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Effect of High Temperature, Daylength, and Reduced Solar Radiation on Potato Growth and Yield

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고온, 일장 및 저일사 조건이 감자 생육 및 수량에 미치는 영향

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ABSTRACT

Potato phenology, growth, and yield are projected to be highly affected by global warming in the future. The objective of this study was to examine the responses of potato growth and yield to environmental elements like temperature, solar radiation, and daylength. Planting date experiments under open field condition were conducted using three cultivars differing in maturity group (Irish Cobbler and Superior as early; Atlantic as mid-late maturing) at eight different planting dates. In addition, 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 using cv. Superior. Tuber initiation onset was found to be hastened curve-linearly with increasing temperature, showing optimum temperature around 22-24°C, while delayed by longer photoperiod and lower solar radiation in Superior and Atlantic. In the planting date experiments where the average temperature is near optimal and solar radiation, rainfall, pest, and disease are not limiting factor for tuber yield, the most important determinant was growth duration, which is limited by the beginning of rainy season in summer and frost in the late fall. Yield tended to increase along with delayed tuber initiation. Within the optimum temperature range (17°-22°C), larger diurnal range of temperature increased the tuber yield. In an elevated temperature treatment of AT+5.0°C, plants failed to form tubers as affected by high temperature, low irradiance, and long daylength. Tuber number at early growth stage was reduced by higher temperature, resulting in the decrease of assimilates allocated to tuber and the reduction of average tuber weight. Stem growth was enhanced by elevated temperature at the expense of tuber growth. Consequently, tuber yield decreased with elevated temperature above ambient and drop to almost nil at AT+5.0°C.

***Key words*: Potato, Climate change, High temperature, Planting date, Tuber initiation, Tuber yield**

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I. 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 and Burton, 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 and 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 lower than 25°C, but due to the reduction of harvest index under higher temperature, optimal temperature of yield is even lower than that of net photosynthesis (Winkler, 1971; Ku *et al.*, 1977; Dwelle *et al.*, 1981). Wheeler and Tibbitts(1986) showed optimal temperature for tuber yield are 20°C and 16°C for daylengths of 12 and 24hours, respectively. However, temperature responses vary among cultivars and development stages, and especially, heat tolerance varies widely (Reynolds *et al.*, 1990). In Korea, low temperature during early stage and high temperature during tuber bulking stage reduce tuber yield and quality for the cultivation in spring (Choi *et al.*, 2014).

Various environmental factors other than temperature affect potato phenology and growth. Photoperiod is one of the most important factors for potato growth and development. Lorenzen and Ewing(1990) showed higher photosynthesis efficiency in short days and Ewing and Wareing(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, interactions between environmental factors have not been 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. The objectives of this experiment are to examine the responses of potato growth and yield to the elevated temperature and the different daylength and solar radiation as changed by planting dates for different cultivars.

II. Materials and Methods

2.1. Planting date experiments

2.1.1. 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 1). Plants were grown under non-water stress condition, irrigated by hose and sprinkler in 2014 and 2015, respectively. Fertilizers were applied by the rates of 100kg ha^{-1} of N, 100kg ha^{-1} of P and 120kg 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 season fertilization. Seed tubers were pre-germinated for two to three weeks and planted at a spacing of 0.7m between rows and 0.25m between plants within row.

2.1.2. Measurements

2.1.2.1. 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 *et al.*, 1979; Manrique and Hodges, 1989). Tuber initiation onsets 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 at an interval of one to three weeks. Vegetative organ was divided into leaf and stem and oven-dried at 80^{o}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.

2.1.2.2. Meteorological data

Throughout the growing season, meteorological elements, such as air temperature and solar radiation were monitored at 5 minutes interval using data-logger (CR1000, Campbell Scientific, USA) equipped with temperature sensor and pyranometer (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.

2.2. Elevated temperature experiments

2.2.1. Experimental setup

This study was conducted under four plastic houses controlled to target temperatures of ambient temperature (AT), AT+1.5^{o}C, AT+3.0^{o}C, and AT+5.0^{o}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.

2.2.2. Measurements

2.2.2.1. Plant growth

General methods for measuring plant growth were identical to the planting date experiments. After emergence, ten plants per treatments were sampled five

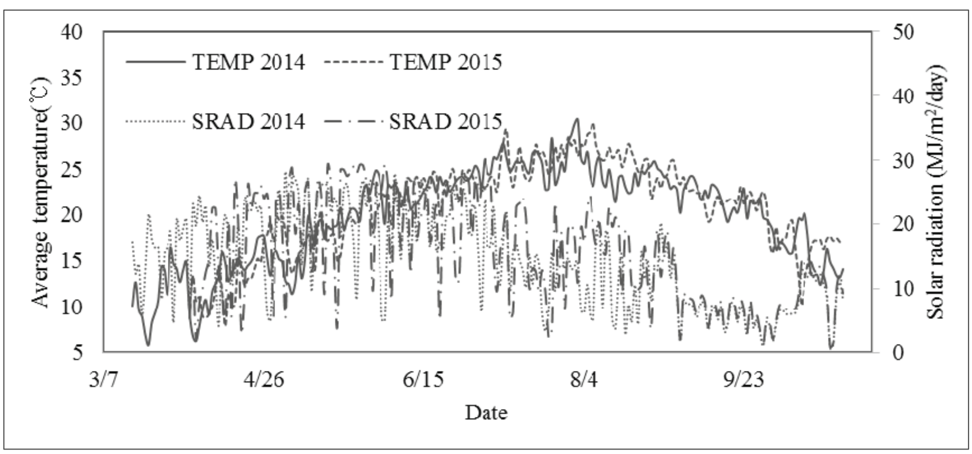

Fig. 1. Daily average air temperature and solar radiation during experimental season in 2014 and 2015.

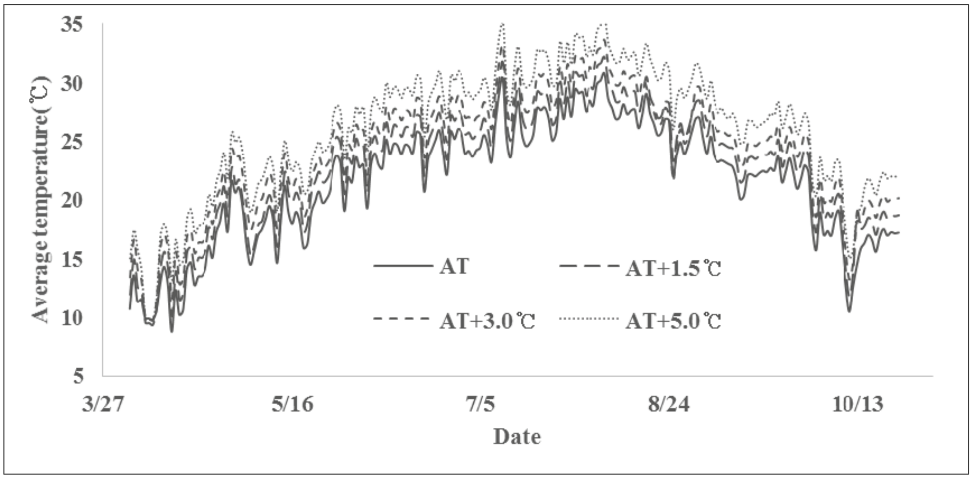

Fig. 2. Daily average air temperature inside the plastic houses which were controlled to different target temperatures in 2015.

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.

2.2.2.2. 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.

2.2.3. Statistical analysis

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

2.3. Effects of environmental factors on tuber growth

Multiplicative models (1) and (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.

$$\mathrm{EM-TIO} = (a_1 \times T_{av}{}^2 + a_2 \times T_{av} + a_3) \times (b_1 \times DL + b_2) \quad (1)$$

for the planting date experiment

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

for the Superior data pooled across the planting date and the temperature elevation experiments

Where $\mathrm{EM-TIO}$, T_{av}, 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.

III. Results

3.1. 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 continuous rainfall, causing shorter daylength throughout the growing season compared to the spring season and the ordinary cultivation period in the fall season (Table 1, 2).

3.1.1. Tuber initiation onset

As shown in the Table 1, tuber initiation onset occurred from 11 to 22 days after emergence according to planting dates and cultivars. In the spring season, Irish Cobbler formed tuber about 1.8 and 5 days earlier than Superior and Atlantic on average. As the temperature increases 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 and McGoldrick, 1941; Tibbitts *et al.*, 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

Table 1. 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 (°C)	Diurnal temperature range (°C)	Daylength (hour)
Irish Cobbler	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

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.

3.1.2. Yield

As presented in Table 2, cultivation periods were shortened by the beginning of rainy season and the frost at the later plantings in the spring and the fall season, 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.

3.2. Responses of potato growth and yield to elevated temperature

3.2.1. Tuber initiation onset

As shown in Table 3, average temperatures of the spring season experiment were approximately 4°C higher than those of the fall experiment, showing similar

Table 2. 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

Table 3. 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

Table 4. 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

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 variations 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 environmental differences between the two experiments were solar radiation and diurnal temperature range (Table 1 and 3).

3.2.2. Growth and yield

As presented in Table 5, 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 4, final yield decreased substantially with temperature elevation above ambient, dropping to almost nil in AT+5°C. As presented in Fig. 3, 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.

3.3. Effects of environmental factors on tuber initiation and growth

3.3.1. Tuber initiation onset

The responses of tuber initiation onset to environments can be explained by the models presented in Table 6. In the open field condition, temperature was an important

Table 5. Growth characteristics of Superior as affected by different temperature regimes

days after emergence	temperature treatments	dry weight(g/plant)				dry weight ratio(g/g)			LAI	tuber number
		leaf	stem	tuber	total	leaf	stem	tuber		
14	AT	2.41	1.70b	0.02	4.14	0.58a	0.41b	0.01	0.42	0.10
	AT+1.5℃	2.46	1.93ab	0.00	4.39	0.56ab	0.44ab	0.00	0.36	0.00
	AT+3.0℃	3.10	2.25ab	0.00	4.65	0.52b	0.48a	0.00	0.42	0.00
	AT+5.0℃	2.45	2.62a	0.00	5.72	0.54ab	0.46ab	0.00	0.36	0.00
	F-value	1.777NS	2.93*	1NS	2.231NS	4.574**	4.781**	1NS	0.902NS	1NS
28	AT	9.57	7.46	6.48a	23.51	0.41	0.33c	0.26a	1.36	3.20a
	AT+1.5℃	9.23	9.85	1.96b	21.04	0.45	0.48b	0.08b	1.35	1.30ab
	AT+3.0℃	9.38	9.92	1.91b	21.21	0.44	0.46b	0.10b	1.14	1.50ab
	AT+5.0℃	8.40	11.28	0.00b	19.68	0.43	0.57a	0.00b	1.11	0.00b
	F-value	0.175NS	1.352NS	7.123***	0.311NS	0.647NS	21.27***	8.313***	0.58NS	6.742**
42	AT	21.30	21.00	25.15a	67.45	0.32	0.31c	0.37a	3.47	4.40a
	AT+1.5℃	20.13	28.87	9.43b	58.43	0.34	0.50b	0.16b	3.48	2.70b
	AT+3.0℃	17.50	24.57	7.27b	49.34	0.36	0.52b	0.12b	2.59	1.60b
	AT+5.0℃	14.70	23.01	0.00b	36.57	0.36	0.64a	0.00b	2.14	0.00c
	F-value	1.465NS	0.765NS	13.18***	2.75NS	1.442NS	24.96***	13.36***	1.889NS	23.34***
56	AT	23.87a	28.06	51.49a	103.43a	0.23bc	0.28c	0.48a	5.21a	4.70a
	AT+1.5℃	30.16a	39.93	37.89ab	107.98a	0.27ab	0.35bc	0.38a	5.56a	5.50a
	AT+3.0℃	18.23ab	36.96	29.81b	85.00a	0.21c	0.42b	0.38a	3.74ab	4.90a
	AT+5.0℃	11.46b	24.76	0.26c	39.48b	0.31a	0.68a	0.01b	2.21b	0.20b
	F-value	6.187**	1.838NS	16.4***	8.907***	8.552***	27.64***	22.34***	5.361**	12.83***
70	AT	16.84	23.15	90.07a	130.06a	0.12c	0.17c	0.70a	5.04	6.40a
	AT+1.5℃	26.16	46.96	63.29b	136.40a	0.19b	0.34b	0.47b	6.50	7.40a
	AT+3.0℃	19.58	42.78	38.41b	100.77ab	0.20b	0.43b	0.38b	5.20	7.00a
	AT+5.0℃	17.17	39.64	0.31c	57.12b	0.30a	0.69a	0.00c	3.21	0.30b
	F-value	2.082NS	2.797NS	34.12***	7.747***	47.05***	91.57***	98.41***	2.635NS	13.28***

NS, *, **, ***, not significant at the 0.05, 0.01, 0.001 significant levels, respectively.

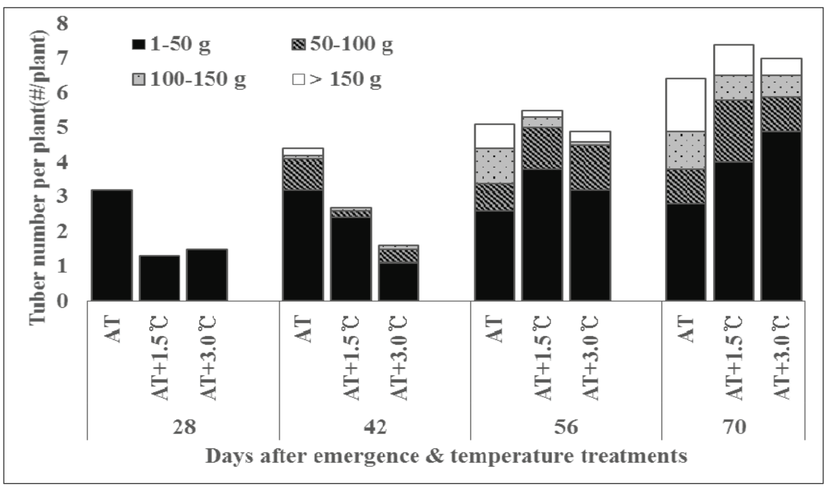

Fig. 3. Temporal changes of tuber number and tuber weight distribution under different elevated temperature treatments.

Table 6. Parameters of the tuber initiation models [equations (1), (2)] obtained by a global optimization by differential evolution (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.

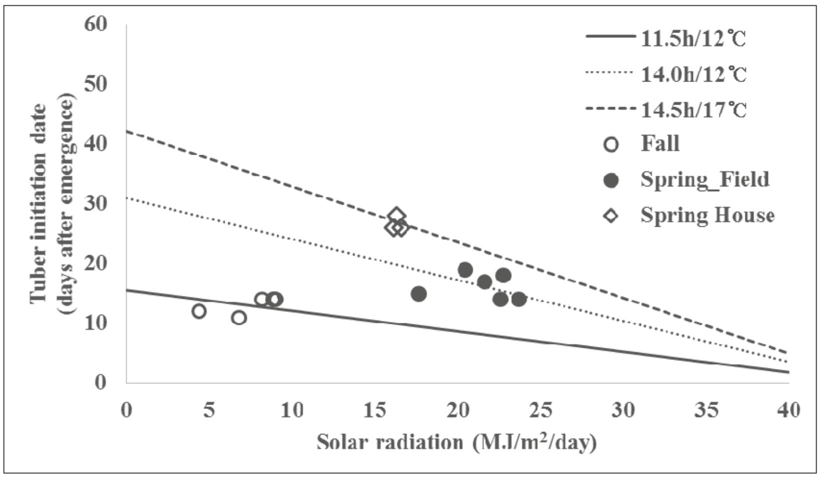

Fig. 4. Relationship of duration from emergence to tuber initiation onset with solar radiation, daylength, and diurnal temperature range in cultivar Superior. Data were pooled across the planting date and the temperature elevation experiments. 11.5/14.0/14.5h and 12/17°C are daylength and daily mean temperature, respectively.

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 the 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

Table 7. 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 (^{o}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(^{o}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.

temperature and lower solar radiation than in the open field. As in Fig. 4, the model using all the data pooled across planting date experiments in open field and elevated temperature experiments in plastic houses shows that the effect of solar radiation on 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.

3.3.2. Yield

Relative importance of yield-related factors was analyzed using ridge regression for open field experimental data as shown in Table 7. 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 planting date experiments in the open field and temperature elevation experiments in plastic houses for cultivar Superior. As shown in Fig. 5, tuber yield showed quadratic response to average air temperature. Tuber yield reached maximum at around 20^{o}C, decreased drastically above this temperature, and dropped to almost nil at 27^{o}C.

IV. 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

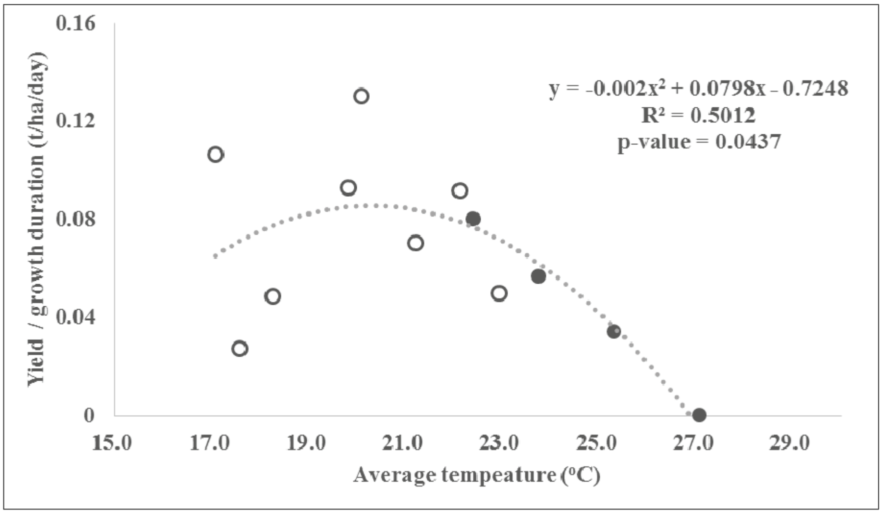

Fig. 5. Quadratic regression of tuber yield divided by growth duration with daily mean temperature averaged throughout the growth period in a cultivar Superior. Open and closed circle represent the planting date experiments data in the open field and the elevated temperature experiment data in the plastic houses, respectively.

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 6). However, tuber initiation will be delayed by the temperature above 22-24°C and Streck *et al.*(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 *et al.*, 1998) 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 1, 3). There were studies suggesting diurnal fluctuations are beneficial to tuber initiation (Werner, 1935; Bennett *et al.*, 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 7). 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. 5. This coincides with the result of 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 *et al.*, 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 (Table 5 and Fig. 3). 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 and 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.

적 요

지구 온난화에 의한 미래의 기후변화는 감자의 생물계절, 생육 및 수량에 지대한 영향을 미칠 것으로 예상되므로 그 영향을 평가하여 적응대책을 수립하여야 한다. 본 연구에서는 고온조건을 포함한 다양한 기상 조건에서 감자의 생육과 수량 변화를 확인하고자 하였다. 작기이동 실험은 2014년과 2015년, 수원의 서울대학교 부속실험농장에서 실시되었으며, 봄 실험에서는 조생종인 남작과 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 촉진되었다. 반면에 고온과 장일 조건에서 적은 일사량은 역시 괴경형성기를 지연시켰다. 공시 품종 모두 괴경형성 적온은 22-24°C 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. 이는 봄 작기 동안의 수원의 평균기온이 감자 수량의 최적온도와 큰 차이를 보이지 않고 2014～2015년 마른장마로 인해 생육시기 동안 충분한 일사량이 확보되어 제한요인으로 작용하지 못하였기 때문이다. 앞당겨진 괴경형성기와 최저기온의 상승은 수량을 감소시켰다. 17-22°C 범위의 평균기온에서는 일교차만이 수량에 큰 영향을 주었다. 고온반응 실험은 2015년에 서울대학교 부속실험농장의 플라스틱 하우스 4개동에서 수행되었다. 대표 품종으로 수미가 이용되었으며, 4월 29일과 9월 17일에 외기온 프라스틱하우스와 외기온보다 1.5°C, 3.0°C, 5.0°C 높게 조절되는 프라스틱하우스에 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 괴경이 형성되지 않았다. 온도 상승에 따라 괴경형성 초기의 괴경 숫자가 감소하여, 괴경으로 전류되는 동화산물과 수확기 괴경의 평균 생서중이 감소하였다. 잉여동화산물은 주로 줄기로 집적되어 왕성한 줄기신장을 보였다. 본 실험 결과에 따르면 이미 수원의 현재 기후는 감자재배의 적온 범위를 벗어나기 시작하였으며, 미래기후에서 고온피해는 더 심각하게 나타날 것이다. 하지만, 감자의 괴경 형성 및 비대에 대한 이해는 아직까지도 부족한 상태이므로 미래 기후 변화 영향을 평가하기 위해서는 고온 하에서 감자의 생리적 반응에 대한 구체적인 연구가 필요할 것으로 사료된다.

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