evolution (DE) introduced by Storn and Price (1997). To analyze the relationship between tuber yield and environmental factors, ridge regression was used to prevent multicollinearity problems among meteorological variables. Linear ridge regression contained in the R package ‘ridge’ was used. Quadratic regression was performed to analyze the relationship between yield and average temperature for cultivar Superior.

$$EM-TIO=(a_1\times T_{av}^2+a_2\times T_{av}+a_3)\times(b_1\times DL+b_2)$$

$$\text{for } the\ planting\ date\ \text{experiment}$$

$$EM-TIO=(c_1\times SR+c_2)\times(d_1\times DL+d_2)\times(e_1\times DTR+e_2) \quad [2]$$

$$\text{for } the\ superior\ data\ pooled\ across\ the\ planting\ date\ \text{and}$$

$$the\ temperature\ \text{experiments}$$

where EM-TIO, Tav, DL, SR, and DTR are days from emergence to tuber initiation onset, average temperature (°C), daylength (hour), daily solar radiation (MJ/m^2/day), and diurnal temperature range (°C), respectively.

4. Modification of SUBSTOR-Potato model

Growth data of both planting dates and elevated temperature experiments for cultivar Superior were used for running the model. Cultivars Irish Cobbler and Atlantic were excluded due to the lack of the growth data under plastic houses.

4.1. General feature of SUBSTOR-Potato model

SUBSTOR-Potato is a potato growth model that simulates plant development, biomass accumulation, and partitioning affected by temperature, photoperiod and light interception (Ritchie, 1995). It is based on the CERES-type crop model, using capacity type models of soil water and nitrogen dynamics (Jones and Kiniry, 1986). Photosynthesis is estimated by using the RUE based model, similar to CERES-type model. The model took no account of yield components, such as tuber number and mean weight of tubers, regarding the storage organ as a single large tuber. As inputs, soil, climate, and cultural management data and genetic coefficients for specific cultivars are required because the model is designed to be used over wide environments and for different cultivars (Ritchie 1995).

4.2. Description of the modifications

4.2.1. Tuber initiation

To estimate tuber initiation date, SUBSTOR-Potato uses a method suggested by Sands (1979) that assumes tuber initiation date as an extrapolation of linear tuber bulking rate to the time axis. This method delays the timing as the initial lag phase of tuber growth is ignored (Ritchie, 1995). The model considers culitvar responses of tuber initiation to both temperature and photoperiod. For temperature function, the model uses 4 parameter dent-like function [3], including one cultivar parameter which is a coefficient of critical temperature for tuber initiation (TC, °C).

$$\begin{array}{ll}
RTF = 0.0 & \text{for } TEMP \leq 4.0 \\
RTF = 1.0 - (\frac{1}{36.0}) \times (10.0 - TEMP)^2 & \text{for } 4.0 < TEMP \leq 10.0 \\
RTF = 1.0 & \text{for } 10.0 < TEMP \leq TC \\
RTF = 1.0 - (\frac{1}{64.0}) \times (TEMP - TC)^2 & \text{for } TC < TEMP \leq TC + 8 \\
RTF = 0.0 & \text{for } TC + 8 < TEMP \\
TEMP = 0.75 \times T_{\min} + 0.25 \times T_{\max} &
\end{array} \qquad [3]$$

where RTF, Tmin, and Tmax are relative temperature factor, daily minimum and maximum temperature, respectively.

For photoperiod longer than 12hours, tuber initiation is assumed to be delayed and degree of delay (RDLF) is calculated considering the length of twilight (twilen) and the cultivar photosensitivity to tuber initiation (P2) by following function;

$$RDLF = 1.0 \qquad \text{for } twilen \leq 12.0$$
$$RDLF = (1.0 - P2) + (\frac{P2}{144}) \times (24.0 - twilen)^2 \quad \text{for } 12.0 \leq twilen \qquad [4]$$

Tuber initiation index (TII) is calculated by the function [5] and tuber initiation date is assumed when the cumulative tuber initiation index reaches 20.

$$TII = RTF \times RDLF + 0.5 \times (1.0 - MIN(SWFAC, NSTRES)) \quad [5]$$

where SWFAC and NSTRES are stress effects of water nitrogen on tuber initiation, respectively.

This approach in the model works well for estimating final yield under suitable climate condition. However, the model does not consider radiation and diurnal temperature under high temperature condition. As a first step of modification, temperature function was changed to a beta function and heat stress was considered when the daily maximum temperature exceed 29.68°C. Afterwards, we added relative radiation factor affecting tuber initiation (RSF) and subsidiary functions of interaction between temperature, daylength and radiation. The assumption was that radiation below the optimum radiation for tuber initiation would be a stress factor which increase linearly with decreasing solar radiation. The optimum radiation was determined by considering the interaction among temperature / daylength and radiation. Also, we used respective maximum tuber initiation rate for each cultivar reflecting the differences of maximum development rate among cultivars. The descriptions of the modification are described in Table 1. In Table 1 and 2, parameters for the modified model were estimated by minimizing root mean square error (RMSE) of tuber initiation date between observed and simulated, using DE.

Table 1. Modifications made to the tuber initiation functions.

Function	Description	Acronym	Parameter	Unit
Temperature	$RTF=\frac{(T_{ceil}-T_{av})}{(T_{ceil}-T_{opt})}\times(\frac{T_{av}}{T_{opt}})^{(\frac{T_{opt}}{T_{ceil}-T_{opt}})}$ for $0 \le T_{av} \le T_{ceil}$ $RTF=0.0$ for $else$ $RTF = 0.5\times RTF$ for $29.68 < T_{\max}$	T_{av}	Daily average temperature	℃
		T_{max}	Daily maximum temperature	℃
		T_{opt}	Optimum temperature for tuber initiation	℃
		T_{ceil}	Ceiling temperature for tuber initiation	℃
Radiation	$RSF=\frac{SRAD}{S_{opt}}$ for $0 \le SRAD \le S_{opt}$ $RSF = 1.0$ for $S_{opt} < SRAD$ or $S_{opt} = 0.0$	SRAD	Daily solar radiation	MJ/m^2/day
		S_{opt}	The least optimum solar radiation for tuber initiation	MJ/m^2/day
Interaction between temperature, daylength, and radiation	$STINTER = \frac{1.0}{1.0+e^{-\alpha\times(T_{av}-(T_{ceil}-\frac{\ln(99.0)}{\alpha})}}$ $\alpha = 2.0\times\frac{\ln(99.0)}{T_{ceil}}$ $SDINTER = 1.0-RDLF$ $S_{opt} = S_{\max}\times STINTER\times SDINTER$ $S_{\max} = 48.691$	S_{max}	S_{opt} when interactions are maximum	MJ/m^2/day
Daily tuber initiation index	$TII = R_{\max}\times RDLF\times RTF\times RSF$ $+0.5\times(1.0-MIN(SWFAC, NSTRES))$	R_{max}	Maximum daily tuber initiation rate	day^{-1}

4.2.2. Tuber bulking rate in early growth stage

The original model estimated tuber growth with a two-step process. For the first, it estimates the proportion of maximum potential tuber growth receiving first priority on assimilates (TIND) by following function;

$$\begin{aligned}
&TIND = \left(\frac{\sum_{i=1}^{3} DTII(i)}{3.0}\right) \times \left(\frac{1.0}{NFAC}\right) \times DEVEFF \quad \text{for } 1.0 < NFAC \\
&TIND = \left(\frac{\sum_{i=1}^{3} DTII(i)}{3.0}\right) \times DEVEFF \quad \text{for } NFAC \le 1.0 \\
&TIND = MAX(TIND, 0.0) \\
&TIND = MIN(TIND, 1.0) \\
&DTII = RTF + 0.5 \times (1.0 - MIN(SWFAC, NSTRESS, 1.0)) \\
&DTII = MIN(DTII, 1.0) \\
&DEVEFF = MIN((XSTAGE - 2.0) \times 10.0 \times PD, 1.0)
\end{aligned} \quad [6]$$

where DTII, NFAC, DEVEFF, XSTAGE and PD are daily tuber initiation index, nitrogen deficit factor, factors that limit carbon demand of tuber immediately after initiation, plant developmental stage and cultivar parameter of tuber bulking determinacy, respectively.

The second step is estimating potential tuber growth rate (PTUBGR) by a function of maximum tuber growth rate (G3) and relative temperature and calculating actual tuber growth rate (GROTUB) by following functions;

$$\begin{aligned}
&PTUBGR = \frac{G3 \times PCO2 \times ETGT}{PLTPOP} \\
&GROTUB = PTUBGR \times MIN(TURFAC, AGEFAC, 1.0) \times TIND
\end{aligned} \quad [7]$$

where PCO2, ETGT, PLTPOP, TURFAC and AGEFAC are effect of CO_2 concentration on plant growth rate, relative temperature factor for tuber growth, plant population per m^2, water and nitrogen stress, respectively.

However, the model does not consider temperature and radiation effects on duration of tuber initiation. High temperature and low radiation prolong the duration, resulting in the delayed onset of linear tuber bulking period and reduced yield. We modified the equation of DTII by adding radiation effect on tuber sink strength during tuber initiation phase as below;

$$TS_{opt} = S_{\max} \times (0.5 + 0.5 \times STINTER)$$

$$TRSF = \begin{cases} 0.0 & \text{for } SRAD < 0.0 \\ \dfrac{SRAD}{TS_{opt}} & \text{for } 0.0 \le SRAD \le TS_{opt} \\ 1.0 & \text{for } TS_{opt} < SRAD \text{ or } TS_{opt} = 0.0 \end{cases}$$

$$CTRSF = CTRSF + TRSF \qquad [8]$$

$$DTII = 0.9 \times RTF + TRSF + 0.5 \times (1.0 - MIN(SWFAC, NSTRES, 1.0))$$

$$\text{for } CTRSF < CTMAX$$

$$DTII = 1.9 \times RTF + 0.5 \times (1.0 - MIN(SWFAC, NSTRES, 1.0))$$

$$\text{for } CTMAX \le CTRSF$$

where TSopt, TRSF, CTRSF, TRSF, and CTMAX are optimum solar radiation for tuber formation after tuber initiation, relative solar radiation factor for tuber initiation duration, cumulative relative factor for tuber initiation duration, and the flag of cumulative relative factor when the tuber formations are completed, respectively.

CTMAX was estimated to 8.55 by minimizing mean absolute percentage error (MAPE) between observed and simulated temporal tuber dry weight using the DE.

4.3. Model evaluation

Prior to the model evaluation, genetic coefficients were estimated by the DE (Table 2), minimizing RMSE and MAPE between observed and simulated results of tuber initiation date and temporal tuber dry weight, respectively. To evaluate the model, RMSE and r^2 for the both models were compared for tuber initiation. For tuber growth and final yield, MAPE and in addition the index of agreement (d) developed by Willmott (1981) were used to compare the temporal data.

Table 2. Genetic coefficients of cultivar Superior in the original SUBSTOR-Potato model and the modified model.

Acronym	Parameter	Units	Value
Original model			
G2	Leaf expansion rate after tuber initiation	$cm^2/m^2/day$	2574.66
G3	Potential tuber growth rate	$g/m^2/day$	27.78
PD	Tuber bulking determinacy		0.34
P2	Sensitivity of tuber initiation to photoperiod		0.00
TC	Sensitivity of tuber initiation to temperature	°C	17.40
Modified model			
G2	Leaf expansion rate after tuber initiation	$cm^2/m^2/day$	2747.40
G3	Potential tuber growth rate	$g/m^2/day$	24.23
PD	Tuber bulking determinacy		0.28
P2	Sensitivity of tuber initiation to photoperiod		0.79
T_{opt}	Optimum temperature for tuber initiation	°C	21.90
T_{ceil}	Ceiling temperature for tuber initiation	°C	30.67
R_{max}	Maximum daily tuber initiation rate	day^{-1}	2.43

Results

1. Responses of potato development and growth to planting dates

Air temperature tends to increase until the beginning of August, reaching average temperature of 30°C in Suwon (Fig. 1). The daylength is near 15 hours at summer solstice which falls on June 21. During the spring season, later planting caused higher temperature and longer days while opposite for the fall season. Plantings in the fall season were delayed by the continuos rainfall, causing shorter daylength throughout the growing season compared to the spring season and the ordinary cultivation period in the fall season (Table 3, 4).

1.1. Tuber initiation onset

As shown in the Table 3, tuber initiation onset occurred from 11 to 22 days after emergence according to planting dates and cultivars. In the spring season, the extremely early culitvar Irish Cobbler formed tuber about 1.8 and 5 days earlier than Superior and Atlantic on average. As temperature increase with delayed planting in the spring, tuber initiations were hastened for Irish Cobbler and Atlantic, except for the last planting of Atlantic. Irish Cobbler and Atlantic are known as non-photosensitive and highly thermo-sensitive cultivars, respectively (Miller, 1941; Tibbitts, 1992). Thus, it could be interpreted as the temperature effects on tuber initiation overcompensated the delaying effect by the lengthened daylength in the later planting. However, Superior did not show consistent response to average temperature change and daylength, but as diurnal temperature range decreased, tuber initiation onset was delayed in the both year. In the fall season, tuber started to form earlier than the spring season, even though average temperature and diurnal temperature range were, respectively, similar and relatively smaller as compared to those at the late planting in the spring season. This indicates that the main meteorological element affecting tuber initiation could be the daylength.

1.2. Yield

As presented in Table 4, at the later plantings in the spring and the fall seasons cultivation period was shortened by the beginning of rainy season and the frost, respectively, resulting in the decreased yield. During the spring experiments, the mean daily average temperature increased from 17.1°C to 22.9°C with delayed planting and diurnal temperature range decreased with the delayed planting dates. Average daily solar radiation was not different among the spring plantings. However, due to the difference of growth duration among the planting dates, meteorological effects on tuber yield are not clearly shown. Among cultivars, when the growth duration exceed 100 days, late-maturing cultivar tends to have higher yield, but no consistent trends were found in the shorter growth duration.

Table 3. Dates of planting, emergence, tuber initiation onset, and meteorological elements averaged during the period from emergence to tuber initiation onset under different planting dates in 2014 and 2015.

Cultivar	Maturity group	Year	Planting date	Emergence date	Tuber initiation onset date	Solar radiation (MJ/m^2/day)	Average temperature (^{o}C)	Diurnal temperature range (^{o}C)	Daylength (hour)
Irish Cobbler	Extremely early	2014	March 19	April 8	April 26	17.5	14.2	13.2	13.0
			April 10	April 29	May 16	22.3	15.8	11.7	13.7
			April 30	May 14	May 25	22.0	19.3	12.2	14.1
		2015	April 10	April 30	May 14	21.3	17.3	12.0	13.7
			May 4	May 17	May 31	23.8	19.3	13.8	14.2
			May 14	May 29	June 10	22.3	21.6	12.0	14.4
Superior	Early	2014	March 19	April 10	April 25	17.7	14.6	13.1	13.0
			April 10	April 30	May 18	22.8	16.1	12.2	13.8
			April 30	May 15	May 29	22.6	20.0	12.3	14.2
			Sep. 12	Sep. 23	Oct. 5	4.4	19.6	8.4	11.7
			Sep. 19	Oct. 1	Oct. 12	6.8	17.7	11.8	11.4
		2015	April 10	April28	May 17	20.5	17.4	11.8	13.7
			May 4	May 18	June 1	23.7	19.5	13.7	14.2
			May 14	May 29	June 15	21.7	22.2	11.5	14.5
Atlantic	Mid-late	2014	March 19	April 12	May 3	17.5	15.0	11.9	13.2
			April 10	May 1	May 20	22.8	16.5	12.5	13.8
			April 30	May 16	June 4	20.6	21.0	11.9	14.2
			Sep. 12	Sep. 22	Oct. 7	4.8	19.3	9.2	11.7
			Sep. 19	Oct. 2	Oct. 15	8.1	17.0	12.0	11.3
		2015	April 10	April 27	May 19	19.7	17.4	11.6	13.7
			May 4	May 18	June 4	24.2	20.0	13.6	14.3
			May 14	May 31	June 18	22.2	22.6	11.5	14.5

Table 4. Yield, growth duration, and meteorological elements averaged throughout the growth period under different planting dates in 2014 and 2015.

Cultivar	Year	Planting date	Days from emergence to tuber initiation onset	Days from planting to harvest	Yield (t/ha)	Solar radiation (MJ/m^2/day)	Average temperature (°C)	Diurnal temperature range (°C)	Daylength (hour)
Irish Cobbler	2014	March 19	18	100	9.2	19.2	17.1	11.3	13.6
		April 10	17	92	7.2	19.6	19.8	10.8	14.0
		April 30	11	72	4.3	20.6	21.2	10.5	14.3
	2015	April 10	14	102	7.0	20.3	20.1	11.2	14.0
		May 4	14	85	5.7	20.3	22.1	10.5	14.3
		May 14	12	75	4.0	20.0	22.9	10.2	14.4
Superior	2014	March 19	15	100	10.6	19.2	17.1	11.3	13.6
		April 10	18	92	8.6	19.6	19.8	10.8	14.0
		April 30	14	72	5.1	20.6	21.2	10.5	14.3
		Sep. 12	12	56	2.7	7.1	18.3	10.7	11.3
		Sep. 19	11	49	1.3	7.3	17.6	11.0	11.1
	2015	April 10	19	102	13.3	20.3	20.1	11.2	14.0
		May 4	14	85	7.8	20.3	22.1	10.5	14.3
		May 14	17	75	3.7	20.0	22.9	10.2	14.4
Atlantic	2014	March 19	21	107	11.2	19.2	17.6	11.2	13.6
		April 10	19	92	8.0	19.6	19.8	10.8	14.0
		April 30	19	72	5.5	20.6	21.2	10.5	14.3
		Sep. 12	15	56	2.5	7.1	18.3	10.7	11.3
		Sep. 19	13	49	0.6	7.3	17.6	11.0	11.1
	2015	April 10	22	102	16.0	20.3	20.1	11.2	14.0
		May 4	17	85	8.7	20.3	22.1	10.5	14.3
		May 14	18	75	5.2	20.0	22.9	10.2	14.4

2. Responses of potato growth and yield to elevated temperature

2.1. Tuber initiation onset

As shown in Table 5, average temperatures of the spring season experiment were approximately 4°C higher than those of the fall experiment, showing similar temperatures between AT of the spring experiment and AT+5.0°C of the fall experiment. Solar radiation of the spring experiment was twice that of the fall experiment and daylength was 2.9 hours longer in the spring experiment.

Tuber initiation onsets were slightly delayed at AT+3.0°C and inhibited at AT+5.0°C in the spring season experiment. In the fall season experiment, there were no variation of EM-TIO among the temperature treatments. EM-TIO in the spring season experiment was twice as long as that of the fall season experiment due to the difference of daylength. Tuber initiation was delayed in plastic houses compared to the open field and the differences between the two experiments were solar radiation and diurnal temperature range (Table 3 and 5).

2.2. Growth and yield

As presented in Fig. 3, total dry weight was reduced significantly with temperature elevation treatments above AT+3.0°C and the total dry weight of AT+5.0°C was lower than a half of that in the other treatments. Tuber dry weight decreased significantly until harvest with temperature elevation. As presented in Table 6, final yield decreased substantially with temperature elevation above ambient, dropping to almost nil in AT+5°C. As presented in

Fig 4, less tubers were formed during the early season of tuber initiation (28-42 days after planting; DAE) under elevated temperature treatments, while no statistical difference in tuber number were found thereafter among temperature treatments except AT+5.0°C. Therefore, proportion of small tubers increased with temperature elevation above ambient. The proportion of assimilates partitioning to stem increased at the expense of tuber growth along with temperature elevation. Dry weight ratio of leaf to stem decreased along with elevated temperature.

Table 5. Tuber initiation onset as affected by elevated temperature treatments and meteorological elements averaged over the period from emergence to tuber initiation onset in a potato cultivar Superior in 2015.

Planting date	Temperature treatments	Emergence date	Tuber initiation onset date	Solar radiation (MJ/m^2/day)	Average temperature (°C)	Diurnal temperature range (°C)	Daylength (hour)
April 29	AT	May 10	June 5(26)	16.2	20.0	17.4	14.2
	AT+1.5°C	May 9	June 4(26)	16.6	21.4	18.9	14.1
	AT+3.0°C	May 10	June 7(28)	16.3	23.1	18.1	14.2
	AT+5.0°C	May 11	Failed	16.1	24.8	17.3	14.2
Sep. 17	AT	Sep. 30	Oct. 14(14)	8.9	16.4	14.4	11.4
	AT+1.5°C	Oct. 1	Oct. 15(14)	9.0	17.7	17.4	11.3
	AT+3.0°C	Sep. 30	Oct. 14(14)	8.9	19.2	17.0	11.4
	AT+5.0°C	Oct. 9	Oct. 23(14)	8.2	20.1	16.5	11.0

( ) is days from emergence to tuber initiation onset.

Table 6. Tuber yield as affected by elevated temperature treatments and meteorological elements averaged throughout the growth period.

Planting date	Temperature treatments	Yield (ton/ha)	Solar radiation (MJ/m^2/day)	Average temperature (°C)	Diurnal temperature range (°C)	Daylength (hour)
April 29	AT	6.4	14.8	22.4	15.2	14.3
	AT+1.5°C	4.5	14.8	23.8	16.1	14.3
	AT+3.0°C	2.7	14.8	25.3	15.7	14.3
	AT+5.0°C	0.0	14.7	27.1	15.9	14.3

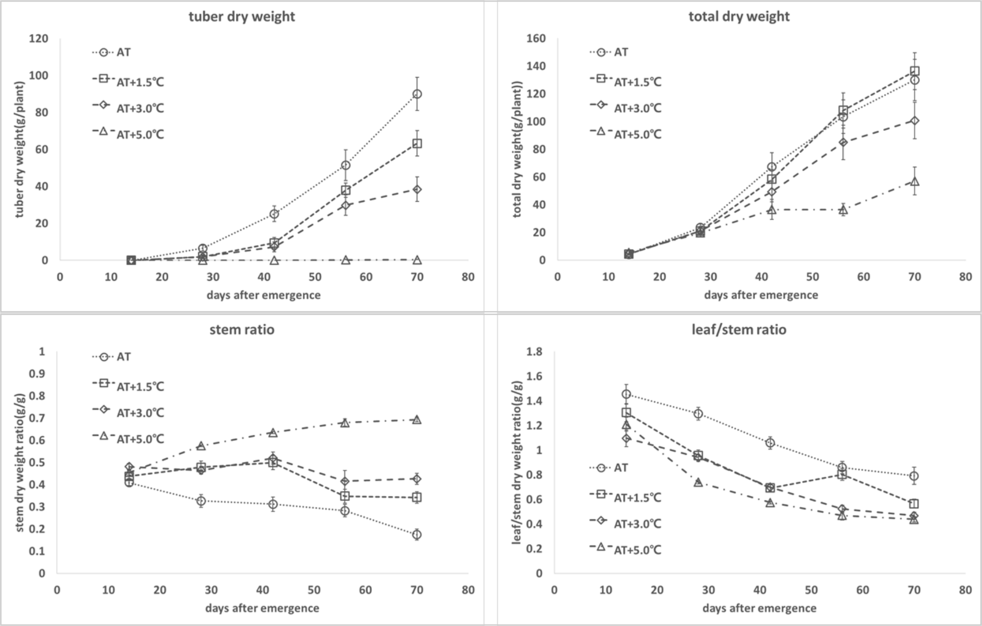

Fig. 3. Temporal changes of tuber dry weight, total dry weight, stem dry weight ratio to total dry weight and leaf dry weight ratio to stem dry weight under different elevated temperature treatments (vertical bars represent standard error).

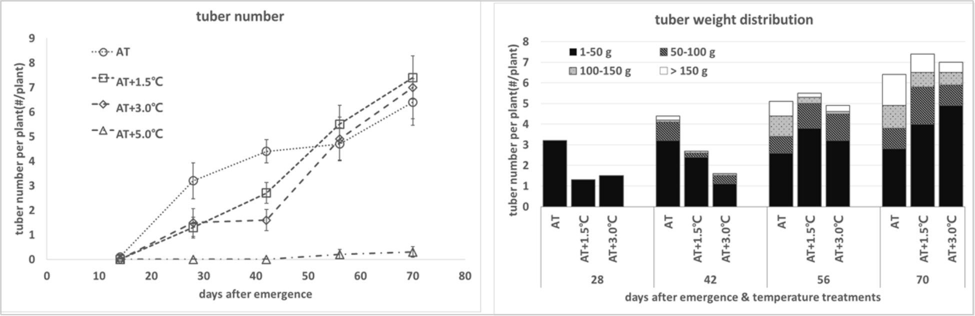

Fig. 4. Temporal changes of tuber number and tuber weight distribution under different elevated temperature treatments (vertical bars represent standard error).

3. Effects of environmental factors on tuber initiation and growth

3.1. Tuber initiation onset

The responses of tuber initiation onset to environments can be explained by the models presented in Table 7. In the open field condition, temperature was an important factor for tuber initiation onset commonly to all the cultivars tested, while daylength was another important factor only in two cultivars Superior and Atlantic except an extremely early cultivar Irish Cobbler. In Irish Cobbler temperature is the sole factor affecting tuber initiation onset. Tuber initiation onset response to temperature was very similar among cultivars, becoming earlier curve-linearly with increasing temperature up to optimum average temperature and showing similar optimum temperature of around 22-24°C. Tuber initiation onset tended to delay with the increasing daylength very similarly in the two cultivars Superior and Atlantic. In these cultivars temperature and daylength seemed to exert effects on tuber initiation onset interactively, exaggerating each other. Only daylength and average temperature were not sufficient for explaining tuber initiation onset variation of Superior at spring season in temperature controlled plastic houses with much larger diurnal ranges of temperature and lower solar radiation than in the open field. As in Fig. 5, the model using all the data pooled across transplanting date experiments in open field and elevated temperature experiments in plastic houses shows that the effect of solar radiation to tuber initiation onset of

Superior varied with different daylength and diurnal temperature range. Solar radiation had relatively small effects on tuber initiation onset under short day in fall season. However, tuber initiation onset was highly affected by solar radiation in the spring season, especially under the plastic houses, where daylength and diurnal temperature range were long and large.

3.2. Yield

Relative importance of yield-related factors was analysed using ridge regression for open field experimental data as shown in Table 8. Tuber yield tended to increase significantly with the increased growth duration and the delayed tuber initiation (longer EM-TIO) regardless of cultivars and planting seasons. Solar radiation showed significantly positive relationship with tuber yield only in cultivar Superior, while average temperature showed significantly negative relationship with tuber yield only in cultivar Irish Cobbler. However, diurnal temperature range showed highly significant positive relationship with tuber yield in all the cultivars tested.

The yield response to average temperature during growth period were analyzed for the data pooled across transplanting date experiments in the open field and temperature elevation experiments in plastic houses for cultivar Superior. As shown in Fig. 6, tuber yield showed quadratic response to average air temperature. Tuber yield reached maximum at around 20°C, decreased drastically above this temperature, and dropped to almost nil at 27°C.

Table 7. Parameters of the tuber initiation models (equation [2]) obtained by DE.

Cultivars	Parameters						r^2
Planting date experiment							
	a_1	a_2	a_3	b_1	b_2	-	
Irish Cobbler	0.104	-4.63	63.2	-	-	-	0.85
Superior	-0.18	8.38	-155.4	-0.03	0.17	-	0.63
Atlantic	0.23	-11.27	207	0.029	-0.15	-	0.75
Pooled with temperature experiment							
	c_1	c_2	d_1	d_2	e_1	e_2	
Superior	-0.28	12.81	3.74	-33.58	0.0062	0.054	0.90

a and b are the coefficients of temperature and daylength for the tuber initiation model of the planting date experiment.

c, d, and e are the coefficients of solar radiation, daylength, and diurnal temperature range for the tuber initiation model of Superior data pooled across the planting date and temperature experiments.

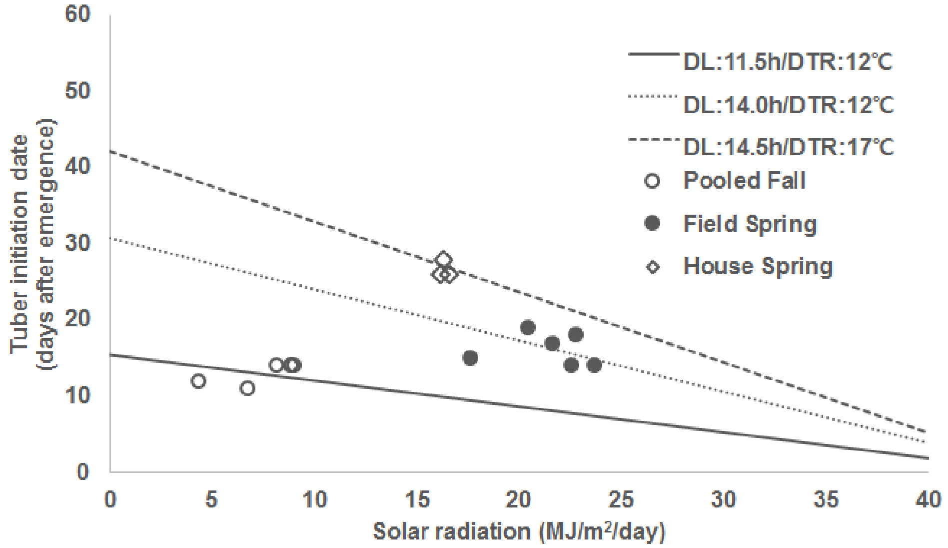

Fig. 5. Relationship of duration from emergence to tuber initiation onset with solar radiation, daylength (DL), and diurnal temperature range (DTR) in cultivar Superior. Data were pooled across the planting date and the temperature experiments.

Table 8. Ridge regression analysis of the relationship of tuber yield with growth duration, tuber initiation duration, and meteorological elements averaged over whole growth period.

Planting season		Spring			Spring+fall	
Cultivar		Irish Cobbler	Superior	Atlantic	Superior	Atlantic
Intercept		1.08	-75.76	-62.78	-36.21	-81.55
Days from planting to harvest	Coef.	0.04	0.19	0.10	0.07	0.09
	SC	1.07	5.36	3.02	3.46	4.98
	Pr(>|t|)	0.008	0.000	0.001	0.000	0.005
Days from emergence to tuber initiation onset	Coef.	0.26	0.03	0.47	0.24	0.47
	SC	1.61	0.16	1.94	1.79	3.68
	Pr(>|t|)	0.007	0.815	0.066	0.030	0.048
Solar radiation (MJ/m^2/day)	Coef.	-0.19	1.76	1.16	0.10	0.03
	SC	-0.22	2.04	1.36	1.57	0.53
	Pr(>|t|)	0.676	0.003	0.244	0.004	0.663
Average temperature (°C)	Coef.	-0.26	-0.03	0.04	-0.09	0.60
	SC	-1.18	0.14	0.18	-0.51	3.27
	Pr(>|t|)	0.007	0.846	0.847	0.442	0.062
Diurnal temperature range (°C)	Coef.	0.66	2.98	2.82	2.73	5.43
	SC	0.64	2.86	2.51	2.69	5.02
	Pr(>|t|)	0.033	0.000	0.000	0.000	0.003
RP		0.03	0.09	0.61	0.71	0.14

Coef., SC, Pr, and RP are represent ridge regression coefficient, scaled ridge regression coefficient, probability, and ridge parameter, respectively

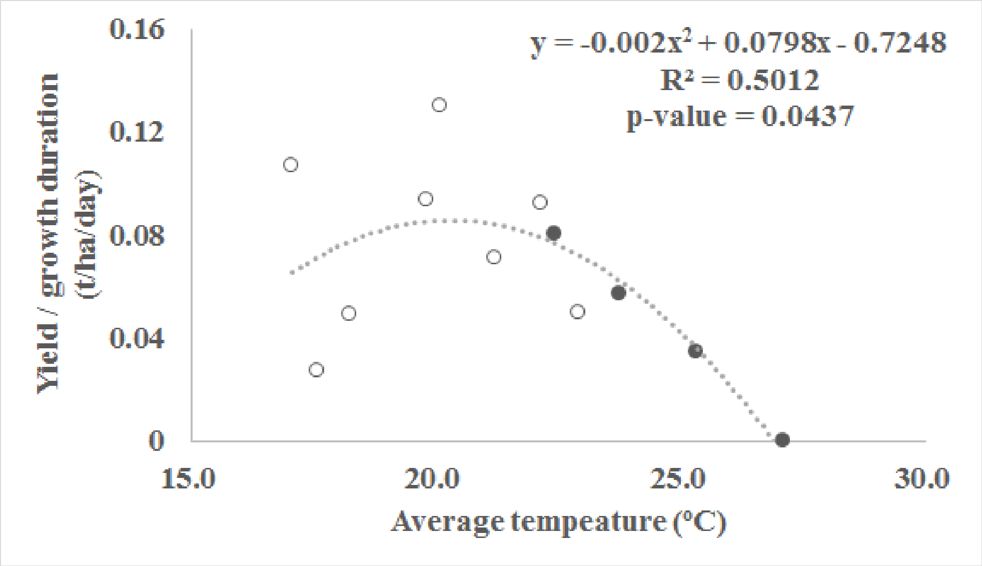

Fig. 6. Quadratic regression of tuber yield divided by growth duration with daily mean temperature averaged throughout the growth period in a cultivar Superior. (Open and closed circle represent the planting dates experiments data in the open field and the elevated temperature experiment data in the plastic houses, respectively.)

4. Modification of SUBSTOR-Potato

4.1. Tuber initiation onset

As shown in Fig 7, the original model failed to estimate tuber initiation under both open field and plastic houses. In the open field experiments and the fall season experiment in the plastic houses, tuber initiation dates were simulated later than the observed ones. As in Table 2, cultivar coefficient of Superior for photosensitivity (P2) was estimated as zero, indicating that Superior is very early cultivar with no photosensitivity. However, Superior was observed to have formed tuber even earlier than the model. The reason is that the original model ignores the lag phase during early tuber initiation phase. Also, the simulated results of tuber initiation were hastened for the spring season experiments in the plastic houses. As mentioned above, tuber initiation could be delayed by low solar radiation and large diurnal temperature fluctuation under high temperature, but the original model does not reflect this phenomenon. The modified model which included these phenomena in predicting tuber initiation onset worked well for both cases, reducing RMSE from 6.57 to 1.32 days as in Fig. 8.

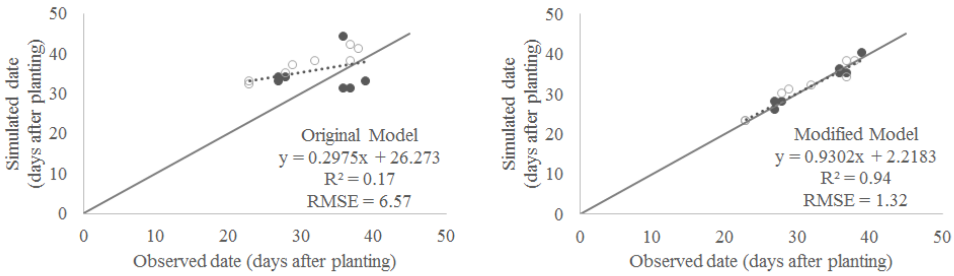

Fig. 7. Comparison between observed and simulated tuber initiation date as simulated by the original and modified SUBSTOR-Potato model. (Open and closed circle represent the planting dates experiments data and the elevated temperature experiment data, respectively.)

4.2. Tuber bulking and yield

As shown in Fig. 8 and Table 9, the modified model predicted tuber bulking until 20 days after tuber initiation onset better than the original model in all the treatments except for AT and

AT+3.0°C. Both models showed poor performances for those two elevated treatments. Judging from the root mean square error and mean absolute percentage error (MAPE), the modified model showed a little better accuracy than the original one in predicting the temporal tuber growth during whole growth period in open field and temperature-controlled plastic house conditions, while the overall performances were found similar showing the same Willmott index.

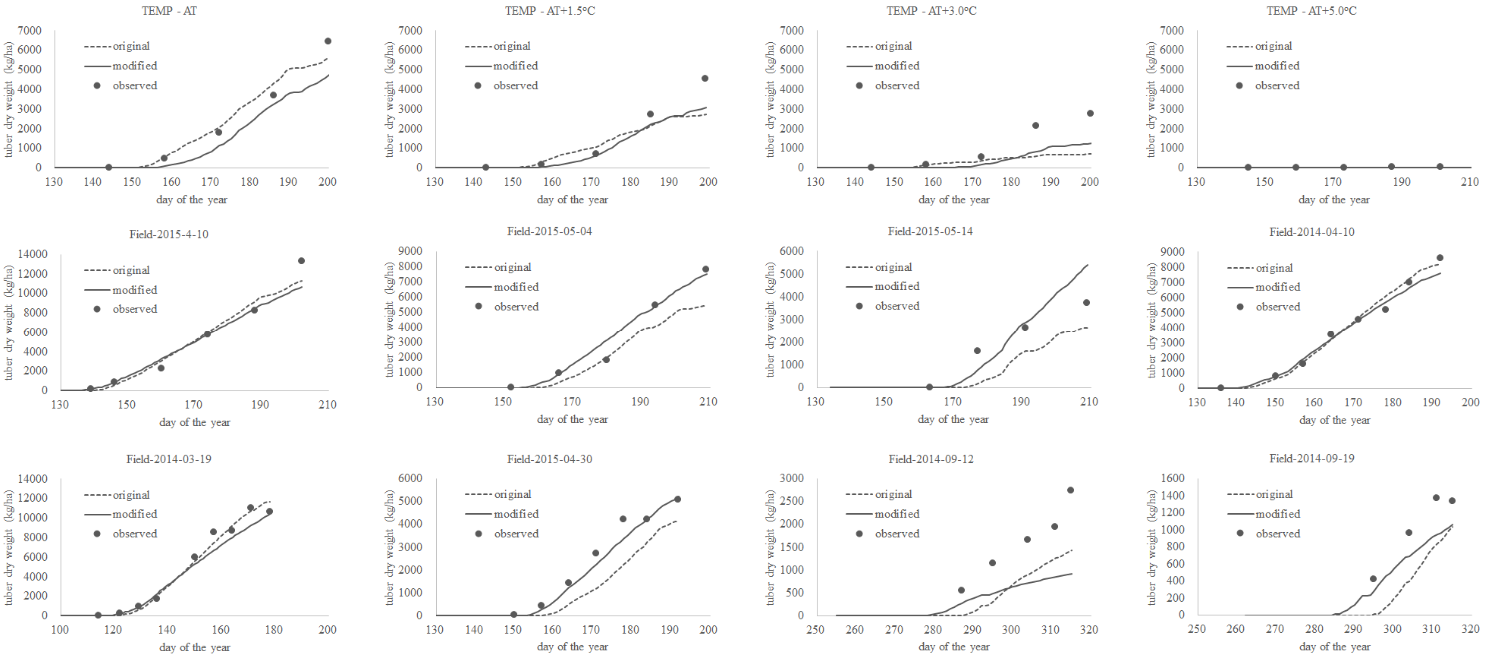

Fig. 8. Comparison between observed and simulated temporal tuber dry weight increases by the original and modified SUBSTOR-Potato models.

Table 9. Comparison of tuber growth and yield simulation performances between the original and the modified SUBSTOR-Potato model.

Parameter			RMSE (kg/ha)		MAPE		R-square		Willmott index	
			Original	Modified	Original	Modified	Original	Modified	Original	Modified
Temporal tuber dry weight increase	During 20 days after tuber initiation		492.1	316.7	0.61	0.41	0.49	0.75	0.80	0.90
	whole growth period	Planting date exp.	893.0	809.2	0.39	0.25	0.95	0.95	0.98	0.98
		Elevated temp. exp.	898.5	846.0	0.48	0.55	0.82	0.95	0.94	0.94
Final tuber yield		Planting date exp.	1363.6	1321.3	0.22	0.21	0.94	0.90	0.97	0.97
		Elevated temp. exp.	1411.8	1337.0	0.57	0.53	0.88	0.97	0.91	0.91

RMSE, MAPE, and Willmott index are root mean square error, mean absolute percentage error, and index of agreement developed by Willmott, respectively.

Discussion

Future potato yield is projected to decrease in many regions because of temperature increase due to global warming (Hijmans, 2003). The yield decreases due to warming would be attributed to the reduced assimilates allocating to tuber, shift of tuber initiation onset and slower tuber formation during the initiation phase, decrease of growing season, etc.

Tuber initiation was hastened by higher temperature under the current climate in Suwon (Table 7). However, tuber initiation will be delayed by the temperature above 22-24°C and Streck (2007) suggest similar optimum temperature for tuber initiation of 15-21°C. Contrast to the common result, tuber initiation was delayed under the plastic house condition due to reduced solar radiation level (16MJ/m^2/day) which was relatively higher than the reported critical solar radiation level of 7MJ/m^2/day (O'brien, 1998a) and larger diurnal range of temperature. Demagante and Vander Zaag (1988) also suggested that reduced solar radiation (thought to be above 10MJ/m^2/day) under high temperature delay tuber initiation. This result would be supported by the report of Jackson (1999) that high temperature, long day, and low solar radiation have similar mechanism of delaying tuber initiation by increasing gibberellin level which is known as an inhibitor of tuber formation. Low radiation seems to intensify the response of tuber initiation onset to daylength and temperature. Also, according to our data, large diurnal temperature range is beneficial for tuber formation under open field condition, but the effect was opposite when the average temperature and fluctuation range exceed 22°C and 17°C, respectively (Table 3, 5). There were studies suggesting diurnal fluctuations are beneficial to tuber initiation (Werner, 1935; Bennett, 1991), but not for the opposite. The previous studies were conducted under short days or daily maximum temperature of 22°C. In our experiments in plastic houses, high diurnal temperature range would have caused daily maximum temperature above 30°C, causing heat stress.

In the current climate in Suwon, where average temperature is around 20°C during the potato growth season, tuber yield is not highly affected by slight temperature elevation, while decrease of diurnal temperature range could be more detrimental to tuber yield than the increase of average temperature (Table 8). However, if average temperature increase more than 2-3°C, tuber yield would decrease drastically and drop to almost nil at 27°C as in Fig. 6. This coincides with the result from Wheeler (1986) that optimum temperature for tuber yield are 20°C and 24°C under daylength of 12 and 16 hour, respectively. In our study and previous research (Timlin, 2006) yield reduction by elevated temperature was mainly due to reduced assimilates partitioning ratio to tuber and enhanced stem growth. Due to reduced sink strength of tuber by elevated temperature, tuber formation was delayed, which coincides with the study (Wardlaw, 1990) that organ initiation often decreases and abortion increases with decreased source strength. Delayed tuber formation leaded to large number of smaller tuber and great yield loss at harvest (Fig. 3, 4). Also, tuber initiation makes diversion of assimilates to tuber, thus early tuber initiations cause small plants and leaf area leading to lower final yield (Ivins and Bremner, 1965;

Bremner & Radley, 1966). Therefore, environmental conditions during the early growth (before tuber initiation and early tuber growth phase) may play crucial role for the late tuber growth. In conclusion, lengthened growth period, delayed tuber initiation onset, higher solar radiation, and current average temperature with large daily temperature fluctuation will increase tuber yield, but temperature above the current will cause yield loss.

The original SUBSTOR-Potato model does not account of radiation and diurnal temperature fluctuation effects on tuber initiation and tuber bulking at early season under high temperature condition. The modified model simulates tuber initiation considering above factors. The modified model performed better for estimating tuber initiation onset and early season tuber bulking, but model failed to simulates tuber bulking for some treatments. Diversion of assimilates among organs and the change of canopy structure under high temperature and so on can exert influences on tuber bulking which are not considered in the model. Therefore, further detailed studies about potato growth under high temperature is needed to improve the model. Also, the model should be validated with individual data set from diverse environmental conditions.

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고온조건에서 감자 생육과 수량 모의 성능 향상을 위한 SUBSTOR-Potato 모델의 온도 반응식 개선

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초록

지구 온난화에 의한 미래의 기후변화는 감자의 생물계절, 생육 및 수량에 지대한 영향을 미칠 것으로 예상되므로 그 영향을 평가하여 적응대책을 수립하여야 한다. 이 연구는 작물모델을 이용하여 기후변화 영향을 평가하기 위한 사전 단계로 감자 생육 모델인 SUBSTOR-Potato 모델의 고온조건에서 생육과 수량 모의 성능 평가 및 개선을 하고자 한 것이다.

작기이동 실험은 2014년과 2015년, 수원의 서울대학교 부속실험농장에서 실시되었으며, 봄 실험에서는 극조생종인 남작, 조생종인 수미 그리고 중만생종인 대서를 세 번의 파종기에 걸쳐 재배하였다. 가을 실험에서는 수미와 대서를 두 번의 파종기에 걸쳐 2014년에만 재배하였다. 괴경형성기는 품종과 파종기에 따라 출아 후 11일부터 22일까지 다양한 시기에 나타났다. 기상요인들이 괴경형성기에 미치는 영향을 분석한 결과, 현재 기후조건에서 괴경형성기는 기온 상승과 단일조건하에서 촉진되었고 또한 고온과 장일 조건에서 일조 부족 역시 괴경형성기를 지연시켰다. 공시 품종 모두 괴경형성 적온은 22-24℃ 내외로 추정되었으며, 기온, 일장 및 일사는 괴경형성에 상승적으로 상호작용하였다. 재배기간,

괴경형성기와 기상요인이 수량에 미치는 영향을 확인하기 위한 능형회귀 결과 가장 큰 영향은 재배기간으로 나타났다. 남한에서 감자의 생육기간은 봄철의 장마와 늦가을의 서리로 제한된다. 앞당겨진 괴경형성기와 최저기온의 상승은 수량을 감소시켰다. 17-22°C 범위의 평균기온에서는 일교차만이 수량에 큰 영향을 주었다.

고온반응 실험은 2015년, 서울대학교 부속실험농장의 플라스틱 하우스 4개동에서 수행되었다. 대표 품종으로 수미가 이용되었으며, 4월 29일과 9월 17일에 외기온 온실과 외기온보다 1.5°C, 3.0°C, 5.0°C 높게 조절되는 온실에 각각 80주씩 파종하였다. 가을실험에서는 출아기와 괴경형성기만을 관측하였다. 괴경형성기는 장일효과로 인해 봄 실험에서 가을 실험에 비해 14일 가량 늦어졌으며, 5.0°C 온실에서는 고온, 저일사와 장일효과로 인해 괴경형성이 억제되었다. 온도 상승에 따라 괴경형성 초기의 괴경 숫자가 감소하여, 괴경으로 전류되는 동화산물과 수확기 괴경의 평균 생서중이 감소하였다. 잉여산물들은 주로 줄기로 집적되어 왕성한 줄기 신장을 보였다.

위의 실험 자료들을 토대로 SUBSTOR-Potato 모델을 평가하였다. 모델에서는 괴경형성기를 선형 외삽법을 이용하여 구해진 괴경비대곡선과 시간축의 교점으로 정의하고 있다. 이로 인해 모의시기는 실측시기보다 지연된다. 이를 개선하기 위해 기존 식을 변경하였으며 고온과 장일 조건하의 일사 반응식을 추가하였다. 그 결과, 새로운 모델은 작기이동 실험 및 고온반응 실험의 괴경형성기를 비교적 정확히 예측하였다. 기존의 모델은 괴경형성초기 고온이 괴경 숫자와 괴경비대속도에 미치는 영향을 반영하지 못하였다. 시계열 자료에서의 괴경비대를 정확히 모의하기 위하여 고온에 따른 괴경형성속도 반응식을 추가하였다.

본 실험 결과에 따르면 이미 수원의 현재 기후는 감자재배의 적온 범위

를 벗어나기 시작하였으며, 미래기후에서 고온피해는 더 심각하게 나타날 것이다. 하지만, 감자의 괴경 형성 및 비대에 대한 이해는 아직까지도 부족한 상태이며, 모델들도 현실적인 고온반응 결과를 보여주지 못하고 있다. 따라서 고온에 대한 감자의 생리적 반응의 구체적인 연구와 이를 모델에 적용시키는 과정이 필요할 것으로 사료된다. 또한, 모델의 활용 전에 다양한 환경조건에서 모델을 검증하는 작업이 선행되어야 할 것이다.

주요어 : 감자, 기후변화, 고온, 모델, 괴경형성기, 괴경비대, SUBSTOR-Potato
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