Effects of Temperature at Different Growth Stages on Nonstructural Carbohydrate, Nitrate Reductase Activity and Yield of Potato

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The effect of temperature (15, 25, 30°C and glasshouse as control) at different growth stages (stage-I: vegetative to tuber initiation, stage-II: tuber initiation to initial tuber bulking and stage-III: tuber bulking to maturity) on leaf nitrate reductase (NR) activity, carbohydrate contents and tuber yield were investigated in potatoes (*Solanum tuberosum* L. cvs. May Queen and Norin 1) as pot experiment in naturally lit glasshouse and phytotron. The high temperature treatment decreased the total dry matter production as well as tuber yield and degraded the tuber quality by reducing the specific gravity. NR activity of leaves was also decreased by high temperature treatment, whereas low temperature increased the activity. Water soluble carbohydrate (WSC) and starch content in leaves were sequentially decreased and as a result total nonstructural carbohydrates (TNC) were also decreased by high temperature. The inhibition of tuber yield by high temperature was due to the limited translocation of carbohydrates from leaves to the tubers, following the reduction of NR activity and the expense of carbohydrates for dark respiration. The maximum yield reduction was observed at high temperature treatment at stage-I which was most critical for tuber yield, and low temperature at stage-II produced the highest yield which was considered as more advantageous step towards yield improvement.

Keywords: growth stages, potato (*Solanum tuberosum* L.), specific gravity, temperature, tuber yield

INTRODUCTION

The major constraints for potato plant growth and tuber yields are environmental stress conditions. Environmental factors such as temperature, moisture, light and fertilizer play key roles in the variation of plant growth and tuber yield. Potatoes are grown all over the world from tropics to cool area. The yield of potato in the warm tropics is limited by high temperatures (Borah and Milthorpe, 1962; Awan, 1964), but there is considerable variation in field production in warm climates (Ewing, 1981). Moreover, the large temperature perturbations above and below normal during the growing season can cause relatively undetermined effects on the growing potato plants. The potential for damage from these temperature variations depends on the stage of crop developments which they occur. There are some reports about the high temperature stress on potato growth and yield (Bodlaender, 1963; Gregory, 1965; Marinus and Bodlaender, 1975; Levy, 1986), but none of them considered the

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growth stages critical for tuber yield.

On the other hand, nitrate is the principal form of nitrogen absorbed by plants. However, it can be used in amino acid for protein synthesis, so it must be reduced to ammonia form. The first step in this reduction process is conversion of nitrate to nitrite by the nitrate reductase (NR) enzyme. Supra-optimal temperatures and moisture deficits result in a relatively rapid decrease or inactivation of NR activity in plants (Mattas and Pauli, 1965; Younis et al., 1965; Schrader et al., 1968). NR seems to be unique among the other enzymes being inactivated by heat stress employed (Onwueme et al., 1971).

It is well known that the carbohydrate synthesis and translocation are affected by temperature (Wolf et al., 1990). In potato plants, there are some reports concerning high temperature effects on carbohydrate metabolism, suggesting the reduction of carbohydrate synthesis and translocation from source leaf to the tubers and reduced the yield (Borah and Milthorpe, 1962; Krauss and Marschner, 1984; Mohabir and John, 1988; Lafta and Lorenzen, 1995).

Even in natural conditions, temperature fluctuation sometimes observed in the potato growing areas which may be happened in the different growth stages during the growing season and can influenced the growth and yield of potato. For that we admixed different temperature treatments at different growth stages.

Considering the above, we conducted the present experiment in order to evaluate the role of different temperature treatments at different growth stages on dry matter production, leaf NR activity and carbohydrate contents in relation to tuber yield and quality, and also to find out the severity of treatments which is more detrimental for tuber yield.

MATERIALS AND METHODS

The experiment was conducted in clay pots (30 cm in diameter and 24 cm in depth) in naturally lit glasshouse and temperature controlled phytotron (Shimadzu, Japan, Model SCN-181) in March 1999. The experimental conditions of different treatments and atmospheric temperature (inside glasshouse temperature varied 1–3°C above depending on weather conditions) at different growth stages are presented in Fig. 1 and Table 1. Each pot was filled with coarse sandy loam soil equivalent to 9.0 kg of dry weight. The field capacity of the soil determined by gravimetric methods was 29.8%. The soil moisture content at 80% field capacity was considered to the optimum for standard growth of the potato plants (Petr et al., 1988) and maintained throughout the season by regular weighing the pot and adding water at 8:00 A.M. According to the fertilizer recommendation based on soil analysis 5.0 g ammonium sulfate, 6.0 g superphosphate and 2.0 g potassium chloride were mixed into the soil prior to seed tuber planting. About 50 g seed tubers were planted in the pots and after germination two stems were kept finally to be grown. Plants were grown in glasshouse and different temperature treatments (15, 25, 30°C) were imposed starting 10 d after germination in the phytotron at three growth stages (stage-I: vegetative to tuber initiation, stage-II: tuber initiation to initial tuber bulking, stage-III: tuber bulking to maturity). Duration of each treatment was 20 d. Two potato cultivars May Queen and Norin 1 different in their growth habit (leafy and stemmy type) were used. There were three replications and the pots were arranged in a randomized block design and each pot was considered as one replication. Plants were sampled at the end of each treatment. Three pots per treatment were sampled and plants were separated into stems, leaf blades, petioles, stolons, tubers and roots. Measurements included the length of the main stem, leaf area, stolon number, tuber number, fresh and dry weight of each organ. For yield determination, three pots per treatment were harvested, and total yield, yield components and dry weight of tubers were recorded. At final harvest, the specific gravity of tuber was measured by the weight in air and in water.

Table 1 Experimental conditions of different treatments and atmospheric temperature (inside GH temperature range 2–3°C above during the daytime) and average relative humidity at different growth stages.

Growth stages	Treatments	Treatment duration			Atmospheric temperature and relative humidity (stage average)			
		20 (d)	20 (d)	20 (d)	Temperature (°C)		Relative humidity (%)	
					Min.	Max.		
	Control (GH)	GH	GH	GH				
Stage-I (Apr. 12–May 1)	15°C (stage-I)	15°C	GH	GH	9.80	19.87	14.33	60.12
	25°C (stage-I)	25°C	GH	GH				
	30°C (stage-I)	30°C	GH	GH				
Stage-II (May 2–May 21)	15°C (stage-II)	GH	15°C	GH	13.05	25.91	19.36	61.32
	25°C (stage-II)	GH	25°C	GH				
	30°C (stage-II)	GH	30°C	GH				
Stage-III (May 22–Jun. 10)	15°C (stage-III)	GH	GH	15°C	15.64	25.62	20.55	71.31
	25°C (stage-III)	GH	GH	25°C				
	30°C (stage-III)	GH	GH	30°C				

Stage-I: vegetative to tuber initiation, stage-II: tuber initiation to initial tuber bulking, stage-III: tuber bulking to maturity. GH, glasshouse.

Fig. 1 Schematic diagram of different temperature treatments.

Solid line indicates GH and broken line indicates temperature treatments in phytotron. O, sampling.

NR activity was determined every 10 d after treatment following in vivo NR assay as described by Kapoor and Li (1982). Fully expanded leaf (third and fourth leaves from the apex) samples were composited (five replicates) and analysis was done in triplicate at three growth stages.

The concentration of carbohydrate was determined from leaf blades at the end of each treatment period at three stages of growth. For water soluble carbohydrate (WSC), 0.1 g dried samples were extracted once with ethanol (80%) at 60°C and twice with distilled water at 70°C. WSC was measured by anthrone method (Yemm and Willis, 1954). The residue was used for starch determination after suspended in distilled water and heated at 120°C for 10 min within an autoclave for gelatinization. After cooling, α -amylase (Wako Pure Chemical

Fig. 2 Effect of different temperature treatments at different growth stages on dry matter production of different plant organs of two potato cultivars just after treatment.

Bars represent standard error. □, 15°C; ■, 25°C; ▨, 30°C; ▩, control.

Industries Ltd., Japan) with phosphate buffer (pH 5.8) was added to the residue and it was incubated for 16 h at 40°C in shaking bath for breakdown of starch. Starch concentration was determined from glucose standard by anthrone method. The sum of WSC and starch was considered as total nonstructural carbohydrate (TNC).

All statistical analyses were performed by software MSTAT package (Michigan State University, USA).

RESULTS

Dry matter production

Dry weights of each organ just after the treatment are shown in Fig. 2. In all growth stages, the total dry matter production was decreased with increasing temperature in both cultivars. This response was due to the decrease in tuber weight with a relatively small response in leaf and stem weight. In stage-I, glasshouse treated (control) plant produced the highest amount of total dry matter followed by 15 , 25 and 30°C treated plants in both cultivars. In stage-II, high temperature decreased the total dry matter in both cultivars, but it increased stem and leaf dry matter. In May Queen, 15°C treated plant produced the maximum amount of total and tuber dry matter followed by 25°C treated plant. In Norin 1, control plant produced the maximum amount of total and tuber dry matter followed by 15°C treated plant. In stage-III, trend in dry matter production was similar in both cultivars and plant treated with 15°C produced the highest amount of total and tuber dry matter. Among all the growth stages, decrease in dry matter production by higher temperature was maximum in stage-I in both cultivars which were 68 and 43% in May Queen and Norin 1 respectively over control.

Nitrate reductase activity

Table 2 shows the effect of different temperature at different growth stages on NR activity at 10 and 20 d from the beginning of treatment. Higher temperature treatment almost decreased the NR activity at all growth stages. In stage-I, 15°C treated plants in both cultivars showed the higher NR activity. Whereas, 25°C treated plant showed the lowest NR activity at 10 d in both cultivars. In stage-II, 15°C treated plants showed the highest NR activity followed by control, 25 and 30°C treated plants. In stage-III, the NR activity showed

Table 2 Effect of different temperature at different growth stages on nitrate reductase ($\mu\text{mol NO}_2 \text{ g fresh wt.}^{-1} \text{ h}^{-1}$) activity of two potato cultivars.

Cultivar	Treatment	Growth stages					
		Stage-I		Stage-II		Stage-III	
		10 ^z	20	10	20	10	20
May Queen	15°C	6.65	8.03	7.23	6.79	3.66	3.56
	25°C	3.47	6.04	2.81	3.20	3.39	3.26
	30°C	4.85	3.09	2.68	2.70	2.75	2.54
	GH	4.03	4.39	6.36	6.12	5.63	4.12
	LSD (0.05)	0.519	0.265	0.501	0.311	0.329	0.131
Norin 1	15°C	3.43	5.04	8.00	5.50	5.89	4.26
	25°C	2.22	3.06	5.72	4.47	4.20	4.71
	30°C	3.41	2.88	3.86	2.29	3.58	3.72
	GH	3.84	3.93	7.40	5.64	5.20	4.38
	LSD (0.05)	0.366	0.195	0.368	0.579	0.138	0.512

^z Days from the beginning of treatments.

Table 3 Effect of different temperature at different growth stages on water soluble carbohydrates (WSC), starch and total nonstructural carbohydrates (TNC) of leaves just after treatment of two potato cultivars.

Cultivar	Temperature regimes	Stage-I			Stage-II			Stage-III		
		WSC	Starch	TNC	WSC	Starch	TNC	WSC	Starch	TNC
May Queen	15°C	6.63	4.46	11.09	16.49	8.72	25.21	15.68	3.92	19.60
	25°C	6.09	4.36	10.45	10.38	8.42	18.8	13.90	5.76	18.66
	30°C	5.31	2.73	8.04	7.57	3.49	11.06	6.68	3.15	9.83
	GH	8.35	5.03	13.38	9.88	4.46	14.34	5.69	5.55	11.24
LSD (0.05)		0.396	0.480	0.367	0.898	0.346	1.033	0.339	0.348	0.632
Norin 1	15°C	7.73	3.06	10.79	9.72	2.53	12.25	14.77	2.91	17.68
	25°C	7.07	2.93	10.00	8.86	1.72	10.58	8.46	2.10	10.56
	30°C	5.03	0.94	5.97	7.60	1.68	9.28	9.49	2.05	11.54
	GH	10.26	3.45	13.71	8.46	1.93	10.39	10.22	3.66	13.88
LSD (0.05)		0.316	0.202	0.444	0.256	0.177	0.319	0.273	0.133	0.329

All the values are in percentage of the dry weight.

variability depending on different treatments. In May Queen, the highest activity was observed in control plants followed by 15, 25 and 30°C treated plants. Whereas, in Norin 1, the highest activity was observed in 15°C treated plants followed by control, 25 and 30°C treated plants. However, on total average 17% activity was increased by 15°C treatment in May Queen and 6% in Norin 1 over control. Whereas, in case of 30°C treatment, 39 and 35% activity was decreased in May Queen and Norin 1, respectively.

Leaf carbohydrate concentration

The effect of temperature on carbohydrate contents of two cultivars having variation in the levels of soluble sugars and starch are shown in Table 3. The WSC concentration was almost higher in Norin 1 than that of May Queen. On the other hand, starch content was higher in May Queen than Norin 1. In all the growth stages, the WSC, starch and TNC levels were decreased with increasing temperature in both cultivars. In stage-I, control plant possesses the higher concentration of WSC, starch and TNC followed by 15, 25 and 30°C plants in both cultivars. But in stage-II and stage-III, 15°C treated plant possesses the higher content of WSC, starch and TNC in both cultivars.

Yield characters

Table 4 shows the effect of different temperature on yield and yield components at final harvest. Tuber number and yield were markedly influenced by different temperature treatment in all the three stages of growth. High temperature treatment (30°C) at stage-I decreased the tuber number maximum than the other stage of growth. Similarly, high temperature treatment at all growth stages decreased the average tuber weight. High temperature treatment at stage-I decreased yield more than the other stages of growth and yield reduction was higher in Norin 1, than May Queen. But in stage-II, low temperature (15°C) treated plant produced the maximum tuber yield in both cultivars, and 30°C treated plant produced the minimum tuber yield. In stage-III, temperature effect was relatively lower than the other stages, though dry tuber yield reduction was observed in higher temperature treated plant. Tuber specific gravity markedly influenced by the different temperature treatments. Higher temperature treatments sequentially decreased specific gravity of tubers at all stages of growth in both cultivars. But the effect of high temperature was more pronounced at last stage of growth. However, cool temperature (15°C) treatment increased the specific gravity of tubers

Table 4 Effect of different temperature at different growth stages on yield and yield components of two potato cultivars at final harvest.

Treatments	Tuber number (plant ⁻¹)		Tuber yield (g plant ⁻¹)		Dry tuber yield (g plant ⁻¹)		Average tuber weight (g)		Tuber specific gravity	
	May Queen	Norin 1	May Queen	Norin 1	May Queen	Norin 1	May Queen	Norin 1	May Queen	Norin 1
Control (GH)	15.0 ab	17.0 ab	345.1 c	316.0 c	58.4 e	54.7 d	23.0 de	18.6 de	1.061 c	1.064 d
15°C (stage-I)	15.7 a	15.7 cd	406.2 b	371.6 bc	73.6 b	69.8 b	25.9 c	23.7 b	1.067 b	1.071 c
25°C (stage-I)	13.0 cd	13.5 e	307.4 e	169.0 f	60.0 de	26.4 g	23.7 d	12.5 f	1.072 a	1.058 e
30°C (stage-I)	10.5 e	3.0 f	197.5 f	39.7 g	35.2 h	4.9 h	18.8 f	13.2 f	1.063 c	1.036 g
15°C (stage-II)	13.0 cd	13.7 e	431.9 a	420.0 a	77.1 a	81.0 a	33.3 a	30.7 a	1.072 a	1.077 b
25°C (stage-II)	13.3 cd	13.7 e	386.6 b	301.8 cd	69.6 c	61.1 c	29.1 b	22.1 c	1.067 b	1.077 b
30°C (stage-II)	12.0 de	16.3 bc	316.2 e	205.2 e	49.6 f	31.9 f	26.5 c	12.6 f	1.054 d	1.055 f
15°C (stage-III)	14.0 bc	15.0 d	323.6 cde	289.1 d	63.7 d	59.5 c	23.2 de	19.3 d	1.073 a	1.080 a
25°C (stage-III)	15.0 ab	17.5 ab	319.4 cde	315.1 c	61.1 de	56.4 d	21.3 e	18.0 e	1.071 a	1.078 ab
30°C (stage-III)	16.0 a	18.0 a	339.7 bed	317.2 c	39.0 g	35.6 e	21.3 e	17.6 e	1.025 e	1.010 h

Data followed by the same letter(s) in a column do not differ significantly.

Table 5 Some simple correlations between yield and some characters ($n=30$).

	May Queen		Norin 1	
	May Queen	Norin 1	May Queen	Norin 1
Yield × tuber no.	0.516**	0.707**	Yield × starch	0.745**
Yield × NR	0.497**	0.752**	Yield × TNC	0.675**
Yield × WSC	0.571**	0.696**	Yield × SG	0.099 ^{ns}

**, *, ^{ns} : significant at 1%, 5% and not significant respectively. SG, specific gravity.

at all stages of growth. The control plants also showed medium specific gravity. The tubers of Norin 1 possessed the higher specific gravity than that of May Queen.

Correlation coefficient between yield and some characters are shown in Table 5. Tuber number showed significant positive correlation with yield in both cultivars. Leaf NR activity, WSC, starch and TNC also maintained significant correlation with yield in both cultivars. Specific gravity of tubers also showed significant correlations with yield in Norin 1, but in May Queen the relation was not significant.

DISCUSSION

The high temperature (30°C) treated plant significantly decreased the total dry matter production at all stages of growth. The effect was more pronounced on tuber than that of leaves and stems dry matter. The major constraints to high temperature treated plants were to completely inhibited the tuber initiation at stage-I, at stage-II decrease the dry matter partitioning to tuber and stage-III greatly decreased the tuber specific gravity. Whereas, low temperature treated plants were favored by tuber initiation and higher dry matter production. Treatment duration was 20 d at different stages of growth and remaining part of growing season the plant were grown in the naturally lit glasshouse. But those 20 d different temperature treatment at three growth stages affected the whole plant growth, dry matter production and tuber yield. There was little difference between the result immediately after temperature treatment and that of the final harvest in terms of tuber yield. Because plant growth pattern was altered by different temperature treatment at different growth stages. High temperature treatment at early growth stages completely inhibited the tuber initiation in both cultivars. Whereas, low temperature and glasshouse treated plants were favored by tuber initiation. And the yield reduction was maximum in high temperature treatment (30°C stage-I) in this stage might be due to the lower tuber number and average tuber weight. At the same time, low temperature treatment in stage-II (15°C stage-II) produced the highest yield in both cultivars than other stage of treatments. The possible reason is due to the higher synthesis and translocation of carbohydrates from source leaves to tuber sink as increased demand of tuber and higher plant growth (Moorby, 1968).

Actually cultivars used in this experiment were not tolerant to high temperature treatments. Both cultivars failed to form tuber at high temperature. And the tuber yield markedly decreased by high temperature treatment. But the tuber yield decreased relatively higher in Norin 1 than that of May Queen. Tuber number also decreased drastically in stage-I at 30°C treated plant in both cultivars than the other stages of growth. The average tuber weight decreased by high temperature treatments in both cultivars at all stages of growth.

The observed NR inactivation during heat stress could reflect a failure of continued enzyme production during stress. Heat stress resulted in growth retardation as well as NR inactivation and an association between the two effects was considered. The reduction in NR levels were directly related to decreased growth subsequent to heat stress. High temperature treated stress plants were significantly smaller in weight than unstressed and low temperature (15°C) treated plant. This indicates a similar degree of growth retardation suggesting that the heat inactivation of NR activity may be directly implicated in the growth retardation. As NR activity showed highly significant positive correlation with yield, so yield reduction may be related to the NR activity retardation (Deckard et al., 1973).

The tuber quality is generally judged by the specific gravity of the tubers. Higher specific gravity of tuber is required for higher cooking quality of the potato processing industry. High temperature treatment deteriorated the quality of tuber by decreasing the specific gravity, whereas low temperature treatment increased the specific gravity. The specific gravity of tuber

was relatively higher in Norin 1 than that of May Queen and Norin 1 showed significant correlation with yield.

Among the kinds of carbohydrate tested in this experiments, WSC is the most sensitive to heat stress. WSC was higher in Norin 1 consequently starch content was higher in May Queen. According to this hypothesis, Norin 1 is more tolerant to heat stress than May Queen. Furthermore, starch accumulation seems to help the heat susceptible genotypes to withstand the conditions of stress. When starch is depleted in the leaves due to midday depression of photosynthesis (Manhas and Sukumaran, 1988), increase in the rate of photorespiration (Ku et al., 1977) or a gradual increase in dark respiration together with an increase in temperature (Winkler, 1971), plant may not withstand heat stress well.

Our observations in this experiment suggested that, inhibition in growth and yield of potato by high temperature was due to reduction in dry matter production as carbohydrate synthesis and translocation limited by heat stress, following the reduction of NR activity and the expense of carbohydrates for dark respiration.

According to the severity of the treatments, the high temperature at stage-I was found to be most critical for tuber yield in both cultivars than that of other stages of growth. Furthermore, the low temperature treatment (15°C) at stage-II produced the highest tuber yield in both cultivars, which was considered as more advantageous step towards the improvement of yield.

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〈和文抄録〉

生育時期別温度処理がバレイシヨの非構造的炭水化物、硝酸還元酵素活性ならびに収量に及ぼす影響

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バレイシヨの生育時期別（Ⅰ期：栄養生長期～塊茎形成期，Ⅱ期：塊茎形成期～塊茎肥大初期，Ⅲ期：塊茎肥大期～成熟期）に異なる温度処理（15，25，30℃およびガラス室）を行い，葉の炭水化物含量，硝酸還元酵素(NR)活性および収量について調べた。供試品種はメークイン，農林1号の2品種である。すべての生育時期を通じ，両品種とも高温は全乾物重，塊茎乾物重を低下させ，塊茎の品質(比重)をも低下させた。葉のNR活性は高温条件で低くなり低温条件では高くなった。葉における水溶性炭水化物およびデンプン含量は高温になるほど低くなり，その結果，全非構造的炭水化物含量も低くなった。高温による塊茎収量の抑制は，NR活性の低下および暗呼吸のための炭水化物消費に伴い，塊茎への炭水化物転流が抑制されたことによる。Ⅰ期における高温条件が最も収量を低下させ，この時期が最大の危険期と考えられた。また，Ⅱ期の低温条件によって収量は最高となり，この時期は収量の向上に対して大きな意義のあることが示唆された。